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Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California



Doctorado en Ciencias en Ecología Marina

Connectivity in the deep water region of the southern Gulf of Mexico based on potential habitat models of selected ichthyoplankton species and circulation numerical models

Tesis para cubrir parcialmente los requisitos necesarios para obtener el grado de Doctor en Ciencias

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Copyright © 2023, Todos los Derechos Reservados, CICESE Prohibida su reproducción parcial o total sin la autorización por escrito del CICESE Resumen de la tesis que presenta **Gonzalo Daudén Bengoa** como requisito parcial para la obtención del grado de Doctor en Ciencias en Ecología Marina

Conectividad en la región de aguas profundas del sur del Golfo de México basado en modelos de hábitat potencial de especies selectas de ictioplancton y modelos de circulación numérica

Resumen aprobado por:

Dra. Sharon Zinah Herzka Llona Directora de tesis

Los peces marinos tienen etapas de vida complejas que requieren diferentes hábitats y condiciones ambientales. El hábitat larvario depende de la distribución y desove de adultos, pero pueden dispersarse a regiones con condiciones inadecuadas que afecten la supervivencia y reclutamiento. En sistemas oceánicos, la circulación de mesoescala influye la dispersión larvaria, la conectividad, dinámica y estructura de poblaciones de peces. Los modelos de circulación son utilizados en experimentos de seguimiento de partículas, aplicando un marco de Lagrange que siguen gran cantidad de larvas virtuales en el espacio y tiempo, examinando dispersión y conectividad. Pueden combinarse con información ecológica (hábitats y períodos de desove) o características biológicas (duración de etapa planctónica, tasas de crecimiento larvaria) obteniendo información sobre interacciones físicas y biológicas y evaluar las vías de dispersión larvaria y conectividad entre regiones. Este estudio, examinó la distribución y densidad de larvas de seis especies en función de variables oceanográficas usando Modelos Aditivos Generalizados (GAM) con datos de 15 cruceros realizados entre abril y noviembre (2011 a 2018) en el Golfo de México (GoM). Doce en aguas profundas (> 1000 m) del sur del GoM (sGoM) y tres en la plataforma de Yucatán. La distribución larvaria de especies oceánicas se relacionó con variables oceanográficas indicativas de mayor productividad, que puede conducir a un mayor éxito alimenticio y supervivencia. Especies neríticas en aguas oceánicas próximas a plataformas probablemente mediado por transporte hacia fuera, puede conducir a una alta mortalidad. En la plataforma de Yucatán, las larvas neríticas se distribuyeron más allá de la isóbata de 40 m, con mayores densidades en el centro. Sus densidades estuvieron relacionadas significativamente con salinidad y velocidad del viento, pero su distribución refleja las regiones y períodos de desove de adultos. Posteriormente se aplicaron los GAM a una climatología de diez años de datos hidrográficos para predecir el hábitat potencial de cada especie y delimitar el origen de dispersión de partículas. Se seleccionaron dos patrones de circulación de mesoescala contrastantes: (1) alto nivel de intrusión de la Corriente de Lazo (LC), sin interacción entre remolinos anticiclónicos (AE) y ciclónico (CE) de la Bahía de Campeche (BoC), y (2) bajo nivel de intrusión de LC, un LC-AE recientemente desprendido e interacciones AE-CE en el Golfo occidental. El transporte se simuló utilizando campos de velocidad del modelo HYCOM. Se sembraron partículas pasivas distribuidas aleatoriamente en hábitats potenciales y advectaron 30 días. Partículas dispersadas desde hábitats dentro del sBoC se retuvieron en el GoM occidental. En aguas profundas la mayor retención fue en períodos de alta actividad e interacción entre remolinos de mesoescala. Cuando la intrusión de LC fue mayor, partículas de hábitats potenciales cercanos se dispersaron hacia el GoM noroccidental y Océano Atlántico. El estudio de la dispersión de especies con historias de vida contrastantes basadas en requisitos ambientales y modelos de circulación oceánica proporcionó información sobre cómo la distribución de larvas y los procesos de circulación de mesoescala pueden afectar la dispersión y la conectividad entre regiones, que influye en la supervivencia y el reclutamiento de poblaciones adultas.

Abstract of the thesis presented **by Gonzalo Daudén Bengoa** as a partial requirement to obtain the Doctor of Science degree in Marine Ecology

Connectivity in the deep water region of the southern Gulf of Mexico based on potential habitat models of selected ichthyoplankton species and circulation numerical models

Abstract approved by:

Dr. Sharon Zinah Herzka Llona Thesis Director

Marine fishes have complex life stages requiring different habitat types and distinct environmental conditions. Larval habitat depends on the adult distribution and spawning, but larvae can be dispersed to regions with unsuitable conditions that may negatively affect survival and recruitment. In oceanic systems, larval dispersion is highly influenced by mesoscale circulation, which influences connectivity, population dynamics and the structure of marine fish populations. Ocean circulation models can be used in particle tracking experiments, thereby applying a Lagrangian framework to follow a large number of virtual larvae through space and time and examine dispersion and connectivity. They can be coupled with ecological information (adult spawning habitat and period) or biological characteristics (planktonic stage duration, larval growth rates) to obtain detailed insight into the physical and biological interactions and evaluate larval dispersion pathways and connectivity between regions. In this study, the larval occurrence, distribution and density of six fish species were examined as a function of oceanographic variables using Generalized Additive Models (GAM) based on data from 15 cruises held from April to November (2011 to 2018) in the Gulf of Mexico (GoM). Twelve cruises covered the southern GoM's (sGoM) deep-water region (> 1000 m) and three the Yucatan Shelf. The distribution of oceanic species was related to oceanographic variables indicative of higher productivity, which may lead to greater larval feeding success and survival. In contrast, the presence of neritic species in oceanic waters close to the shelves is likely mediated by regional cross-shelf transport and may lead to high mortality. On the Yucatan Shelf, neritic larvae were distributed beyond the 40 m isobath, with the highest densities in the central shelf. Larval densities were significantly related to salinity and wind speed, but their distribution reflects adult spawning regions and periods. GAMs were subsequently applied to a ten-year climatology of hydrographic data to predict each species' potential habitat and delimit the origin of the particle dispersion pathways. Two contrasting mesoscale circulation patterns were selected: (1) a high level of Loop Current (LC) intrusion and no interaction between anticyclonic eddies (AE) and the cyclonic eddy (CE) of the Bay of Campeche (BoC), and (2) a low level of LC intrusion, the presence of a recently detached LC-AE, and AE-CE interactions in the western Gulf. Larval transport was simulated using the HYCOM model's velocity fields. Randomly distributed, passive particles were seeded in predicted potential habitats and advected for 30 d. Dispersed particles from potential habitats within the sBoC were mainly retained in the western GoM. There was higher retention in the deep-water region during periods of high mesoscale activity due to interactions between eddies. Particles from potential habitats close to the LC were dispersed to the northwestern GoM and the Atlantic Ocean when its intrusion was higher. Studying the dispersion of species with contrasting life histories based on environmental requirements and ocean circulation models provided insight into how larval distribution and mesoscale circulation processes may impact dispersion and connectivity between regions, which will influence survival and the recruitment of adult populations.

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1.1 Background

Marine fishes have complex life cycles that encompass the embryonic, larval, juvenile, and adult stages, requiring different habitat types with distinct environmental conditions (Fuiman & Werner, 2002). Marine fish habitats can also be defined according to the characteristics and depths where adults reside and spawn (Kingsford, 1993). In oceanic regions, fish species are distributed at particular ranges of the water column, and their habitat can be classified as those that occupy epipelagic (0-200 m), meso- (200-1000 m), and bathypelagic (1000-4000 m) waters (Fahay, 2007). In contrast, neritic species are found from the coastline to the edge of the continental shelf (at depths < 200 m).

Fish larvae inhabit the euphotic zone (De Macedo-Soares et al., 2014), where primary production takes place (Hidalgo-González & Álvarez-Borrego, 2008; Yamaguchi et al., 2019) and where there is greater food availability that favors increased larval survival and recruitment (Fuiman & Werner, 2002). Larval habitat is also influenced by the adult distribution, spawning region, and seasonality, as well as environmental requirements (Caiger et al., 2021; Marancik et al., 2005) and transport processes (Largier, 2003; Milligan & Sutton, 2020).

The survival and recruitment of marine fish larvae is critical for sustaining populations through time (Rothschild, 2000, Govoni, 2005; Kingsford, 1993). Understanding the spatial and temporal distribution and density of the larvae relative to environmental conditions allows for the definition of their ecological requirements and understanding of recruitment variability. However, in marine systems, larval sampling and identification are frequently patchy, with intensive and expensive labor, and obtaining a comprehensive characterization of a species' distribution is challenging and often limited. One approach that complements in situ sampling is the definition of stage-specific potential habitats (Rooker et al., 2013). A potential habitat can be defined as a region with a set of suitable environmental conditions that is species-specific and can vary among life stages (Planque et al., 2007). Potential habitats can be predicted based on several approaches, such as presence-absence or density models (e.g., Borchers et al., 1997; Torrejón-Magallanes et al., 2019). They can be useful for identifying habitat size and distribution shifts through time due to anthropogenic impacts such as oil spills (Langangen et al., 2017; Rooker et al., 2013), overfishing and climate change (Muhling et al., 2011; Petitgas et al., 2013), which influence survival and

recruitment during the early life of marine fishes (De Mitcheson & Erisman, 2012; Lindo-Atichati et al., 2012).

During the early life stages of fish, larvae can be passively transported over long distances to areas that can increase or decrease growth and survival (Cowen & Sponaugle, 2009; Govoni, 2005). Due to the lack of well-developed horizontal swimming abilities in the earlier stages of development, passive transport is mainly responsible for establishing connectivity between regions (Clark et al., 2005; Leis, 2020). Specifically, the level of connectivity between regions is regulated by the retention and dispersal of larvae (Cowen et al., 2006; Lett et al., 2008). Connectivity during the dispersive larval stage is critical in determining population structure and the potential for recolonization after disturbances such as oil spills (Hogan et al., 2012; McCrea-Strub et al., 2011).

Connectivity studies also contribute to inferring larval origin, identifying retention areas and estimating the time elapsed between spawning and recruitment to nursery habitats (Compaire et al., 2021; Johnson et al., 2013; Leis et al., 2015). One approach to analyzing transport mechanisms, larval dispersal and connectivity among regions (Compaire, et al., 2021; Johnson et al., 2017) is using ocean circulation models (e.g., Basterretxea et al., 2012; Lett et al., 2008; Morey et al., 2020), which provide high-resolution horizontal velocity components at different depths. Ocean circulation models can be coupled with species-specific characteristics such as egg and larval distribution and seasonality, egg buoyancy, or larval mortality rates (Basterretxea et al., 2012; Mariani et al., 2010; Parada et al., 2003; Paris et al., 2013). Comprehending the transport mechanisms and evaluating marine fish larval connectivity in the context of a given species' ecological and biological characteristics can provide a better understanding and assessment of population structure, population resilience and recruitment variability (Basterretxea et al., 2012; Cowen et al., 2006).

The circulation of the Gulf of Mexico's (GoM) deep-water region (> 1000 m), which occupies 70 % of its total area (Heileman & Rabalais, 2009), is highly influenced by the Loop Current (LC) and mesoscale eddies (Biggs, 1992; Weisberg & Liu, 2017). The LC connects the Caribbean Sea to the GoM through the Yucatan Channel and becomes the Gulf Stream in the Atlantic Ocean once it passes through the Florida Straits (Flór, 2010). The northern GoM is characterized by periodically detached LC anticyclonic eddies (LC-AE) that travel westward as their energy dissipates until they interact with the western slope (Dubranna et al., 2011; Leben, 2005; Weisberg & Liu, 2017). Cyclonic features known as LC frontal eddies also play an essential role in driving mesoscale circulation (Hamilton et al., 2016; Sheinbaum et al., 2016). These mesoscale features determine the transport of water masses into the GoM (Cowen & Sponaugle, 2009;

Johnson et al., 2017), and can also transport fish larvae from the Caribbean Sea into the GoM (Echeverri-García et al., 2022; Jochens & DiMarco, 2008; Lindo-Atichati et al., 2012).

The oceanic region of the southern GoM (south of 22 °N), which encompasses the Bay of Campeche (BoC), is characterized by higher primary and secondary productivity in comparison with the central and northern GoM (Martínez-López & Zavala-Hidalgo, 2009; Vázquez de la Cerda et al., 2005). Higher nutrient availability to the euphotic layer is due to the presence of a semi-permanent cyclonic eddy (CE) that shallows the pycnocline in the western BoC (Dubranna et al., 2011; Pérez-Brunius et al., 2013) and to wind-driven upwelling near the BoC's eastern shelf (Merino, 1997; J. Zavala-Hidalgo et al., 2003). In addition, the transport of river runoff from the Grijalva-Usumacinta River System toward the deep waters of the BoC also contributes to its productivity (Signoret et al., 2006). The processes that drive higher productivity and food availability contribute to larval survival (Fuiman & Werner, 2002). LC-AEs and non-LC AEs may interact with the CE in the BoC (Pérez-Brunius et al., 2013), forming fronts that also increase productivity and prey availability and can sustain high larval growth rates that decrease the duration of the larval stage and cumulative mortality (Bakun, 2006). These fronts, and the circulation in the GoM, will determine larval connectivity in the oceanic waters of the GoM (Johnson et al., 2017; L. Sanvicente-Añorve et al., 2014). In addition, the upper layer is influenced by seasonal variability that controls environmental conditions and circulation in the euphotic zone (Muller-Karger et al., 2015; Jorge Zavala-Hidalgo et al., 2006).

In contrast to oceanic species, fish larvae of neritic species are mainly distributed over the continental shelf; however, they can be dispersed toward oceanic waters due to seasonal cross-shelf transport (Compaire et al., 2021; Echeverri-García et al., 2022; Johnson et al., 2013). Understanding the mechanisms that transport larvae to and from suitable habitats is vital because the loss of those larvae can influence recruitment and population size.

1.2 Objectives

1.2.1 General objective

This study aimed to evaluate the dispersal of several marine fish species with contrasting life history strategies from predicted potential habitats using a high-resolution ocean circulation model to asses connectivity among regions of the GoM's deep-water region.

1.2.2 Specific objectives

- Describe the density and distribution of fish larvae of six species with contrasting life history strategies collected in the GoM deep-water region whose adults occupy oceanic and neritic habitats in the GoM.
- Evaluate the relationship between larval density and distribution of neritic and oceanic species with environmental conditions based on samplings in the deep-water region of the GoM.
- Evaluate the relationship between environmental conditions and the density and distribution of two commercially critical neritic species based on sampling over the Yucatan Peninsula's continental shelf.
- Predict the potential habitat of the larvae of species with contrasting life histories based on a 10year climatology of environmental conditions in the GoM's deep water region.
- Couple species-specific predicted potential habitats with ocean circulation models to examine larval dispersal and connectivity in the GoM's deep-water region under two contrasting conditions: (1) a year with a high level of LC intrusion and low interaction between AEs of the northern GoM and the semi-permanent CE in the BoC, and (2) a year with a low level of LC intrusion and high level of interaction between AEs in the northern GoM and the CE in the BoC.

Chapter 2. Distribution and densities of fish larvae species with contrasting life histories as a function of oceanographic variables in the deep-water region of the southern Gulf of Mexico

2.1 Introduction

Comparing the distribution, density and habitat characteristics of species with contrasting life history strategies can provide insight into how similar processes structuring biogeographical provinces and driving connectivity might relate differently among these species. This would allow for the evaluation of the specific relationship between environmental conditions and how connectivity can affect survival during the early life stages.

Marine fish species can be classified according to the habitat characteristics and depths where adults reside and spawn (Espinosa-Fuentes & Flores-Coto, 2004). Neritic species are found from the coastline to the edge of the continental shelf (at depths < 200 m) and their spawning period is generally between spring and summer (Froese & Pauly, 2021; Richards, 2006). Spawning normally occurs in the upper water column or in shallow demersal habitats such as coral reefs (Flores-Coto et al., 2000; Grüss et al., 2018), where wind-driven long-distance transport tends to occur along-shelf (Gómez-Valdivia & Parés-Sierra, 2020; Gough et al., 2019), although cross-shelf transport can also cause larvae to be transported off the continental shelf toward deeper oceanic waters (Compaire et al., 2021; Martínez-López & Zavala-Hidalgo, 2009; Otis et al., 2019). Larval stage duration in most neritic species is 16 to 40 d (De Vries et al., 1990; Houde & Richard, 1969; Leis et al., 2006). Species that live in oceanic waters can be classified in those that live in epipelagic waters (0-200 m), meso- (200-1000 m) and bathypelagic (1000-4000 m) regions (Fahay, 2007).

While epipelagic species usually spawn between spring and summer (Collette & Aadland, 1995; Froese & Pauly, 2021), mesopelagic species mostly spawn throughout the year, although some present one or two spawning peaks (April-May, August-September; Froese & Pauly, 2021; Richards, 2006). However, fecundity is typically lower in oceanic species than in neritic species (Catul et al., 2011; Goodwin IV & Funicane, 1985; Macias et al., 2006). Meso- and bathypelagic species' spawning occurs mainly above 500 m (Caiger et al., 2021; Hulley & Prosch, 1987), and eggs are fertilized as they rise to a specific vertical position in the water

column as a function of the lipid and protein content of the yolk sac (Catul et al., 2011; Marshall, 1979; Sundby & Kristiansen, 2015). The larval stage of many mesopelagic species lasts ~ 50 d (Gartner, 1993; Landaeta et al., 2015). Therefore, adult distribution and spawning period and region will influence original fish larvae distribution.

The survival and successful recruitment of the early life stages of fishes (eggs, larvae and juveniles) is crucial to sustaining adult populations through time (Rothschild, 1986). Ichthyoplankton distribution and density are dependent on adult population size, spawning regions and seasonality, and whether their environmental requirements are met (Cowen & Sponaugle, 2009; Miller, 2007). In addition, due to the larval weak swimming ability, mainly until notochord flexion is completed (Clark et al., 2005; Gawarkiewicz et al., 2007), some can be passively transported horizontally over tens to hundreds of kilometers (Compaire et al., 2021; Cowen & Sponaugle, 2009; Govoni, 2005), during which time they are exposed to varying environmental conditions. Spatial and temporal variability in environmental conditions can lead to changes in the physiology and behavior (e.g., swimming or feeding) of ichthyoplankton, affecting larval survival and recruitment (Fuiman & Werner, 2002). Understanding the spatial and temporal density of the larvae relative to oceanographic conditions allows for defining habitat requirements, as well as identifying habitat shifts caused by anthropogenic impacts such as oil spills, overfishing and climate change, all of which affect survival and recruitment during the early life of marine fishes (De Mitcheson & Erisman, 2012; Lindo-Atichati et al., 2012; Rooker et al., 2013).

The Gulf of Mexico (GoM) is a semi-enclosed large marine ecosystem in which the central oceanic region encompasses 70 % of its total area (Heileman & Rabalais, 2009). The circulation is dominated by mesoscale features including the Loop Current (LC), detached LC anticyclonic eddies (LC-AE), non-LC anticyclonic eddies (AC) and cyclonic eddies (CE) (Gómez-Valdivia & Parés-Sierra, 2020; Pérez-Brunius et al., 2013; Weisberg & Liu, 2017). The LC connects the Caribbean Sea to the GoM through the Yucatan Channel, and becomes the Gulf Stream in the Atlantic Ocean once it passes through the Straits of Florida (Flór, 2010). LCEs travel westward in the central GoM over time periods ranging from months to one year (Leben, 2005; Weisberg & Liu, 2017); when they reach the slope and the continental shelf their energy dissipates (Dubranna et al., 2011). In the LC and warm core eddies (LC-AEs and ACs), the pycnocline deepens due to the anticyclonic circulation and the productivity is lower (Biggs, 1992). The southern GoM (sGoM) is characterized by a semipermanent cyclonic eddy in the Bay of Campeche (BoC; South of 22 °N; Pérez-Brunius et al., 2013), which provides nutrients to the surface due to a shallowing of the pycnocline (Salas de León & Monreal Gómez, 2005). Coupled with regional upwelling, the BoC exhibits higher productivity than the central gulf (Martínez-López & Zavala-Hidalgo, 2009; Vázquez de la Cerda et al., 2005). While

circulation and productivity of the oceanic GoM are mainly influenced by mesoscale features, the continental shelf is primarily affected by wind direction and speed, seasonal surface and water column temperature variations (Muller-Karger et al., 1991; J. Zavala-Hidalgo et al., 2003), salinity shifts and nutrient inputs driven by river discharges (e.g., Mississippi river in the north and the Grijalva-Usumacinta riverine system in the south). In addition, the GoM's circulation and environmental conditions in the surface layer are heavily influenced by atmospheric cold fronts during fall and winter (Salas-Pérez & Granados-Barba, 2008; Jorge Zavala-Hidalgo et al., 2014), and by tropical storms and hurricanes during summer and fall (Gutiérrez de Velasco & Winant, 1996). The circulation and environmental conditions of the oceanic and neritic regions may cause changes in the adult spawning areas and the spatial distribution of the suitable habitat of the larvae, affecting their distribution and density (Domingues et al., 2016; Lindo-Atichati et al., 2012).

Larval fish studies in the GoM that include species with contrasting life histories have mainly focused on larval fish assemblages, in which groups of species are considered an entity (Daudén-Bengoa et al., 2020; Muller-Karger et al., 2015). For example, Muhling et al. (2012) examined data from 20 years of SEAMAP surveys (from the coast to 2000 m) in the northern GoM and found an increase in the density of oceanic families and a decrease in neritic families over time. Inner shelf species' larval density was positively related to shrimp-trawling effort and with the Mississippi River outflow, while those of outer shelf species were positively correlated with mean SST and with plankton density, which influences larvae survival through food availability. Studies of fish larvae in the deep-water region have also focused on commercially important species such as tunas and billfishes (Scombridae and Istiophoridae; Domingues et al., 2016; Rooker et al., 2008, 2012) as well as snappers and runners (Lutjanidae and Carangidae; Goodwin IV and Funicane, 1985; Johnson et al., 2013; Leak, 1981), but these studies have focused on the US Exclusive Economic Zone (EEZ) and have not been extended to the southern gulf. However, a comparative approach that examines the distribution and habitat characteristics of species with different life histories in the GoM's deep-water region is lacking.

For the Mexican EEZ, Sanvicente-Añorve et al. (2000) identified four assemblages in BoC's shelf and oceanic regions, which varied spatially and seasonally. They suggested that adult habitat, seasonality and transport processes led to distinct ichthyoplankton assemblages. Compaire et al. (2021) used backward-tracking particle experiments to explain the presence of coastal and neritic species in the oceanic waters of the western GoM, thus providing insight into the transport of larvae from the continental shelf to the deep-water region. Daudén-Bengoa et al. (2020) suggested that adult distribution and spawning drove the species composition and distribution of larval assemblages of lanternfishes (Myctophidae) in the deep-

water region, rather than larval transport. Therefore, this study will allow comprehend how the same environmental conditions correlate differently depending on the species' contrasting life histories.

The aim of this study was to describe the larval distribution and density relative to environmental conditions of six species with contrasting life history strategies and adult habitats, based on surveys performed in the deep-water region of the sGoM. The relationship with in situ and satellite-based oceanographic parameters during two seasons (spring and early summer, and late summer and autumn) was examined based on the analysis of an extensive dataset integrated from 12 cruises performed between 2011 and 2018. We hypothesized that oceanic mesopelagic species would be broadly distributed and that their density would be related to variables indicative of mesoscale cyclonic and anticyclonic eddies. In contrast, the distribution of neritic species should be more limited to stations close to the edge of the continental shelf in areas where cross-shelf transport is observed, and there should not be a relationship with oceanographic variables. Since mesopelagic species usually spawn throughout the year, temporal variability in density between seasons should not be observed, unlike for neritic species in which spawning seasonality predominates.

2.2 Material and methods

2.2.1 Sampling design

Samples were collected during 12 oceanographic cruises (Table 1), XIXIMI (18 to 25 °N, 86 to 97 °W), SOGOM (18 to 23 °N, 86 to 92 °W) and PERDIDO (24 to 26 °N, 95 to 97 °W; Figure 1) on board the R/V *Justo Sierra*. The cruises were all conducted under a single multi-institutional research project funded by the Mexican National Council for Science and Technology - Mexican Ministry of Energy - Hydrocarbon Fund (project 201441) and covered different regions of the sGoM's deep-water region with some spatial overlap (Figure 1). Cruises were classified into season I comprising spring to early summer (April to July) and season II encompassing late summer to autumn (August to October). This division was based on the increasing stratification that is observed in late summer and early fall compared to spring and early summer and allowed for a balanced pooling of the sampling effort (n = 6 cruises per season). It is also supported by significant differences (Wilcox Test, p < 0.05) between seasons in all oceanographic variables selected for the statistical analysis (Table 3). Although our approach is not conducive to examining larval distribution over the temporal scale of a specific cruise, the seasonal pooling of density data for cruises conducted over

several years (Gartner, 1993; Ochoa-Muñoz et al., 2018; Laura Sanvicente-Añorve et al., 1998; Shulzitski et al., 2015) allowed us to include more data and obtain more robust statistical analyses that reflect a larger sampling effort that encompasses interannual variability.

Cruise	Dates	Season	No. of stations
XIXIMI 02	01-15 July 2011	I	34
SOGOM 01	3-27 June 2015	I	51
XIXIMI 04	27 August - 16 September 2015	II	34
PERDIDO 01	12-21 May 2016	I	13
XIXIMI 05	10-24 June 2016	I	32
SOGOM 02	31 August - 20 September 2016	II	48
PERDIDO 02	28 September - 7 October 2016	II	12
SOGOM 03	21 April - 23 May 2017	I	51
PERDIDO 03	6-21 June 2017	I	13
XIXIMI 06	1-31 August 2017	II	36
PERDIDO 04	19 September - 1 October 2017	II	12
SOGOM 04	29 August - 22 September 2018	II	49

Table 1. Cruises in which larval fish sampling surveys were conducted presented in chronological order. Cruises were classified into Season I (April-July) or II (August-October).

All stations were located beyond the edge of the continental shelf in the deep-water region (> 1000 m) of the Mexican EEZ, and covered the sGoM and Yucatan Channel (Figure 1). Stations in the Yucatan Channel were only sampled in season II. Some of the stations of the SOGOM and XIXIMI cruises located south of 22 °N share the same coordinates, but were covered during different seasons if held in the same year.

Ichthyoplankton samples were collected from 200 m to the surface with oblique bongo tows fitted with 335 µm mesh nets. To estimate filtration volumes, net mouths were equipped with General Oceanics flowmeters. Each sample was fixed immediately either in 96 % ethanol or 7 % formalin buffered with sodium borate. Ichthyoplankton was sorted in the laboratory and identified to the lowest possible taxonomic level based on morphometric and meristic characteristics (Fahay, 2007; Richards, 2006). Densities were standardized as larvae per 1000 m-3 of filtered water. To compare temporal differences between species and seasons, the average standardized density was calculated (mean ± standard deviation) by grouping the data for all cruises within each season.



Figure 1. Ichthyoplankton sampling stations covered during cruises held between 2011-2018 in the southern Gulf of Mexico. PERDIDO (squares), SOGOM (circles) and XIXIMI (triangles) cruises. To allow for the visualization of multiple samples collected at a given station, their location is represented as a grid. Yucatan Channel stations were only sampled in season II. Continuous and dashed lines represent the 200 m and the 1000 m isobaths, respectively.

2.2.2 Species selection

A preliminary list of dominant species was generated, and then specific taxa with contrasting life histories and ecological or economic importance were selected. Six target species were then selected to include taxa with contrasting adult habitats and early life history characteristics, as well as families with ecological and economic importance (Table 2). The species were *Benthosema suborbitale* and *Notolychnus valdiviae* (lanternfishes; Myctophidae), *Bregmaceros atlanticus* (codlets; Bregmacerotidae), *Caranx crysos* (jacks; Carangidae), *Cubiceps pauciradiatus* (drift fishes; Nomeidae), and *Auxis* spp. (Scombridae; which includes larvae of *A. rochei rochei* and *A. thazard thazard*, known as bullet and frigate tuna, respectively). Both *Auxis* species were grouped into genus since their larvae cannot be distinguished morphologically and molecular identification is necessary (Catanese et al., 2008; Ochoa-Muñoz et al., 2018). Nevertheless, both species share very similar distribution, habitat, depth range and spawning periods in the GoM (Collette & Nauen, 1983; Froese & Pauly, 2021; Richards, 2006). **Table 2.** Species selected for GAM analysis, according to ecological and life history characteristics and/or commercial importance. For descriptive purposes, adult habitats are divided into their horizontal (H: neritic, oceanic) as well as their vertical habitat (V: epipelagic, mesopelagic, bathypelagic).

	Adult habitat	Adult depth range (m)		Ecological or	
Species			Spawning season	commercial	Literature
				importance	
					(Ditty et al., 2004; FAO,
				Commercial fisheries	2020; Felder & Camp,
Caranx crvsos	(H) Neritic	0-100	Apr to May	Sport / recreational	2006; Froese & Pauly,
,	(V) Epipelagic	0 100	Aug to Sep	fishing	2021; Goodwin IV &
				5966 t (2011)	Funicane, 1985;
					Richards, 2006)
					(Catanese et al., 2008;
					Collette & Aadland,
					1995; Collette & Nauen,
			No	Commencial Colorian	1983; Espinosa-Fuentes
	(H) Neritic and		Year around		& Flores-Coto, 2004;
Auxis spp.	oceanic	10-100	spawning	Sport / recreational	FAO, 2020; Felder &
	(V) Epipelagic		Peak: Jan to Apr &	Tisning	Camp, 2006; Froese &
			Jun to Aug	172693 t (1996)	Pauly, 2021; Muñoz
					Expósito et al., 2017;
					Ochoa-Muñoz et al.,
					2018; Richards, 2006)
	(H) Neritic and oceanic (V) Mesopelagic	50-2000	Year around spawning		(Clancey, 1956; Cohen et
				Biogeographic	al., 1990; Felder &
				indicator	Camp, 2006; Froese &
Bregmaceros atlanticus				Trophic link	Pauly, 2021; Richards,
				6500 t (1973)	2006; Zavala-García &
					Flores-Coto, 1994)
					(Bard et al., 2002;
				Prey for commercial	Butler, 1979; Cervigón,
	(H) Oceanic		Intermittent	species	1994; Felder & Camp,
Cubiceps pauciradiatus	(V) Epi -	50-820	spawner	Potential future	2006; Froese & Pauly,
	Mesopelagic		Peak: Dec to Apr	fishery	2021; Lamkin, 1998;
				Trophic link (fish,	Richards, 2006;
				birds, mammals)	Romanov, 2002)
	(H) Oceanic		Vear around		
Benthosema suborbitale		50-750	spawping	المطريمة وتجا فحجا	(Catul at al. 2011)
	(v) Epi -	50-750	Spawining	industrial tood	(Catul et al., 2011;
	wiesopeidgic		rean. Ividy lu jui	production	Feider & Camp, 2006;
			Veene	hirds manager	Froese & Pauly, 2021;
Notolychnus valdiviae	(H) Oceanic (V) Epi - Mesopelagic		rear around	Dirus, mammals)	Garmer, 1991, 1993;
		25-800	spawning	Biogeographic	Gjøsæter & Kawaguchi,
			Peak: Jan to Mar &	indicator	1980)
			Jul to Nov		

2.2.3 Oceanographic variable selection and processing

Hydrographic parameters were characterized through in situ measurements and remote sensing. In situ variables including temperature, salinity and fluorescence were measured at each station with a SBE 9Plus CTD equipped with a Seapoint chlorophyll a (chl a) fluorometer. Mean water column temperature over the sampling depth range (0-200 m), as well as temperature at 200 m, were also calculated because it is a key parameter linked to the development and growth of fish larvae (Hermann et al., 2001; Walsh, 1987). The 0-200 m mean salinity can be used to detect freshwater transport to offshore waters (Ditty et al., 2004; Flores-Coto et al., 2014). The depth of 17 °C isotherm and nitracline depth (density 25.3 mg m⁻³) are considered proxies of mesoscale structures (LCEs, non-LC anticyclonic eddies and cyclonic eddies) in the GoM (Martin & Richards, 2001; Pasqueron De Fommervault et al., 2017). Stratification (J, zero for a well-mixed layer and increases with stratification; J. H. Simpson et al., 1981) was used as an in situ indicator of vertical mixing since it has been related to nutrient and prey availability in the euphotic zone in oceanic waters (Hidalgo-González & Álvarez-Borrego, 2008; Yamaguchi et al., 2019).

Sea surface temperature (SST; product id 010_005, 0.25° x 0.25° spatial resolution, gap-free gridded data after validation process) and sea surface height (SSH; product id 008_047, 0.25° x 0.25° spatial resolution, gap-free gridded data after validation process) were also used as indicators of mesoscale features. Sea surface chl a concentration (product id 009_082, ~ 0.04° x 0.04° spatial resolution, gap-free gridded data after validation process) was used as proxy of phytoplankton biomass and indicator of food availability (Hamilton et al., 2016; Pasqueron De Fommervault et al., 2017). Satellite variables were obtained from the E.U. Copernicus Marine Service Information (CMEMS; CMEMS, 2020) (http://marine.copernicus.eu/). Spatial data for SST, SSH and sea surface chl a corresponded to the date on which each station was sampled. Wind surface speed (WS; ERA5 dataset, 31 km spatial resolution, gap-free gridded data after validation process) was downloaded from COPERNICUS (https://cds.climate.copernicus.eu/; Hersbach et al., 2018) and was calculated from wind surface speed vectors (u, v) using the coordinates for each station. WS was used as an indicator of turbulence, which has been related to larval feeding success (Kloppmann et al., 2002; Mackenzie & Kiørboe, 2000). Data were averaged for the 4 d prior to the sampling date, because wind events such as northern fronts and southern winds in the GoM, are usually observed over the time periods of 3 to 7 d. Additionally, the bathymetry from ETOPO1 1 Arc-Minute Global Relief Model (Amante & Eakins, 2009) was used since species from coastal and oceanic habitats were compared. Additionally, the location of each station (latitude and longitude) was added as a smoothed interaction term to consider spatial effects and account for spatial autocorrelation (García-Fernández et al., 2021; Rooker et al., 2012). Outliers were visualized using Cleveland dotplots (Zuur et al., 2010) and only the variables that met the requirements of low correlation (Spearman ρ , r < 0.70) and a variance inflation factor (VIF) lower than 3 (Zuur et al., 2010) were included in the statistical analyses: Mean salinity 0-200 m, SSH, SST, stratification, surface chl a and wind speed (Table 3).

2.2.4 Data and statistical analysis

Temporal differences in the densities of larvae and oceanographic variables were compared with a Kruskal-Wallis (rank sums; $\alpha = 0.05$) as an alternative to one-way analysis of variance (ANOVA). This nonparametric method does not assume a normal distribution, which was required since densities and oceanographic variables did not follow a normal distribution (Shapiro-Wilk normality test performed), and some of the variables did not show homogeneity of variance (Bartlett test performed).

Generalized additive models (GAMs) were used to examine the relationship between oceanographic conditions and the standardized density of each species. GAMs, an extension of generalized linear models, are a nonparametric and nonlinear regression technique that do not require a priori specifications of the functional relationship between the response and predictor variables (Hastie & Tibshirani, 1986; Simon N. Wood, 2017). In the GAM equation (1):

$$E[y] = g^{-1}\left(\beta_0 + \sum_k S_k(x_k)\right) \tag{1}$$

E[y] equals the expected values of the response variable (standardized density of each species), g represents the link function, β_0 equals the intercept, x represents each of k explanatory variables, and Sk represents the smoothing function for each of the explanatory variables.

Since all oceanographic variables were significantly different between seasons (Wilcox Test, p<0.05; Table 3) the GAMs were performed separately for each season. This strategy was chosen as it also allows for the characterization of the potential habitat distribution for the target species on a seasonal basis (see Rooker et al., 2013). For comparative purposes, GAMs using season as a categorical variable and as a categorical smoothing term were also performed (Table 12, Figure 19 and 20). However, the percent of variance explained was generally lower than the GAMs with the split seasonal database. Models were built with a logarithmic link function and using smoothing splines. The smoothing splines flexibility is associated with

the degrees of freedom (1 = linear model; > 1 = nonlinear model; Wood, 2006). The Tweedie distribution (part of the exponential dispersion model family) was used since the response variable (standardized densities) had a high proportion of zeros and were non-negative (Arcuti et al., 2013; Dunn & Smyth, 2005). The percentage of zero densities for each response variable is reported in the result section (Table 5). The power value of the model, which indicates whether the data exhibited a gamma-like (power value close to 1) or a Poisson-like (power value close to 2) distribution is also reported. The Restricted (Residual) Maximum Likelihood (REML) was used as a smoothing parameter estimation method. To avoid overfitting in the model, variables were limited to a maximum 4 k parameters except latitude and longitude. The gam function from the "mgcv" package was used for the models and the gam.check function for model validation (Simon N. Wood, 2018).

A stepwise manual backward procedure to identify the variables that had no effect on the explanatory variable (p > 0.05) was used (e.g., Rooker et al., 2012; Torrejón-Magallanes et al., 2019). This process was halted when all explanatory variables were significant (p < 0.05). Deviance explained was used as a measurement of goodness of fit (Simon N. Wood, 2017). If no variables were significantly related to a species' density, or the explained deviance in the final model was lower than 10 % (Deviance explained < 0.1) the model was discarded.

Once the models were defined, the relative importance of each oceanographic variable was determined by examining the differences in the model with and without the variables by removing them one by one (Rooker et al., 2012). To assess the latter, the change in explained deviance and in AIC (Akaike information criteria) were used. In order to determine if the relationship between the density and the environmental variable was linear, the estimates of degrees of freedom were examined. The R–project 3.4.1 (R Core Team, 2021) statistical program was used for all analyses.

2.3 Results

2.3.1 Larval standardized density and distribution

The lanternfish *N. valdiviae* showed the highest larval density in both seasons, while the neritic species *C. crysos* presented the lowest (Table 3). When comparing between seasons, the mean density of *C. crysos* was almost three times higher in season II, although statistical differences were not found. *C. pauciradiatus*

presented significantly higher mean larval density in season I, and *B. atlanticus* in season II. The density of the lanternfishes (*B. suborbitale* and *N. valdiviae*) did not differ between seasons.

Table 3. Mean seasonal density (larvae 1000 m⁻³) for cruises (6 per season) and total density conducted between 2011 and 2018 in the deep-water region of the southern GoM. Results of one-way ANOVAs are reported between parentheses. Species with significant differences in mean density between seasons are in bold.

	Mean density \pm Std. Deviation		
	Season I	Season II	
	(April-July)	(August-October)	
Carapy crusos (p = 0.340)	0.25 ± 1.34	0.62 ± 2.52	
Curuix (19303 (p = 0.340)	0.45 ±	2.06	
4uxis spn (n = 0.898)	4.07 ± 10.20	4.09 ± 11.06	
Auxis spp. (p = 0.050)	4.08 ± 10.66		
Breamaceros atlanticus ($n = 0.019$)	4.41 ± 8.70	5.77± 12.59	
Dregmaceros ananticas (p = 0.015)	5.14 ± 10.98		
Cubicens nauciradiatus (n = 0.045)	9.59 ± 21.90	5.75 ± 12.56	
	7.67 ± 17.95		
Benthosema suborbitale (n = 0.068)	12.10± 16.98	9.26± 14.96	
	10.57 ± 15.96		
Notolychnus valdiviae (p = 0,175)	20.97 ± 26.47	15.51 ± 17.30	
	18.02 ±	22.13	

Auxis spp. was mostly distributed in the central gulf during season I in comparison to season II, when the highest densities were found in the BoC (Figure 2). *C. crysos'* distribution was mainly limited to stations closer to the continental shelf during season II, and some stations in the north-western and south-eastern gulf. However, in season I, larvae were found at some stations far from the continental shelf, in the central GoM.

The distribution of *B. atlanticus* was patchy during both seasons, and high densities were found in the BoC although larvae were collected throughout the deep-water region. The spatial distribution of mesopelagic species was more homogeneous than that of neritic species, and species-specific seasonal variation was observed. While the spatial distribution of *B. suborbitale* and *N. valdiviae* was very similar between seasons, *B. suborbitale* was more abundant in the southern region of the study area in season II. The mesopelagic *C. pauciradiatus* showed the highest density in almost all stations in the northern region and a higher degree of stations with larval absence were observed in the southern gulf during season I. In season II the distribution included more stations in the BoC.



Figure 2. Season-specific spatial distribution of density of larval fish taxa. A: *Auxis* spp., B: *Caranx crysos*, C: *Bregmaceros atlanticus*, D: *Cubiceps pauciradiatus*, E: *Benthosema suborbitale*, F: *Notolychnus valdiviae*. First (second) column with red (blue) dots represents season I: April-July (season II: August-October). Circle size represents the density (larvae 1000 m⁻³) for a given location, with the scale adjusted for each species. Overlapping circles indicate samples from different cruises. Black dots indicate the absence of larvae. Continuous and dashed lines represent the 200 m and the 1000 m isobaths, respectively.

2.3.2 Relationship with oceanographic variables

All oceanographic variables were significantly different between seasons (Wilcox Test, $\alpha = 0.05$). Surface chl a and WS were significantly higher during season I (Table 4). Conversely, stratification, mean salinity, SST and SSH had significantly higher values in season II.

Table 4. Oceanographic variables comparison between seasons for cruises (6 per season) conducted between 2011 and 2018 in the deep-water region of the southern GoM. Kruskal-Wallis test results are reported between parentheses. Variables with significant differences (p <0.05) between seasons are in bold.

	Mean ± Std. Deviation			
	Season I Season II			
	(April-July)	(August-October)		
Wind speed (ms ⁻¹) (p < 0.001)	4.70 ± 1.59	4.04 ± 1.46		
Surface chl a (mg m ⁻³) (p = 0.014)	0.11 ± 0.04	0.09 ± 0.04		
Mean salinity 0-200 m (psu) (p = 0.002)	36.56 ± 0.08	36.60 ± 0.08		
SST (°C) (p < 0.001)	28.40 ± 0.95	30.03 ± 0.41		
Stratification (J) (p < 0.001)	1537.24 ± 395.69	1784.35 ± 282.62		
SSH (m) (p < 0.001)	0.35 ± 0.09	0.41 ± 0.11		

GAMs were constructed for five species: *Auxis* spp. (neritic and epipelagic), *B. atlanticus* (neritic and mesopelagic), and *B. suborbitale*, *C. pauciradiatus* and *N. valdiviae* (mesopelagic) (Table 5). The models for the neritic *C. crysos* had a very low explained deviance (< 0.1) in both seasons and were discarded. For *Auxis* spp., season I was the model with the highest explained deviance, and all models in season I presented higher deviance explained than in season II. In addition, station position was also influenced in several models. The relationship between the raw data of all species' standardized densities and oceanographic variables are presented in Figure 21.

Table 5. Final GAMs for each target species with significant environmental and spatial variables per season (Season I: April to July; Season II: August to October). DE and AIC columns indicate the model's final values without the variable. Zero (%) indicates the percentage of zero values in the response variable (larval density).

Auxis spp.					
SEASON I	Zero (%): 63		SEASON II	Zero (%): 74	
power = 1.30	DE = 47.3%	AIC = 421.03	power = 1.41	DE = 35.8%	AIC = 515.13
Depth			Depth		
Stratification			Stratification	27.30	522.50
Salinity			Salinity		
SST	33.5	438.80	SST	30.90	520.04
SSH	43.7	424.86	SSH		
Chl	41.6	427.04	Chl	22.20	529.98
Wind speed	35.4	433.90	Wind speed	25.60	528.98
Lat, Lon			Lat, Lon		
		Benthosemo	a suborbitale		
SEASON I	Zero (%): 32		SEASON II	Zero (%): 41	
power = 1.23	DE = 24%	AIC = 907.46	power = 1.38	DE = 23.5%	AIC = 978.28
Depth			Depth		
Stratification	19.60	912.70	Stratification		
Salinity	12.50	923.18	Salinity		
SST			SST	16.50	990.97
SSH			SSH		
Chl	21.20	910.83	Chl	12.40	998.49
Wind speed	17.30	916.79	Wind speed	16.70	992.39
Lat, Lon			Lat, Lon		
		Bregmacero	os atlanticus		
SEASON I	Zero (%): 53		SEASON II	Zero (%): 45	
power = 1.22	DE = 43.7%	AIC = 551.89	power = 1.35	DE = 22.7%	AIC = 867.52
Depth			Depth		
Stratification	33.40	570.24	Stratification		

Salinity			Salinity		
SST	36.90	567.02	SST		
SSH			SSH		
Chl	41.80	559.86	Chl		
Wind speed			Wind speed		
Lat, Lon	18.90	566.68	Lat, Lon	22.70	867.52
	·	Cubiceps p	auciradiatus		
SEASON I	Zero (%): 50		SEASON II	Zero (%): 69	
power = 1.38	DE = 45.6%	AIC = 686.81	power = 1.27	DE = 38.3%	AIC = 596.06
Depth	35.70	700.77	Depth		
Stratification	40.40	692.78	Stratification		
Salinity			Salinity		
SST	34.90	704.81	SST	18.60	626.83
SSH	37.70	697.77	SSH		
Chl	40.20	693.01	Chl		
Wind speed			Wind speed	14.70	635.19
Lat, Lon			Lat, Lon		
		Notolychn	us valdiviae		
SEASON I	Zero (%): 18		SEASON II	Zero (%): 22	
power =1.37	DE = 44.4%	AIC = 1119.96	p=1.37	DE =18.8%	AIC = 1248.43
Depth			Depth		
Stratification	41.50	1123.74	Stratification		
Salinity			Salinity		
SST	39.60	1126.85	SST		
SSH			SSH	17.50	1248.43
Chl			Chl		
Wind speed	37.20	1133.59	Wind speed		
Lat, Lon	24.80	1142.28	Lat, Lon	5.80	1268.66

For season I, the final *Auxis* spp. model included 4 oceanographic variables that were significantly related to larval density: SST, WS, chl a and SSH (listed in order of the highest explained deviance contributed to the model). For season II, 4 variables were included in the model (chl a, WS, stratification and SST); higher values of SST were related to higher densities, similar to what was observed for season II (Figure 3). A positive nonlinear relationship between density and chl a was observed for both seasons, although a decrease in density was observed in values > 0.15 mg m⁻³ in season II. Higher densities were related to lower WS in season I and to higher WS in season II. However, during both seasons most of the observations fell along intermediate WS values (3 to 6 m s⁻¹). A linear negative relationship between SSH and density

was observed for season I with most observations around intermediate to low values, while stratification was only significant in season II, with an increase in density at values < 1600 J, after which density decreased.



Figure 3. Response plots of the oceanographic variables' additive effect on the density of *Auxis* spp. Season I (April-July) in red and season II (August-October) in blue. Smoothed values represented by a continuous line, and shaded color indicates 95% confidence intervals. variables with non-significant additive effects (p > 0.05) for a given season are not presented.

B. suborbitale's final model included 4 variables for season I (mean salinity, WS, stratification and chl a). For season II, the variables included in the models were only chl a, SST and WS. Most of the observations in relation with chl a were in low concentration values, however, while in season I, a linear and negative relation was observed, in season II a positive non-linear relation was observed with a peak around 0.13 mg m⁻³ of chl a. WS showed an opposite relationship with density between seasons: it was negative and nonlinear in season I (Figure 4), with lowest densities between 5 to 8 m s⁻¹, and with a linear and positive relationship for season II. Additionally, in season I mean salinity (the most powerful variable) was related with higher densities until a salinity of approximately 36.6 and stratification with values between 1500 -2000 J. In season II SST was positively and non-linear related with B. suborbitale's density.

The density of *B. atlanticus* in season I was related to station location, stratification, SST and chl a, while in season II the explained deviance (DE = 22.7%) was only explained by station location. The three environmental variables were linear and positively related with larval density (Figure 5). Although, the greatest number of observations varied between the variables' ranges. The majority of observations were in low stratification values (< 1600 J), while SSTs were above 28 °C.



Figure 4. Response plots of the oceanographic variables' additive effect on the density of *Benthosema suborbitale*. Season I (April-July) in red and season II (August-October) in blue. Smoothed values represented by a continuous line, and shaded color indicates 95% confidence intervals. Variables with non-significant additive effects (p > 0.05) for a given season are not presented.



Figure 5. Response plots of the oceanographic variables' additive effect on the density of *Bregmaceros atlanticus*. Season I (April-July) in red and season II (August-October) in blue. Smoothed values represented by a continuous line, and shaded color indicates 95% confidence intervals. variables with non-significant additive effects (p > 0.05) for a given season are not presented.

For *C. pauciradiatus*, SST was included in both models. For season I the explaining variables were SST, depth, SSH, chl a and stratification, while in season II WS and SST. A positive relationship between density

and SST was found for both seasons (Figure 6); however, for season I the relationship was linear and the highest densities were observed at temperatures higher than 28 °C; and for season II maximum densities were > 30 °C. Regarding the variables in season I, higher densities were found in deeper stations (< -3000 m), although densities increased in shallower waters than -2000 m deep. With regard to stratification, the highest densities were found at low values (1100 to 1600 J).

SSH showed a nonlinear positive relationship with density in season I, with most of the observations found at low values (0.25 to 0.5 m), and a maximum at high SSH values (> 0.55 m), although this corresponded to very few observations. Thus, this relationship should be interpreted cautiously. Similar to previous models, larval density increased with chl a concentration. In season II, WS was positive and linearly related to density.

For *N. valdiviae*, the variables retained for season I were station location, WS, SST and stratification, while for season II were station location and SSH. The relationship with stratification included was non-linear and positive, although most of the observations were found in values lower than 1700 J (Figure 7). An increase in density was found between 28 to 29 °C of SST and a density peak was found at average WS values (4 to 5 m s⁻¹). In season II a dome-like distribution was found in the relationship between density and SSH, with a maximum between 0.4 and 0.5 m.



Figure 6. Response plots of the oceanographic variables' additive effect on the density of *Cubiceps pauciradiatus*. Season I (April-July) in red and season II (August-October) in blue. Smoothed values represented by a continuous line, and shaded color indicates 95% confidence intervals. variables with non-significant additive effects (p > 0.05) for a given season are not presented. Y axis scale in season I plots were modified to allow for a better interpretation.



Figure 7. Response plots of the oceanographic variables' additive effect on the density of *Notolychnus valdiviae*. Season I (April-July) in red and season II (August-October) in blue. Smoothed values represented by a continuous line, and shaded color indicates 95% confidence intervals. variables with non-significant additive effects (p > 0.05) for a given season are not presented.

2.4 Discussion

In the deep-water region of the sGoM, the distribution and density of the larvae of fish species with contrasting life histories varied spatially and between seasons. Larvae of adults from neritic habitats were mostly captured closer to the slope and less abundant, compared to those from epi- or mesopelagic species that were more homogeneously distributed throughout the deep-water region. Additionally, the oceanographic variables that had a significant correlation with density, and thus some predictive power for delimiting their spatial and temporal distribution, varied among species. Although our approach is not conducive to examining larval distribution over the temporal scale of a specific cruise, the seasonal pooling of density data for cruises conducted over several years allowed us to include more data and obtain more robust statistical analyses.

2.4.1 Spatial and temporal patterns

Spawning of the two neritic species occurs from March to April and June to August in *Auxis* spp. and April to May and August to September in *C. crysos* (Collette & Nauen, 1983; FAO, 2020; Froese & Pauly, 2021;
Richards, 2006), which is consistent with their presence during the two seasons considered in this study. These two species showed a more limited spatial distribution and lower densities than mesopelagic species, which agrees with our hypothesis. The adults of *C. crysos* live over the continental shelf at depths < 100 m (Felder & Camp, 2006; Froese & Pauly, 2021). The distribution of their larvae described by Ditty et al. (2004) for the northern GoM resembles our results, since they also reported a limited presence and low density beyond the continental slope. Likewise, Espinosa-Fuentes and Flores-Coto (2004) found lower densities of *C. crysos* at stations between the outer shelf and oceanic waters of the sBoC compared to more coastal stations, coinciding with our findings for the south-eastern BoC. On the other hand, *Auxis* spp. is considered mainly neritic (Boehlert & Mundy, 1994; Espinosa-Fuentes & Flores-Coto, 2004; Sabatés & Recasens, 2001), but adults and larvae have also been caught in oceanic waters (Collette & Nauen, 1983; Klawe, 1963). Espinosa-Fuentes and Flores-Coto (2004) found twice the density of *Auxis* spp.'s larvae in the outer shelf and over the slope in comparison with the inner shelf; larvae were absent at coastal stations. These results suggest that *Auxis* spp. spawn over the shelf as well as in oceanic waters in contrast to the neritic *C. crysos*, as suggested by Lindo-Atichati et al. (2012) in the northern GoM and reported by Klawe (1963) in the eastern Pacific Ocean, and Matsuura and Sato (1981) in southern Brazilian waters.

The presence of larvae of strictly neritic species in the deep-water region is likely explained by their offshore advection by local currents in the BoC, in the north-western gulf and north and east of the Yucatan shelf. Martínez-López and Zavala-Hidalgo (2009) describe the seasonal offshore cross-shelf transport and high chl a surface waters off the Tamaulipas-Veracruz (TAVE; western GoM) shelf and in the south-eastern BoC, which is produced by the convergence of seasonal winds along the shelf. This is observed during spring/early summer in TAVE, and in the southern BoC in the fall (see also Zavala-Hidalgo et al., 2003, 2006). Specifically, the higher density of neritic larvae in the deep-water region of the south-eastern BoC during season II, is consistent with the peak river discharges from the Grijalva-Usumacinta riverine system that coincides with offshore advection and high surface chl a concentration in the bay's central region (Martínez-López & Zavala-Hidalgo, 2009). The presence of C. crysos and Auxis spp. larvae off the western Yucatan shelf (YS) is also consistent with wind-driven westward circulation along the YS and towards the deep waters of the BoC (Ruiz-Castillo et al., 2016) that is intensified during strong wind events that occur in autumn and winter (Gutiérrez de Velasco & Winant, 1996). Once offshore transport occurs, the limited presence and relatively low density of these larvae in the central GoM could also be a result of their quicker development (16 to 40 d; De Vries et al., 1990; Houde and Richard, 1969; Leis et al., 2006), in comparison with mesopelagic larvae, or cumulative mortality if the environmental conditions are unfavorable for their growth and survival (Houde & Richard, 1969). Whether or not these larvae are recruited to favorable nursery habitats is unknown.

Our results clearly show that *C. pauciradiatus* is distributed throughout the oceanic waters of the southern gulf. Houde et al. (1979) and Felder and Camp (2006) limited the distribution of *C. pauciradiatus* larvae to the north-eastern and north-western GoM, this was likely due to limited surveys in the sGoM. We found significantly higher larval density between April and July. This is consistent with Lamkin's (1998) report of spawning in April in the oceanic waters of the northern GoM. The spawning of *B. atlanticus* occurs throughout the year in the Atlantic Ocean and GoM, off the central coast of Brazil (Namiki et al., 2007) and in the Straits of Florida (Clancey, 1956). Zavala-García and Flores-Coto (1994) analyzed the species' density based on eight cruises, and observed the highest average density (average of 6 larvae 1000 m⁻³) in August, compared with 2 larvae 1000 m⁻³ in November to December and 1.4 larvae 1000 m⁻³ between March and May. We also found significantly higher densities during season II, which included August (5.8 larvae 1000 m⁻³).

Our results and those of Zavala-García and Flores-Coto (1994) suggest a spawning peak between August and September. This spawning period overlaps with the transport of high-nutrient river plumes offshore observed in the sGoM from July to September (Martínez-López & Zavala-Hidalgo, 2009), which drive higher productivity and hence food availability for the larvae, likely contributing to their survival.

The lack of significant differences in the seasonal density of the lanternfishes (*B. suborbitale* and *N. valdiviae*) is consistent with the year-around spawning of the adults (Bard et al., 2002; Catul et al., 2011; Gartner, 1993). For the northern oceanic GoM, Milligan and Sutton (2020) found that larvae of *B. suborbitale* and *N. valdiviae* had limited variations in density between early summer (April-June) and late summer (July-September). Rodríguez-Varela et al. (2001) after conducting three cruises between May and July in the Mexican EEZ, also reported that *B. suborbitale* was homogeneously distributed in the inner GoM, and *N. valdiviae* had higher densities in the BoC, coinciding with the distribution found in our results. Additionally, the broader distribution of larvae from mesopelagic species (Parada et al., 2003; Sundby, 1991) could be due to the widespread occurrence and high abundance of adults in mesopelagic waters, where environmental conditions are more homogenous (Pérez-Brunius et al., 2017) compared to surface waters (H. Furey et al., 2018; Pérez-Brunius et al., 2013).

In addition, adults reproduce and spawn at around 800 m (Marshall, 1979; Sundby & Kristiansen, 2015) and there is passive horizontal transport during the ascent of eggs and larvae toward the surface and the larval stage is relatively long (Gartner, 1993; Landaeta et al., 2015), which might increase the larvae's distribution.

2.4.2 Relationship with oceanographic variables

When relating the density of *C. crysos* with the oceanographic variables in the GAMs, very low correlation power was obtained. As we hypothesized, neritic larvae that are transported offshore did not show a correlation with environmental variables. The presence of *C. crysos* in the deep-water region away from suitable habitat for the larvae will likely lead to the loss of those individuals. However, further research is needed.

The relationship between the oceanographic variables and larval density observed in the response plots from the GAMs for *Auxis* spp., *B. atlanticus*, *C. pauciradiatus*, *B. suborbitale* and *N. valdiviae* were very similar (e.g., higher density at high SSTs or high surface chl a concentrations). Surface chl a concentration, WS and SST (in order of their explanatory power in most models), showed to have an impact on habitat suitability, which is often interlinked (Owen, 1989; J. J. Simpson & Dickey, 1981) with the survival of the early life stages of fish (see Fuiman and Werner, 2002; Houde and Zastrow, 1993).

Surface chl a concentration is usually used as a proxy for phytoplankton biomass and an indicator of food availability (Hamilton et al., 2016; Pasqueron De Fommervault et al., 2017), and higher chl a concentrations are commonly found at higher WS (McGillicuddy et al., 2008), lower stratification (Moyano & Hernández-León, 2009) and lower SSTs (Belkin et al., 2009). Despite the significantly positive correlation between chl a and the density observed for *Auxis* spp. (season I and II), *B. atlanticus* and *C. pauciradiatus* (season I) and *B. suborbitale* (season II), most of the observations of larval presence were found at low concentrations (0.05 and 0.12 mg m⁻³), typical of the deep-water region. Nevertheless, the positive relationship may indicate a higher prey availability for the larvae, which could lead to faster growth and survival and higher density (Houde & Zastrow, 1993). In the GoM, higher chl a concentrations may be associated with fronts generated by the interaction between cyclonic and LC-AEs and AC eddies in the central GoM (Biggs, 1992; Martínez-López & Zavala-Hidalgo, 2009; Jorge Zavala-Hidalgo et al., 2006), as well the semi-permanent cyclonic eddy that is characteristic of the BoC (Pérez-Brunius et al., 2013), or due to wind-driven seasonal upwelling in the western and southern shelves of the GoM (Jorge Zavala-Hidalgo et al., 2006) and in the western YS (Ruiz-Castillo et al., 2016).

The overall shape of the additive effect response plots of WS and density exhibited greater variation among models compared with other variables. In season I, the relationship between density and WS varied between species, and greater variability in density was observed at higher WS values (> 7 m s⁻¹), while in season II, WS did not exceed 6 m s⁻¹ and the relationship with larval density was generally positive.

According to Mackenzie and Kiørboe (2000) and Kloppmann *et al.* (2002), high WS drives mixing in the surface layer and increases turbulence (Owen, 1989; J. J. Simpson & Dickey, 1981), favoring primary production, supporting an increase in zooplankton biomass and increasing the encounter rate between the larvae and their prey. However, WS that are too high will decrease the feeding success of larvae, as the prey capture success decreases (Hillgruber & Kloppmann, 2000; Peterman & Bradford, 1987). Our results showed that most of the larval observations during both seasons were found at intermediate WS (Season I: $4.62 \pm 1.64 \text{ m s}^{-1}$; Season II: $4.01 \pm 1.45 \text{ m s}^{-1}$). These results are consistent with Lasker's (1981) "stable ocean" hypothesis, in which he proposed that strong winds can negatively influence larval feeding success.

The spatial variation in SSTs in the GoM's deep-water region is small (Muller-Karger et al., 2015) compared to what is observed over the continental shelf (Ruiz-Castillo et al., 2016; J. Zavala-Hidalgo et al., 2003). In this study, a positive relationship between SST and larval density was found in every species. Most of the observations and higher densities in season I were between 28 and 30 °C (63%), and 29.5 to 31 °C for season II (90%), with few observations in either colder or warmer waters. According to Fuiman and Werner (2002), fish growth rates are typically highest at intermediate temperatures within their environmental tolerance scope, which may be reflected in higher densities due to lower cumulative mortality. However, temperature-dependent growth rates of our target species are lacking, and SSTs do not reflect the vertical thermal structure of the water column, therefore future studies should examine the relationship between larval growth rates and in situ temperature.

Our results indicated that the distribution of larvae and higher densities were largely restricted to stations with low stratification values; 63% of the observations were between 1100 and 1700 J. Studies such as Franco-Gordo *et al.* (2002) for the central Pacific coast of Mexico or Moyano and Hernández-León (2009) along the Gran Canaria Island shelf have reported that stratification, which is driven primarily by SST and WS (see Seo et al., 2019; Vallis, 2000; Yamaguchi and Suga, 2019), can define the distribution of larvae close to the continental slope. Lower stratification is usually related to greater WS and mixing in the surface layer, which can provide nutrients to the euphotic zone (Hidalgo-González & Álvarez-Borrego, 2008; Yamaguchi et al., 2019) yielding greater food availability, hence higher larval survival and recruitment (Fuiman & Werner, 2002).

The remaining variables considered in this study (depth, SSH and salinity) were retained in only one model and had a low influence in the final explained deviance. For example, the limited relationship between bottom depth and *C. pauciradiatus'* density in season I is reasonable for a mesopelagic species were found basin-wide, which coincides with the wide adult distribution (Felder & Camp, 2006; Lamkin, 1995). Likewise, the small correlation between SSH and *C. pauciradiatus*' density in season I and *N. valdiviae*'s in season II, reflect the oceanic habitat that adults of these species occupy and in which they spawn (Catul et al., 2011; Felder & Camp, 2006; Lamkin, 1998). Additionally, the highest abundances were found at intermediate SSH values for mesopelagic species, such as *C. pauciradiatus* suggesting that adults can be found and spawn at frontal environments (e.g., in regions of interaction between AC and CE), where an increased concentration of prey can be found (Lamkin, 1995). Mean salinity was only significantly related to *B. suborbitale* in season I, with a steep decrease in density at salinities higher than 36.55 psu. These salinities are toward the highest values reported for surface waters of the GoM (Cervantes-Díaz et al., 2022; Portela et al., 2018), and according to Fuiman and Werner (2002) salinity influences the development of fish larvae, although to a lesser extent than temperature.

2.5 Conclusions

In this study, we highlight the importance of the contrasting early life stages of fish and their relationship with oceanographic variables for a better understanding of the distribution and density patterns of larvae in the southern GoM's deep-water region. The GAMs allowed us to examine how the same oceanographic conditions related differently to the density of larvae. In addition, analyzing each species model provided further insight into the suitable habitat conditions of larvae in species with contrasting life histories.

Pooling several cruises into a pre-defined season might conceal the relationship between specific oceanographic phenomena and species-specific larval fish density. However, it provides (1) a more integrative description of larval distribution and variations in density between seasons, and (2) a more robust examination of how the densities of different species relate to a uniform set of oceanographic variables. Further studies might consider encompassing both the continental shelf and the deep-water region to describe the distribution gradients in species that occupy the whole basin, and exploring the consequences of finding the larvae of neritic species in the deep-water region. Our results will provide a useful baseline for future studies that delimit the potential habitat distribution under the same oceanographic conditions and for evaluating the impact of climate change on pelagic ecosystems.

Chapter 3. Relationship between oceanographic variables and ichthyoplankton of two commercially important species (*Auxis* spp., Scombridae; *Caranx crysos*, Carangidae) on the Yucatan Peninsula's continental shelf.

3.1 Introduction

The survival and recruitment of larvae is critical for sustaining neritic species' populations through time (Govoni, 2005; Kingsford, 1993; Rothschild, 1986). The distribution and density of marine fish larvae are highly influenced by hydrodynamic conditions as well as environmental factors (Legendre & Demers, 1984). Although the initial spatial and temporal distribution of the early life stages of marine fishes is defined by spawning region and seasonality (Marancik *et al.*, 2005), larval distribution and density are also influenced by temperature and salinity variations (Fuiman & Werner, 2002), fronts and currents (Compaire et al., 2021), as well as food availability and the presence of predators (Olivar et al., 2010).

Continental shelves are recognized for their economic importance due to their role in fisheries production and oil extraction, and are therefore subject to intense exploitation (Adams et al., 2004; Falfan et al., 2007; Ruiz-Fernández et al., 2019). They also serve as important spawning and nursery grounds for many fisheries species (Cornic et al., 2018; Dance & Rooker, 2019). The Yucatan Peninsula, located in southeastern Mexico, has a broad continental shelf with a maximum extension into the Gulf of Mexico (GoM) of approximately 250 km to the north. However, the eastern Yucatan Shelf (YS) is narrower, with an abrupt bathymetric drop into the Yucatan Channel through which the Yucatan Current flows. The interaction between the rapid Yucatan Current and the slope causes upwelling which is advected from approximately 250 m to the shelf, and the water mass is characterized by lower temperatures (16.8 to 22.58 °C) and salinities (36.1 to 36.6 psu) than the surface (Jouanno et al., 2018; Merino, 1997). The strong upwelling intensifies during spring and summer near Cabo Catoche (eastern YS), as well as along the continental slope, providing nutrients to the YS that supports higher productivity (Merino, 1997; Reyes-Mendoza et al., 2016; Medina-Gómez, 2020). This greater productivity sustains higher zooplankton biomass that can provide higher food availability for fish larvae (Stoecker & Capuzzo, 1990). According to Zavala-Hidalgo et al. (2006) the upwelled water can be found near the surface along the peninsula's coast due to the easterly winds that drive westward circulation over the shelf throughout the year (see also Jouanno et al., 2018; Ruiz-Castillo et al., 2016). However, during autumn and winter, the prevailing easterly winds can be interrupted by strong winds from the north, which are associated with cold fronts that decrease water temperature (Medina-Gómez et al., 2020; Reyes-Mendoza et al., 2016). These winds, known locally as "nortes" (Gutiérrez de Velasco & Winant, 1996), diminish the stratification over the YS (Merino, 1997) and increase chlorophyll a (chl a) concentrations in the middle and outer shelf, while lower concentrations are found near the coast (Zavala-Hidalgo et al., 2006; Medina-Gómez et al., 2020). Surface warming and higher stratification is observed from spring through autumn throughout the YS (Medina-Gómez et al., 2020), with higher chl a concentrations near the coast in summer (Zavala-Hidalgo et al., 2006; Medina-Gómez et al., 2020). Spring (March to May) is considered the dry season, and during the rainy season that extends from early summer until autumn (June to October), below-ground freshwater discharge along the coast due to the peninsula's karstic system (Merino-Ibarra et al., 1990; Null et al., 2014). This decreases salinity and provides nutrient inputs that stimulates phytoplankton biomass (Aranda-Cirerol et al., 2006). Hence, the seasonal variations in oceanographic conditions may influence the distribution of adults spawning habitat, as well as larval distribution and survival (Fuiman & Werner, 2002; Houde, 1997).

Marine fish larvae of neritic species are mainly planktonic (Cushing, 1969). The larvae of *Auxis* spp. (*A. thazard thazard* and *A. rochei rochei*, frigate and bullet tunas respectively; Scombridae) are found globally (Mediterranean Sea, and Atlantic, Indian and Pacific Oceans) in pelagic and neritic habitats (Froese & Pauly, 2021). *Caranx crysos* (Blue runner; Carangidae) is found in subtropical western and eastern Atlantic Ocean (Froese & Pauly, 2021). *Caranx crysos* (Blue runner; Carangidae) is found in subtropical western and eastern Atlantic Ocean (Froese & Pauly, 2021). Additionally, these species are found throughout the GoM's continental shelves (Felder & Camp, 2006; Richards, 2006). Both scombrids and blue runners are captured by sport and commercial fishermen for bait, food and sport (Catanese et al., 2008; Falfan et al., 2007; Goodwin IV & Funicane, 1985; Yáñez-Arancibia et al., 1985), and they are prey for commercially important species such as blue marlin (*Makaira nigricans*), dolphinfish (*Coryphaena hippurus*), yellowfin tuna (*Thunnus albacares*) and wahoo (*Acanthocybium solandri*; Franks et al., 2007; Rudershausen et al., 2010).

Most studies on fish larvae from the shelves of the Yucatan Peninsula have focused on the Mesoamerican Barrier Reef System (MBRS) in the Caribbean (e.g., Álvarez-Cadena et al., 2007; Carrillo et al., 2017; Muhling et al., 2013). Additionally, studies such as Álvarez-Cadena et al. (2007) and Muhling et al. (2013) focus on larval fish assemblages. However, studies that encompass the extensive northern YS, and the relationship between species with and the environmental conditions are much more limited.

Previous studies indicate that the distribution and density of *Auxis spp.* and *C. crysos* is located east and west off Cabo Catoche respectively, and their spawning period is mainly limited to spring and summer in the YS (Falfan et al., 2007; Ordóñez-López et al., 1991). This contrasts with other GoM's shelves where larvae distribution extends to the whole western Florida Shelf throughout the year for *Auxis* spp. and *C. crysos* in the southern half of the west Florida shelf in summer (Houde et al., 1979; Leak, 1981) or in the entire Bay of Campeche (BoC) during summer for *Auxis* spp. and during spring and summer in the southwestern shelf of the BoC for *C. crysos* (Espinosa-Fuentes & Flores-Coto, 2004; Laura Sanvicente-Añorve et al., 2000).

The aim of this study was to describe the frequency of occurrence and density of the larvae of *Auxis* spp. and *C. crysos* relative to *in situ* and satellite-based oceanographic parameters over the YS based on three cruises held in summer and fall (2015 to 2018). We hypothesized that *Auxis* spp. and *C. crysos* would be distributed along the continental shelf, with lower *Auxis* spp. and higher *C. crysos* densities at stations closer to the shore (and vice versa), and higher densities in areas with colder water and higher surface chl a concentration that are indicative of higher food availability, such as the upwelling region of Cabo Catoche. Based on their summer spawning (Falfan et al., 2007; Houde et al., 1979; Leak, 1981; Ordóñez-López et al., 1991), we expected higher larval densities in summer compared to autumn. This study provides a baseline for future comparisons of the species' distributions to evaluate habitat changes due to intense disturbances such as overfishing, climate change, oil spills or invasive species, which can affect survival and recruitment during the early life stages of fish.

3.2 Materials and methods

3.2.1 Sampling design

Samples were collected during three oceanographic cruises (Figure 8) covering the YS (20 to 24 °N, 86 to 95 °W), GOMEX-04 (2-20 November 2015, 55 stations), GOMEX-05 (23 September to 10 October 2016, 59 stations) and GOMEX-06 (7-18 July 2018, 78 stations). Although the fixed station grid included a few stations on the slope, only those with depths less than or equal to 200 m were selected for the analyses. Ichthyoplankton samples were collected near the surface (0-10 m) with bongo net tows. Filtration volumes were obtained with General Oceanic Model 2030 flowmeters placed at the mouth of each net. Each sample was fixed immediately in 96 % ethanol.



Figure 8. Ichthyoplankton sampling stations covered during three cruises held between 2015-2018. GOMEX-04 (November 2-20 2015), GOMEX-05 (September 23 to October 10 2016) and GOMEX-06 (July 7-18 2018). All stations \leq 200 m. To allow for visualization of multiple samples from a given station, each fixed station is represented as a grid. Dotted, dashed and continuous lines represent the 40 m, 200 m and 1000 m isobaths, respectively.

3.2.2 Species selection

In the laboratory, ichthyoplankton was sorted and identified to the lowest possible taxonomic level based on morphometric and meristic characteristics (Fahay, 2007; Richards, 2006). Larval densities were standardized to larvae per 1000 m⁻³. *Auxis* spp. includes *A. rochei rochei* and *A. thazard thazard* larvae because the two species cannot be distinguished morphologically during the earlier stages and molecular identification is necessary (Catanese *et al.*, 2008; Ochoa-Muñoz *et al.*, 2018).

Since *A. rochei rochei* and *A. thazard thazard* share very similar distribution, habitat, depth ranges and spawning period in the GoM (Collette & Nauen, 1983; Froese & Pauly, 2021; Richards, 2006), we consider the distribution of both species as broadly representative of each one.

3.2.3 Oceanographic conditions and Generalized Additive Models

To examine the adjustment of the relationship between the species' standardized density and oceanographic conditions, generalized additive models (GAMs) were used. Hydrographic parameters were characterized by *in situ* measurements and remote sensing. *In situ* variables (temperature and salinity) were measured at each station with a Seabird 25 Plus CTD. Mean water column temperature and salinity from near the surface to about a depth of 10 m were calculated since they reflect the environmental conditions over which tows were performed and the vertical distribution of the larvae is unknown. Mean water temperature is a key parameter linked to the development and growth of fish larvae (Hermann et al., 2001; Walsh, 1987), and mean salinity can be used to track groundwater inflow (Ditty et al., 2004; Flores-Coto et al., 2014). Nitracline depth, as indicated by a density of 25.3 mg m⁻³ as a proxy (Pasqueron De Fommervault et al., 2017) and the depth of the 22.5 °C isotherm (Medina-Gómez et al., 2020) were used as upwelling indicators. Stratification (J m⁻³; Simpson et al., 1981) was used as an *in situ* indicator of vertical mixing; values close to zero indicates a well-mixed layer and higher values indicate increasing stratification (Dubranna et al., 2011; Hidalgo-González & Álvarez-Borrego, 2008).

Sea surface temperature (SST; product id 010_005, 0.25° x 0.25° spatial resolution, gap-free gridded data after validation process) was also used as an upwelling indicator. Sea surface chl a concentration (product id 009_082, ~ 0.04° x 0.04° spatial resolution, gap-free gridded data after validation process) was selected as proxy for phytoplankton biomass and food availability for the larvae (Hamilton et al., 2016; Sánchez-Velasco and Flores-Coto, 1994) Surface wind speed (WS; product id 012_004, 0.25° x 0.25° spatial resolution, gap-free gridded data after validation process), which is related to turbulence, has been associated with larvae feeding success (Kloppmann et al., 2002; Mackenzie & Kiørboe, 2000). All satellite-based variables were obtained from the E.U. Copernicus Marine Service Information (CMEMS; CMEMS, 2020) (http://marine.copernicus.eu/). Data of SST and chl a correspond to the sampling date for each station. WS was calculated from wind surface speed vectors (u, v), and the data were averaged over the 4 d prior to the sampling date since wind events in the GoM (e.g., "nortes" and southerly winds) usually occur over a time scale of 3 to 7 d.

Bathymetry from ETOPO1 1 Arc-Minute Global Relief Model (Amante & Eakins, 2009) longitude and latitude were included to represent station depth and location, and cruise was included as a categorical variable to test for spawning seasonality. After removing outliers when necessary (using Cleveland dotplots; Zuur et al., 2010), variables that presented low correlations (Spearman ρ , r < 0.70) and collinearity (variance inflation factor; VIF) < 3 (Zuur et al., 2010) were selected in the GAMs. To assess if

significant differences were found in the variables among cruises, non-parametric Kruskal-Wallis and pairwise Wilcox tests with the Holm method of adjustment were performed ($\alpha = 0.05$).

GAMs are a nonparametric and nonlinear regression technique that does not require *a priori* specifications of the functional relationship between the response and predictor variables (Hastie & Tibshirani, 1986; S. N. Wood, 2006). A general form of the GAM equation (2) is:

$$E[y] = g^{-1}\left(\beta_0 + \sum_k S_k(x_k)\right)$$
⁽²⁾

Where E[y] equals the expected values of the response variable (standardized density of each species), g represents the link function, β_0 equals the intercept, x represents each of k explanatory variables, and S_k represents the smoothing function for each of the explanatory variables.

Only larvae densities from GOMEX-05 (23 September to 10 October 2016) and GOMEX-06 (7-18 July 2018) were included in the GAMs since *Auxis* spp. was not caught in GOMEX-04 and there were very few *C. crysos* larvae (Figure 9). A logarithmic link function with smoothing splines (which are associated with the degrees of freedom; Wood, 2006) was used to build the GAMs. Due to the presence of a high proportion of zero densities and non-negative values of the response variables (i.e. standardized densities) a Tweedie distribution (part of the exponential dispersion model family) was used (Arcuti et al., 2013; Dunn & Smyth, 2005). The model's power, which indicates the data's distribution (power value close to 1 = gamma-like; power value close to 2 = Poisson-like) is reported. To avoid overfitting, variables were limited to a maximum 4 *k* parameters (in exception to latitude and longitude).

For identification of non-significant (p > 0.05) variables, a stepwise backward manual procedure was used (e.g., Randall et al., 2015; Rooker et al., 2012). If the deviance explained in the final model was lower than 10% (DE < 0.1) the model was discarded. To evaluate the relative importance of each variable, models were run with and without each variable (Rooker et al., 2012; Torrejón-Magallanes et al., 2019); the change in deviance explained and Akaike Information Criteria was used to determine the variables' power within the model. The degrees of freedom were examined to determine whether the relationship between the environmental variables and the species' density was linear (df = 1) or non-linear (df > 1). The R–project 3.4.1 (R Core Team, 2021) statistical program was used for all analyses using the gam function from the "mgcv" package and the gam.check function for validation (Simon N. Wood, 2018).

3.3 Results

3.3.1 Standardized density and distribution

Auxis spp. presented higher density than *C. crysos* during GOMEX-05 and -06, but no captures in GOMEX-04 (Table 6). For both *Auxis* spp. and *C. crysos*, the density during GOMEX-06 (July 2018) was an order of magnitude greater than GOMEX-05 (September-October 2016). While *Auxis* spp. presented significant differences among the three cruises (Pairwise Wilcox Test, p < = 0.05), no significant difference between GOMEX-05 and GOMEX-06 was observed for *C. crysos*. Both species were more abundant at stations beyond the 40 m isobath, and their density in GOMEX-05 was more evenly distributed throughout the shelf, while in GOMEX-06, there were higher densities in the northern shelf and lower densities in the southwest (Figure 9). Higher densities of *Auxis* spp. were observed in the central YS and stations near the eastern YS slope. While for *C. crysos*, higher densities were present in the central YS (between -90 and -88 °W), and lower densities were in the southeastern YS.



Figure 9. Spatial distribution of standardized density (larvae 1000 m⁻³) of *Auxis* spp. and *C. crysos*. GOMEX-04 (November 2-20 2015), GOMEX-05 (September 23 to October 10 2016) and GOMEX-06 (July 7-18 2018). All stations \leq 200 m. Dotted, dashed and continuous lines represent the 40 m, 200 m and 1000 m isobaths, respectively.

Table 6. Mean standardized densities \pm SD (larvae 1000 m⁻³) and frequency of occurrence (%; in parenthesis) of *Auxis* spp. and *Caranx crysos* during GOMEX cruises (2015 to 2018) covering the Yucatan Shelf. Post-hoc comparisons using a Pairwise Wilcox Test with Holm's method of adjustment are reported. Letters show significant differences in density at the alpha = 0.05 level.

	GOMEX-04	GOMEX-05	GOMEX-06	
<i>Auxis</i> spp. (p < 0.001)	0 ª (0)	4.7 ± 10.5 ª (45.8)	70.7 ± 146.2 ª (61.7)	
Caranx crysos (p = 0.003)	0.2 ± 0.5 ^{ab} (8.9)	0.8 ± 1.7 ª (30.5)	3.4 ± 7.2 ^b (35.8)	

3.3.2 Relationship with oceanographic variables

All of the oceanographic variables presented significant differences (Pairwise Wilcox Test, p < = 0.05) among cruises (Table 7). However, only chl a, WS and the depth of the 22.5 °C isotherm showed significant differences (p < 0.001) among the three cruises, being chl a and WS the highest values in GOMEX-04 (November 2015). The 22.5 °C isotherm was found in three stations at depths between 100 and 120 m deep in the northern YS, indicating that there was almost no upwelling in GOMEX-04.

For GOMEX-05 (September-October 2016) a shallower isotherm was observed (10 to 70 m) in stations close to the continental slope in the east and the north and in Cabo Catoche. During GOMEX-06 (July 2018), the presence of the 22.5 °C isotherm depth ranged between 10 m in shallower waters and 150 m near the slope, covering the eastern shelf, north off Cabo Catoche and the whole YS slope, plus some stations in front of the western Yucatan Peninsula.

The greatest concentrations of chl a (> 1.5 mg m⁻³) were found near shore (< 40 m depth) in all cruises, followed by stations near Cabo Catoche (0.4 to 0.8 mg m⁻³; Figure 10). WS values showed limited variability throughout the YS during GOMEX-06 (4 to 5 m s⁻¹), while in GOMEX-04 the greatest WS (> 7 m s⁻¹) was found in the western YS and Cabo Catoche. Salinity values lower than 24 were found in GOMEX-05 mainly close to shore (Figure 11), with the lowest values (8 and 13) at two stations between the 40 and 200 m. The temperature range was similar throughout the YS during GOMEX-04 (26 to 29 °C), while in GOMEX-05 and -06 the near-surface waters were colder (24 to 25 °C) closer to shore and warmer (> 29 °C) beyond the 40 m isobath.



Figure 10. Surface chl a concentration (row 1), depth of the 22.5 °C isotherm (row 2) and wind speed (row 3). GOMEX-04 (November 2-20 2015), GOMEX-05 (September 23 to October 10 2016) and GOMEX-06 (July 7-18 2018). All stations \leq 200 m. Dotted, dashed and continuous lines represent the 40 m, 200 m and 1000 m isobaths, respectively.



Figure 11. Mean salinity 0-10 m (row 1), sea surface temperature (row 2) and mean temperature 0-10 m (row 3). GOMEX-04 (November 2-20 2015), GOMEX-05 (September 23 to October 10 2016) and GOMEX-06 (July 7-18 2018). All stations \leq 200 m. Dotted, dashed and continuous lines represent the 40 m, 200 m and 1000 m isobaths, respectively.

	GOMEX-04	GOMEX-05	GOMEX-06
Stratification (J m ⁻³) *	120.7 ± 243.3 ^{ab}	2929.1 ± 4520.9 ª	371.7 ± 349.2 ^b
Mean temperature 0-10 m (°C) *	27.9 ± 0.8 °	29.1 ± 1.5 ^{ab}	27.9 ± 1.5 ^b
Mean salinity 0-10 m (psu) *	36.5 ± 0.4 ^{ab}	34. ± 5.5 ª	35.4 ± 1.5 ^b
Sea surface temperature (°C) *	28.1 ± 0.5 ª	29.7 ± 0.6 ^{ab}	28.2 ± 0.7 ^b
Chl (mg m ⁻³) *	0.6 ± 0.6 ª	0.25 ± 0.27 ª	0.4 ± 0.4 a
Wind speed (m s ⁻¹) *	5.5 ± 1.2 ª	2.7 ± 0.9 ª	4.4 ± 0.5 ^a

Table 7. Mean ± SD values of oceanographic variables for the three GOMEX cruises (2015 to 2018) over the YucatanShelf. Post-hoc comparisons using Pairwise Wilcox test with the Holm method of adjustment are reported. Lettersshow significant mean differences at the alpha = 0.05 level (* significant differences p < 0.001).

The GAM model for *Auxis* spp. had a higher explained deviance (DE = 70.6 %) than that for *C. crysos* (DE = 58.9%). Station location (longitude and latitude) and cruise were the only variables that were kept in both models (Table 8). While the *Auxis* spp. model included mean salinity and WS, for the *C. crysos* model there was no relationship between density and the environmental variables.

Table 8. Final GAM model for each target species. The power (p) indicates the model distribution (p close to 1 = gamma-like; p close to 2 = Poisson-like). The deviance explained (DE) and the Akaike Information Criteria (AIC) are reported with and without each variable.

Auxis spp.	DE =	AIC =	Caranx crysos	DE =	AIC =
(p = 1.5)	70.6%	829.9	(p = 1.3)	58.9%	377.9
Stratification (J m ⁻³)			Stratification (J m ⁻³)		
Mean salinity 0-10 m	69.0	833.6	Mean salinity 0-10 m		
Mean temperature			Mean temperature		
0-10 m (°C)			0-10 m (°C)		
SST (°C)			SST (°C)		
Chl a (mg m ⁻³)			Chl a (mg m ⁻³)		
Wind speed (m s ⁻¹)	69.7	831.8	Wind speed (m s ⁻¹)		
Depth of the 22.5 °C			Depth of the 22.5 °C		
isotherm (°C)			isotherm (°C)		
Lat + Lon	33.1	886.9	Lat + Lon	11.1	411.4
Cruise	59.0	857.1	Cruise	46.2	399.4

For the *Auxis* spp. GAM model, the density was correlated with station position (Lat + Lon), seasonality (cruise), mean salinity 0-10 m and WS (listed in order of higher to lower explained deviance). The relationship between density and station location's additive effect indicated that the highest densities of *Auxis* spp. were found in the northeastern region of the YS, and the lowest abundances were found in stations sampled closer to the shore and near the Yucatan Channel (Figure 12). Higher densities of *Auxis* spp.'s larvae were found at a station with a salinity of 13 (93 m depth), while at two other stations with low salinities (8 and 16) located at 39 and 19 m respectively, no larvae were found. The highest densities were found between salinities of 35 and 37 in both cruises. Higher densities of *Auxis* spp.'s at relatively low WS (1.5 to 2.5 m s⁻¹) were observed during GOMEX-05, and at high WS (> 4 m s⁻¹) for GOMEX-06. Overall, WS was very similar in all the study area during GOMEX-06, while in GOMEX-05 the greater speeds were observed in the eastern slope of the YS, and were the greatest near Cabo Catoche and the Yucatan Channel.

Despite the non-significant correlation between *Auxis* spp. and *C. crysos* densities and SST and mean temperature 0-10 m, both species greatest densities were between 29.5 and 30.5 °C in GOMEX-05 (September-October 2016) and from 28 to 29 °C for GOMEX-06 (July 2018). Scatterplots of the species densities and their relationship with the oceanographic variables are presented in Figure 22.



Auxis spp. (power = 1.5) DE = 70.6% AIC = 829.9





Figure 12. Response plots of the oceanographic variables' additive effect on the density of *Auxis* spp. and *C. crysos.* Smoothed values are represented by a continuous line, and the shaded color indicates 95% confidence intervals. Non-significant additive effects (p > 0.05) for a given season are not presented.

3.4 Discussion

Auxis spp. and *C. crysos* are considered cosmopolitan species in neritic waters of the GoM (Felder & Camp, 2006) and Atlantic Ocean (Froese & Pauly, 2021; Richards, 2006). The highest densities of *Auxis* spp. larvae were found in the northern YS beyond the 40 m isobath during the July cruise. Despite the temporal gap between samplings, this was similar to that found by Houde *et al.* (1979) for the western Florida shelf based on the analysis of 17 cruises (1971-1974). They found significantly higher densities in the summer cruises (July and August) compared to those in autumn (October and November). Hence, our results are consistent with the summer spawning period previously reported (see also, Cornic et al., 2018; Habtes et al., 2014; Uchida, 1981). In addition, Houde *et al.* (1979), found that most larvae were in waters beyond the 50 m isobath, which resembles to our results. Sanvicente-Añorve *et al.* (2000) also found that *Auxis* spp. larvae were found beyond the 36 m isobath in BoC's continental shelf, and with higher densities in May and August, compared to lower densities reported for November and February by Espinosa-Fuentes and Flores-Coto (2004). Therefore, this spatial and temporal distribution of *Auxis* spp. larvae over the YS, which also resembles other studies outside the GoM such as Sabatés and Recasens (2001) in the northwestern Mediterranean Sea or Klawe (1963) in the Pacific Ocean suggest that adult spawning in intermediate and outer shelf waters during summer.

The spatial distribution of *C. crysos'* larvae, in which there were higher densities in July than in the September-October cruise and at stations with depths > 40 m resembles Ordóñez-López *et al.* (1991) study in the YS that described the highest abundances of *C. crysos* in May and very few in November. Additionally, these spawning periods and distribution coincide with Ditty *et al.* (2004) study in the central and western northern GoM's shelf (mainly 50 to 200 m) and Leak's (1981) study in the north-western Florida shelf (beyond 50 m), or Flores-Coto (2004) in the BoC's continental shelf with the higher densities in May and August cruises compared to November and February. This suggests that *C. crysos'* spawning period is year around, although with higher densities in summer months with a spawning peak in July. These results and those cited in the literature indicate that despite *Auxis* spp. and *C. crysos* are cosmopolitan in the GoM, these species are not equally distributed in all neritic waters of the GoM.

When relating the species' densities with the oceanographic variables, *Auxis* spp. was correlated with salinity and WS. The salinity range (25 to 36) at which *Auxis* spp. larvae were caught in this results matches those in the western Florida shelf by Houde (1979). Additionally, in our study the highest densities in both cruises were found around salinity values of 35, which resembles Reglero et al. (2012) in the western Mediterranean Sea, who found the highest densities near the salinity value of 36. The absence of larvae

at stations with low salinity values, such as those near submerged freshwater inflow near the coastal YS might relate with that *Auxis* spp. spawning is where salinity is more homogenous (Alvarez-Berastegui et al., 2014). Therefore, the presence of a few *Auxis* spp. larvae at stations with low salinities might be due to a shelf westward circulation from spawning areas with more homogenous salinity driven by the easterly winds (see Jouanno et al., 2018; Ruiz-Castillo et al., 2016). Additionally, according to Fuiman and Werner (2002), overall low salinity can negatively impacts egg development providing smaller and less developed fish larvae, which may induce mortality.

The low but significant correlation between WS and *Auxis* spp. density could be attributed to the limited WS variability between cruises. However, there was a higher average WS $(4.4 \pm 0.5 \text{ m s}^{-1})$ and density (70.7 \pm 146.2 larvae 1000 m⁻³) during the July cruise compared with the September-October cruise (WS: 2.7 \pm 0.9 m s⁻¹; density: 4.7 \pm 10.5 larvae 1000 m⁻³). This may indicate that higher WS provides a greater mixing in the surface, which increases turbulence favoring primary production (McGillicuddy et al., 2008; Walker et al., 2005) and zooplankton density (Stoecker & Capuzzo, 1990) and decreases stratification (Ruiz-Castillo et al., 2016). Additionally, an increase in the encounter rate between prey and larvae is observed at WS between 2 to 6 m s⁻¹ (Daskalov, 1999; Kloppmann et al., 2002; Sundby et al., 1994). These results also relate with finding the higher densities in areas with lower stratification.

Over the YS, the highest densities of *Auxis* spp. larvae were found between 28 and 29 °C in both cruises. Pruzinsky et al. (2020) indicated that *A. thazard* spawns at SSTs from 21.6 to 30.5 °C in the oceanic GoM. Additionally, Cornic et al. (2018) found high larvae density of scombrids in areas with warmer waters (around 29 °C) for the northern GoM, and noted their distribution was influenced by warm core eddies with greater SSTs. Temperatures ranging from 28 to 29°C are key for successful hatching and larval development of some scombrids (*T. albacares, T. obesus* and *T. atlanticus*; Reglero et al., 2014; Wexler et al., 2011). Additionally, studies of *A. thazard* in the Southeastern Brazilian Coast (Vieira et al., 2022) and *A. rochei* in the Balearic Sea (Laiz-Carrión et al., 2013) reported that larvae presented significantly greater sizes in warmer waters, which may increase survival rates (Fuiman & Werner, 2002).

The correlation between salinity and temperature and *C. crysos* density resembled the results provided by Houde et al. (1979) and Leak (1981) in the western Florida Shelf. *C. crysos* larvae were found at salinities between 31 and 36, and SSTs between 29 and 30 °C, similar to what the higher densities were found in the July and September-October cruises. These salinity ranges also coincide with observations of *C. crysos* larvae and juveniles found by Mohan et al. (2017) in the northern GoM, which might indicate the species' tolerance to these variables during this stage in the GoM. Additionally, the fact that the higher densities in both cruises were observed in areas with a shallower 22.5 °C isotherm (10 to 20 m), lower stratification (200 to 700 J m⁻³) and higher WS (4 to 5.5 ms⁻¹) may indicate that *C. crysos* larvae are distributed in upwelling areas, such as the northern and eastern YS and near Cabo Catoche (Medina-Gómez et al., 2020), areas of higher nutrient availability and zooplankton biomass (Merino, 1997; Stoecker & Capuzzo, 1990), which may increase larvae survival (Govoni, 2005).

3.5 Conclusions

The results obtained in this study in addition to literature from the GoM (e.g., Espinosa-Fuentes and Flores-Coto, 2004; Houde et al., 1979; Leak, 1981; Sanvicente-Añorve et al., 2000) provide insight about the spawning period and the larval distribution of the two commercially important and cosmopolitan species *Auxis* spp. and *C. crysos*. Suggesting a spawning period during the months of July and August in waters beyond the 40 m isobath in the YS. The lack of a significant correlation between some oceanographic variables and *Auxis* spp.'s density or with any variable and *C. crysos* density might be related to a small variation in the oceanographic variables along the YS within each cruise, which might indicate that larvae of these species can develop along the entire shelf, in contrast with the strong correlation with seasonality.

Additionally, this work yields a baseline for future studies that might consider studying offshore larval transport from the YS since these species has been reported in the GoM's deep-water by several authors (e.g., Compaire et al., 2021; Daudén-Bengoa et al., 2023; Ditty et al., 2004; Lindo-Atichati et al., 2012), in order to describe fish larvae dispersion and possible survival and recruitment to optimal recruitment areas. However, little is known about the adult distribution in the YS and the GoM's deep-water region. Considering that these species are important social and economic resources for coastal communities, this study will supply greater knowledge for conservation and management of the Yucatan's Peninsula shelf.

Chapter 4. Coupling of potential habitat models with particle transport experiments to examine dispersal and connectivity of fish larvae in the Gulf of Mexico's deep water region

4.1 Introduction

Marine fishes have complex life stages in which the embryos, larvae, early juveniles, subadults and adults require different habitat types with distinct environmental conditions. While larval habitat depends on adult distribution and spawning (Caiger et al., 2021; Espinosa-Fuentes & Flores-Coto, 2004), larvae can be passively dispersed to areas that affect survival and recruitment (Cowen & Sponaugle, 2009). Connectivity studies are conducive to estimating the time that it takes between spawning and recruitment to nursery habitats (Johnson et al., 2013), as well as identifying larval origin (Compaire et al., 2021) and retention areas (Paris et al., 2005). Retention and dispersal are two key factors that determine the level of connectivity between regions and the environmental conditions that larvae will experience (Cowen et al., 2006; Lett et al., 2008). They also play a role in determining and maintaining population structure and the potential for recolonization following disturbances such as oil spills or hurricanes (Johnson et al., 2009; Rooker et al., 2013). Evaluating connectivity, and understanding the underlying transport processes, is therefore key to comprehending recruitment variability (Basterretxea et al., 2012; Cowen et al., 2006).

While fish larvae of some species can perform limited diel vertical migrations during the earliest life stages to capture food and evade predators (Garrido et al., 2009; Leis, 2020; Olivar et al., 2018), strong horizontal swimming abilities appear during later stages of development (Clark et al., 2005; Leis, 2020). This implies that marine fish larvae can be passively transported great distances (Cowen & Sponaugle, 2009; Govoni, 2005), during which they can be exposed to varying environmental conditions that may be conducive or detrimental to larval growth survival, thus impacting recruitment success.

Since tracking fish larvae in the open ocean is challenging due to their small size (approximately 1 to 10 mm; Richards, 2006), studies simulating the transport of the early life stages through numerical circulation modeling have provided insight into larval dispersion (Basterretxea et al., 2012; Peguero-Icaza et al., 2008), natal origin and transport mechanisms (e.g., Compaire et al., 2021; Paris et al., 2005). These studies commonly use a Lagrangian particle-tracking framework coupled with ocean circulation models to follow

the pathways of a large number of individuals (virtual fish larvae) through space and time (Paris et al., 2013; L. Sanvicente-Añorve et al., 2014; Werner et al., 2007). Additionally, some studies couple Lagrangian dispersion models with ecological information such as adult spawning habitat and period, or biological characteristics such as egg type, planktonic stage duration, larval growth rates or vertical position in the water column (Christensen et al., 2007, 2018; Sponaugle et al., 2002), allowing for a more detailed analysis of physical and biological interactions and therefore a more accurate evaluation of larval dispersion (Cowen et al., 2006).

The high temporal and spatial variability that is typically observed in the distribution and abundance of fish larvae (Fuiman & Werner, 2002) makes it challenging to define the region in which virtual larvae should be seeded in particle tracking experiments. The potential habitat of a species can be defined as the region(s) with a suitable set of environmental conditions that are associated with a particular place and time, and can be stage-specific (Planque et al., 2007). Several approaches have been used to generate potential habitats, including acoustic surveys (Georgakarakos & Kitsiou, 2008), presence-absence models (Borchers et al., 1997), fish density models (García-Fernández et al., 2021), and delta models (Torrejón-Magallanes et al., 2019), in which presence-absence and density models are combined. Likewise, potential habitats can be predicted based on empirical relationships between density and distribution and environmental conditions, using statistical approaches such as linear or logistic regression models or generalized additive models, or GAMs (Chapter 1 and 2; García-Fernández et al., 2021; Meinert et al., 2020). These habitat models contribute to the assessment of the potential impacts of natural variability and anthropogenic disturbances on distribution and abundance (Le Pape et al., 2014; Planque et al., 2007).

Neritic species mainly occupy habitats from the coastline to the continental shelf's edge (200 m). Their spawning period is mainly limited to spring and summer (Froese & Pauly, 2021; Richards, 2006) and it occurs near the surface (Flores-Coto et al., 2000; Grüss et al., 2018) with larval stage durations ranging between 16 to 40 d (De Vries et al., 1990; Houde & Richard, 1969; Leis et al., 2006). In contrast, oceanic taxa can be classified based on the depths of their habitat into epipelagic (0-200 m), mesopelagic (200-1000 m) and bathypelagic (1000-4000 m) species (Fahay, 2007). Spawning in epipelagic species occurs between spring and summer (Collette & Aadland, 1995; Froese & Pauly, 2021), but mesopelagic species mostly spawn throughout the year with some taxa presenting seasonal peaks, and they typically have lower fecundity than neritic species (Richards, 2006; Froese and Pauly, 2021). Meso- and bathypelagic species spawn at around 800 m (Caiger et al., 2021; Hulley & Prosch, 1987), and fertilized eggs rise to the upper levels of the water column as they develop due to positive buoyancy from the high lipid content in

the yolk sack (Sundby & Kristiansen, 2015). In many mesopelagic species, the larval stage duration lasts around 50 d (Gartner, 1993; Landaeta et al., 2015).

In the Gulf of Mexico's (GoM) epipelagic habitat of the deep-water region (defined as depths > 1000 m) previous studies indicate that high larval densities of many neritic species can be found among those of mesopelagic species (Compaire et al., 2021; del Pilar Echeverri-García et al., 2022; Ditty et al., 2004; Muhling et al., 2012). This generally occurs close to the slope and shelves due to the interaction of currents over the slope with the shelf, which can transport larvae toward deeper oceanic waters, or to the convergence of currents over the shelves that lead to offshore transport (Compaire et al., 2021; Guerrero et al., 2020; Martínez-López & Zavala-Hidalgo, 2009; Otis et al., 2019).

In the GoM's deep-water region, the main oceanographic feature that modulates the circulation is the Loop Current (LC), which exhibits different degrees of intrusion (Biggs, 1992; Weisberg & Liu, 2017). During periods of high LC intrusion, anticyclonic eddies (LC-AE) of varying sizes can form and detach from the LC, subsequently traveling westward over 6 to 11 months. This transports water masses and plankton from the Caribbean to the central and western gulf (Jochens & DiMarco, 2008; Lindo-Atichati et al., 2012). LC-AEs eventually interact with the slope and dissipate near the western or southwestern shelf (Dubranna et al., 2011; Leben, 2005; Weisberg & Liu, 2017) although the exchange with surrounding waters begins earlier (Meunier et al., 2019). The position of the LC and LC-AEs can influence the transport and retention of pelagic plankton within the Gulf and their transport through the Florida Straits and out of the Gulf (Cowen & Sponaugle, 2009; Johnson et al., 2017).

In the southern GoM (sGoM), the western Bay of Campeche (BoC; south of 22 °N) is characterized by the presence of a semi-permanent cyclonic gyre (CE) (Pérez-Brunius et al., 2013) that interacts with the slope and shelf (Guerrero et al., 2020) and provides nutrients to the euphotic layer due to a shallowing of the pycnocline (Salas de León & Monreal Gómez, 2005). Wind-driven upwelling in the southeastern BoC near the Yucatan shelf (YS) (J. Zavala-Hidalgo et al., 2003) and river runoff from the Grijalva-Usumacinta river system that is transported toward the deep waters of the GoM (Signoret et al., 2006) leads to higher productivity in the BoC than the central gulf (Martínez-López & Zavala-Hidalgo, 2009; Vázquez de la Cerda et al., 2005). Additionally, LC-AEs and non-LC anticyclonic eddies (AE) can interact with the BoC's CE (Guerrero et al., 2020; Pérez-Brunius et al., 2013), creating jets that can enhance larval growth due to higher prey availability (Bakun, 2006), and may also disperse larvae to other regions of the GoM, thus increasing larval connectivity (L. Sanvicente-Añorve et al., 2014).

The BoC has been described as a region with relatively high retention and weak interaction with the rest of the GoM regions (Damien et al., 2018; Miron et al., 2017). Miron et al. (2017) constructed a Lagrangian dynamical geography for the gulf's surface waters based on a matrix of transitional probabilities of more than 3000 daily satellite-tracked surface drifters trajectories deployed in the GoM from 1994 to 2016. They indicated that the BoC acts as a weakly interacting province, which implies limited dispersion toward the northwestern GoM. The BoC's retention in the upper layer is mainly associated with the presence of the semipermanent CE (Pérez-Brunius et al., 2013). Perez-Brunius et al. (2013) observed this overall retention based on analyzing three years of data from surface drifters, deep current meter moorings and satellite altimetry. Nevertheless, they also observed a northward circulation in the central and eastern basins due to convergence of locally generated AEs and interaction with the CE, which changes in position, size, and intensity as a result. Thus, the position and intensity of the CE and its interaction with locally generated ACs or LC ACEs may influence larval dispersal pathways and therefore connectivity in the wGoM.

The GoM's upper layer is subject to seasonal variability that influences environmental conditions and circulation in the euphotic layer (Muller-Karger et al., 2015; Jorge Zavala-Hidalgo et al., 2006). Modeling results suggest that on the Tamaulipas-Veracruz (TAVE) shelf (western GoM south of 26 °N) upwelling peaks in July, and wind-driven currents are northward along the shelf providing offshore transport from April to August between 20 and 22 °N (J. Zavala-Hidalgo et al., 2003). During fall and winter, atmospheric cold fronts lead to a southward circulation along the Gulf's western shelf, which reaches the southernmost BoC, where it meets an opposing current, generating offshore transport (Martínez-López & Zavala-Hidalgo, 2009; J. Zavala-Hidalgo et al., 2003). Another region of along-shelf confluent currents is in the Perdido Foldbelt of the northwestern GoM (nwGoM) during April and May. Offshore transport in this region has been observed as high chlorophyll (chl a) plumes detected through remote sensing (Compaire et al., 2021; Martínez-López & Zavala-Hidalgo, 2009). Additionally, offshore transport in the western Gulf can also be due to jets formed during the interaction between mesoscale eddies and the slope and outer shelf (Guerrero et al., 2020; J. Zavala-Hidalgo et al., 2003). Along the western YS, there is westward circulation throughout the year, with the strongest offshore transport between July and August (J. Zavala-Hidalgo et al., 2003). The seasonal variations in circulation patterns and environmental conditions modify larval habitat suitability, influencing species' distribution and density (Domingues et al., 2016; Lindo-Atichati et al., 2012) and dispersal (L. Sanvicente-Añorve et al., 2014).

This study examines the dispersal of virtual larvae (passive particles) in the GoM's deep-water region from potential habitats of four species with contrasting life histories using a high-resolution ocean circulation model. Given the BoC's higher productivity (Martínez-López & Zavala-Hidalgo, 2009; Vázquez de la Cerda

et al., 2005) and its importance for fishery production (Falfan et al., 2007; St. John et al., 2016), the study focuses on retention within the BoC and its connectivity to the rest of the GoM, as well as the dispersal in the region of influence of the LC. First, we generated species-specific predictions of potential habitats based on the results of generalized additive models (GAMs) applied to *in situ* larval distributions for the sGoM (Chapter 1). Second, the retention and dispersal of virtual larvae for each species were examined using particle tracking experiments during two periods with contrasting mesoscale circulation: (A) a high level of LC intrusion, absence of a recently detached LC-AE, and no interaction between AE and CE in the BoC, and (2) a low level of LC intrusion, a recently detached LC-AE in the central Gulf, and AE-CE interaction in the BoC and western Gulf. Third, to complement the interpretation of the dispersal of virtual larvae from their potential habitats, the results were compared to a null model in which particles were seeded throughout the BoC.

It was hypothesized that the spatial distribution of each species' potential larval habitat plays a central role in determining the pattern of particle retention and dispersion. Specifically, we posit that strong interactions between mesoscale features in the BoC will lead to less retention within the Bay. We also hypothesized that a high level of intrusion of the LC into the GoM will lead to the transport of virtual larvae from north of the Yucatan Peninsula through the Florida Straits to the Atlantic Ocean, compared with the low intrusion level in which greater retention in north off the YS will be observed. The use of numerical circulation models coupled with the spatial distribution of fish larvae can provide insight into the retention and dispersal level of fish larvae and the connectivity between regions in the GoM's deep-water region, and hence to a better understanding of population connectivity.

4.2 Materials and methods

4.2.1 Study area and oceanographic conditions

The study area for the dispersion experiments covered the GoM's deep-water region (depths > 1000 m; Figure 13). Two contrasting conditions were selected for the experiments: (1) July 1st to 30th 2011, when there was a high LC intrusion and no recently detached LC-AE in the central Gulf, the BoC's CE was relatively small and weak and there was no interaction between mesoscale features (hereafter referred to as HLC/low interaction), and (2) July 1st and 30th 2016, when the LC's eddy Olympus ("huge" size category, https://www.horizonmarine.com/loop-current-eddies) had detached leading to a low level of LC intrusion and traveled westward, and there was an interaction between the BoC's CE and AEs (hereafter referred to as LLC/high interaction). Since the goal of the study was to characterize the differences in larval dispersion among contrasting conditions, only one example of each condition was used in the dispersion models.



Figure 13. Schematic representation of the circulation and mesoscale features in the GoM's deep-water region during the particle tracking experiments. The two upper rows correspond to HLC/low interaction conditions (2011) and the two lower rows correspond to LLC/high interaction (2016). Column 1: July 1st, column 2: July 15th and column 3: July 31st. Colored maps represent sea surface height (SSH, m) and the contour lines indicate the -0.1, 0 and 0.2 m. Vector maps indicate surface velocities (m s⁻¹).

4.2.2 Species selection

The species selected to run the particle dispersion models were *Notolychnus valdiviae* (lanternfishes; Myctophidae), *Cubiceps pauciradiatus* (drift fishes; Nomeidae), *Bregmaceros atlanticus* (codlets; Bregmacerotidae) and *Auxis* spp. (Scombridae; which includes larvae of *A. rochei rochei* and *A. thazard thazard*, known as bullet and frigate tuna, respectively). Both *Auxis* species were grouped into their genus since their larvae cannot be distinguished morphologically during the early life stages and molecular identification is necessary (Catanese et al., 2008; Ochoa-Muñoz et al., 2018). Nevertheless, both species share very similar distribution, habitat, depth range and spawning periods in the GoM (Collette & Nauen, 1983; Froese & Pauly, 2021; Richards, 2006). These species present contrasting adult habitats and early life history characteristics, and belong to different families with ecological and economic importance (see Chapter 1).

4.2.3 Prediction of potential spawning habitat from hydrographical parameters

To predict each species' potential habitat in the GoM's Mexican EEZ (south of 26 °N), the species' densities and GAMs from Chapter 1 were applied to hydrographic data corresponding to a ten-year climatology spanning 2009 to 2018 and encompassing the late spring and summer (April 1st to July 31st). Gridded explanatory variables from Chapter 1 (resized to 0.25° resolution) were linked using the predict.gam function from the "mgcv" package (Simon N. Wood, 2018) to estimate the species density in each grid quadrant using the R–project 3.4.1 (R Core Team, 2021) statistical program. Predictions of the larval density for each species are presented in Figure 23.

4.2.4 Particle tracking experiments

Numerical simulations used the HYCOM + NCODA circulation model (Chassignet et al., 2007), which provides horizontal velocity components (u and v, eastward and northward respectively). The velocity values corresponded with the smallest spatial and temporal resolution available (1/25 th degree, ~3.5-km horizontal resolution and 1-hour temporal resolution) to reduce simulation errors (Compaire et al., 2021). Passive particle advection was calculated using a fourth-order Runge-Kutta algorithm. The HYCOM + NCODA model includes 17 depth levels (z) between 0 and 200 m (the depth range corresponding with the oblique plankton tows used for larval sampling; Chapter 1). Five depth levels were selected for particle

seeding (z: 0, 50, 100, 150 and 200 m). The first 200 m of the water column is where both neritic and mesopelagic larvae inhabit during their development (Alvarez et al., 2021; Catul et al., 2011; Wang et al., 2021) and where most nutrients and phytoplankton that sustain secondary production (including prey for larvae) are present (Biggs & Ressler, 2001; Linacre et al., 2015), and corresponds to the average seasonal thermocline in the GoM (Advocate & Hood, 1993).

A subset of the predicted potential habitat for each species was used for particle seeding to focus on areas of the highest predicted larval density irrespective of the absolute predicted density, which varied among species. Normalized densities were obtained by scaling each species' predicted densities, where 1 represents the maximum predicted density and 0 the absence of larvae. To visualize the dispersion patterns and simplify the interpretation, particles were seeded in predicted areas where the normalized predicted density (PD) was > 0.4 (hereafter PD > 0.4). Since the BoC has been described as a region with relatively high retention and weak interaction with the rest of the GoM's regions (Damien et al., 2018; Miron et al., 2017), a null model encompassing the entire BoC's deep water region serving as potential habitat was included for comparative purposes (Figure 14).

The number of randomly seeded particles at t = 0 d (e.g., July 1st 2011 and July 1st 2016) was proportional to the area of each potential habitat subset, where the smallest area *B. atlanticus* 1 (1076 km²) received 2500 particles (500 at each depth; Table 9), and the largest potential habitat was over 12 times larger (*N. valdiviae*) and was consequently seeded with 31,565 particles. From *B. atlanticus'* potential habitat, two habitat subsets were obtained according to the PD > 0.4.

Species habitat	Potential habitat seeding area (km²)	Areas relative to smallest habitat subset	Number of seeded particles at t = 0 d	
B. atlanticus 1	1076	1	2500	
B. atlanticus 2	2530	2.43	6080	
Auxis spp.	2815	2.62	6545	
C. pauciradiatus	2943	2.80	6995	
BoC (null model)	11999	11.23	28065	
N. valdiviae	13462	12.63	31565	

Table 9. Particle numbers deployed at the 5 depth layers (z: 0, 50, 100, 150 and 200 m) based on each species' predicted potential habitat area. Seeding areas were those with normalized predicted densities > 0.4 (PD > 0.4).

To calculate particle transport to different locations throughout the GoM, 35 quadrants were generated by gridding the entire GoM's deep-water region in a 2 by 2-degree latitude and longitude matrix (Figure 14). This spatial resolution was selected since it resembles the size of mesoscale features and the spatial lifetime scale of ichthyoplankton (Haury et al., 1978; Hunt & Schneider, 1987).



Figure 14. Particle dispersion areas in the Gulf of Mexico consist of a 2 by 2-degree grid covering the deep-water region. Numbers indicate particle arrival quadrants. The red polygon represents the BoC's null model. Dotted, dashed and continuous (smoothed) lines represent the 40, 200 and 1000 m isobaths.

Particles were advected forward in time for 30 d based on the average development time for neritic and mesopelagic larvae (Blas-Cabrera et al., 2006; Conley & Gartner, 2009; Lespilette et al., 2003; Margulies, 1997; Núñez & Baumar, 2018). Additionally, a midpoint (t = 15 d) was included to aid the interpretation of the particle dispersion evolution through time. The same time was applied to all species, and the null model, to allow for examination of particle dispersion without the confounding effect of varying larval stage duration, although this ignores the fact that greater dispersal distances can be achieved in species with longer larval stage duration, and that this has been shown to increase connectivity (Cowen et al., 2006).

In the particle dispersion models, the number of particles present at each depth (z) in a certain final quadrant (j) at a given time (t = {0:1/24:30} d with hourly resolution) were counted (N_j (t), with j = [1,2, ..., 35], to obtain the percentage (%) of particles that arrived in quadrant (j). Additionally, the percentage of particles (P) that (a) remained within each species' habitat subset (PD > 0.4), (b) that were dispersed in the deep-water region ($N_{1000 \text{ m}}$; particles that stayed at locations with depths equal or greater to 1000 m deep) and (c) that were dispersed beyond the 200 m isobath ($N_{200 \text{ m}}$; particles that stayed at locations with depths equal or greater to 200 m deep) after a given time (t) was calculated. $N_{1000 \text{ m}}$ and $N_{200 \text{ m}}$ were used to calculate the number of particles between the 200 and 1000 m isobath.

Particle connectivity maps were created to depict the percentage of particles that were retained and dispersed from the BoC at the time of seeding the particles (t = 0 d), after t = 15 d and t = 30 d. Additionally, a matrix of the percentage of particles arriving at each quadrant from each habitat subset under both contrasting conditions was calculated.

It is possible that these experiments present several limitations, such as not incorporating vertical larval migration, which was addressed by modeling particle dispersion in several of the depths where vertical migration occurs. In addition, variations in the period of dispersion (e.g., larval development time) for each species were not considered. These factors were not included in the models in order to be able to isolate the effect of the size and distribution of the species' predicted potential habitat and distinguish its implications for larval dispersion and connectivity. This study focuses on understanding the dispersion patterns and connectivity of fish larvae in the deep-water region of the GoM by comparing several species of ecological or economic importance under different circulation scenarios, in comparison with other studies that focus on a single species or circulation pattern (Johnson et al., 2017; Lara-Hernández et al., 2019; Paris et al., 2005).

4.3 Results

4.3.1 Species potential habitat

Each species' potential habitat had a limited and differing distribution (Figure 15). Those of *Auxis* spp., *N. valdiviae* and one of the two subsets of *B. atlanticus* potential habitat were limited to the southern BoC (sBoC), with the greatest proportion of larvae predicted close to the continental slope (except for *N.*

valdiviae, which had a larger predicted potential habitat encompassing most of the BoC). In contrast, the potential habitat of *C. pauciradiatus* was just north of the BoC. The largest PD > 0.4, corresponded to *N. valdiviae*, with an extension of 13,462 km², while the smallest was for *B. atlanticus* in the BoC with 1,076 km². However, a second PD > 0.4, was found for *B. atlanticus* north of the YS, and it was 1.5 times larger than the one in the sBoC.



Figure 15. Species-specific larval potential habitats. Normalized larval densities. A: *Auxis* spp., B: *B. atlanticus*, C: *C. pauciradiatus* and D: *N. valdiviae*. The red bold line indicates areas within which predicted densities > 0.4 are found (PD > 0.4) and which were used for particle seeding in tracking experiments. Two potential habitat areas with PD > 0.4 were predicted for *B. atlanticus* in the deep-water region. Dotted, dashed and continuous lines represent the 40, 200 and 1000 m isobaths.

4.3.2 Simulation of larval transport

After 30 d the overall retention in the deep-water region was greater under the LLC/high interaction condition (> 77% in all cases). However, *Auxis* spp. and *B. atlanticus* in the sBoC had greater retention of total released particles in the deep-water region under HLC/low interaction conditions (3 % and 10% higher, respectively) than with LLC/high interaction conditions (Table 10). This contrasts with a greater

percentage of retained particles within the deep-water region for *B. atlanticus* in the north of YS (3 %), *C. pauciradiatus* (6 %) and *N. valdiviae* (5 %) with the LLC/high interaction. The percentage of retained particles in the deep-water region of *N. valdiviae* was very similar to that observed in BoC's null model, which presented the same percentage of retention (77 %) under both conditions. Overall, less than 10 % of the particles were dispersed onto the continental shelf, independent of the conditions.

Table 10. Percentage of seeded particles at t = 30 d that were retained or dispersed in particle seeding experiments. LLC/high interact: low level of intrusion of the Loop Current and interaction between mesoscale features (2011). HLC/low interact.: high level of Loop Current intrusion and no interaction between mesoscale features. BoC: Bay of Campeche. Deep-water region (depths > 1000 m). Upper slope: 200 to 1000 m isobath. Continental shelf: < 200. Bold values indicate the largest value.

Spacios	Retained	d in the	Retained in the deep-		Dispersed to the		Dispersed to the	
species	potential habitat (%)		water region (%)		upper slope (%)		continental shelf (%)	
	HLC/low	LLC/high	HLC/low	LLC/high	HLC/low	LLC/high	HLC/low	LLC/high
	interact.	interact.	interact.	interact.	interact.	interact.	interact.	interact.
Auxis spp.	13	18	87	84	11	11	2	5
B. atlanticus 1	0	0	86	76	13	20	1	4
B. atlanticus 2	55	73	79	92	14	4	7	4
C. pauciradiatus	15	52	87	93	11	6	2	1
N. valdiviae	66	47	72	77	20	14	8	9
BoC (null model)	40	30	77	77	17	14	6	9

The dispersion of the particles seeded in the null model was limited to the wGoM (west of 92 °W). For the HLC/low interaction, most particles were transported toward the north along the western continental slope during the first 15 d, and after 30 d, particles reached the northwestern shelf and a few were dispersed to the deep-water region due to a non-LC AE in the nwGoM (Figure 16 A). In contrast, under LLC/high interaction, the northward transport after 15 d extended throughout the deep-water region to a greater extent (Figure 16 B), and some particles were also dispersed to the shelf (< 200 m). After 30 d, particles reached the central GoM from the northwestern region and others from the central BoC. For *N. valdiviae's*, the dispersal pattern was similar to that observed for the BoC's null model (Figure 16 C and D), reflecting the large overlap in the spatial distribution between its PD > 0.4 and the BoC. However, more particles reached the northcentral GoM (28 °N, 90 °W) after 15 and 30 d from *N. valdiviae's* PD > 0.4.

In comparison, particles seeded in at PD > 0.4 of *Auxis* spp. (Figure 16 E and F) and *B. atlanticus* in the sBoC (Figure 17 A and B) were transported northward along the western continental slope, but their dispersion was less extensive than what was observed for *N. valdiviae's* potential habitat and BoC's null model. For

Auxis spp., after 15 d of dispersal under HLC/low interaction, the particles remained within the BoC, with very few particles transported to the upper slope (Figure 16 E). In comparison, during LLC/high interaction (Figure 16 F), particles reached 25 °N along the GoM's western slope. After 30 d, particles reached the nwGoM (including the shelf) due to northward along-slope transport under HLC/low interaction, while under LLC/high interaction, more particles were retained in the deep-water region near the northern limit of the BoC (22 °N). Additionally, particles that reached the nwGoM were dispersed eastward by anticyclonic circulation in the western Gulf. The distribution of the dispersed particles from the sBoC subset of *B. atlanticus*, was similar to that of *Auxis* spp., which is to be expected based on the similarity in the spatial distribution of both potential habitats.

The dispersal of particles from *B. atlanticus* north of the YS with PD > 0.4 (Figure 17 C and D), indicated that after 15 d there was more widespread particle advection under HLC/low interaction conditions compared with LLC/high interaction. Particles reached the northern GoM's shelf near the Mississippi Delta and the eastern BoC when the LC extended far into the Gulf (Figure 17 C). After 30 d, particles were transported through the Florida Straits and more particles were dispersed beyond the 1000 m isobath toward the continental slope (14 %) and inside the continental shelf (7 %). Under LLC/ high interaction conditions, the low level of intrusion of the LC led to greater retention of particles within or close to PD > 0.4 as well as some advection to the sGoM, reaching the potential habitat of *B. atlanticus*. Additionally, the lack of intrusion of the LC in the GoM led to more particles remaining inside the deep-water region (HLC/low interaction: 79 %; LLC/ high interaction: 92 %).

The overall dispersion from *C. pauciradiatus* potential habitat subset differed between conditions. Under HLC/low interaction, particles traveled westward after 15 d of dispersion (Figure 17 E). In contrast, with LLC/high interaction conditions (Figure 17 F), particles remained close to PD > 0.4 due to the retention anticyclonic features that interacted with the northern BoC.

By the end of the dispersal period, particles under HLC/low interaction were transported out of the potential habitat toward the Texas shelf and some particles reached the continental slope, while under LLC/high interaction, more particles remained in *C. pauciradiatus* PD > 0.4 and some were advected to the sBoC.



Bay of Campeche (Null model)

Figure 16. Particle dispersion experiments for BoC's null model (A, B), *N. valdiviae* (C, D) and *Auxis spp.* (E, F) over gridded regions. First column: species-specific PD > 0.4 area of seeded particles at t = 0 d. Second column t = 15 d and third, t = 30 d. HLC/LI: High Loop Current Intrusion/Low Interaction; LLC/HI: Low Loop Current Intrusion/High Interaction. Rows A, C and E correspond to HLC/LI (July 2011), and rows B, E and F to LLC/HI (July 2016). Red dots are seeded particles released at five depths (z = 0, 50, 100, 150 and 200 m). $N_{1000 \text{ m}}$: Number of particles retained from 1000 m and deeper and $N_{200 \text{ m}}$: Number of particles retained from 200 m and deeper (including the deep-water region). The gray continuous line corresponds to the smoothed 200 m isobath, and the black line surrounding the 2 by 2-degree grid corresponds to the smoothed 1000 m isobath.



Figure 17. Continuation of particle dispersion experiments for *B. atlanticus* 1 (A, B), *B. atlanticus* 2 (C, D) and *C. pauciradiatus* (E, F) over gridded regions. First column: species-specific PD > 0.4 area of seeded particles at t = 0 d. Second column t = 15 d and third, t = 30 d. HLC/LI: High Loop Current Intrusion/Low Interaction; LLC/HI: Low Loop Current Intrusion/High Interaction. Rows G, I and K correspond to HLC/LI (July 2011), and rows H, J and L to LLC/HI (July 2016). Red dots are seeded particles released at five depths (z = 0, 50, 100, 150 and 200 m). N_{1000} m: Number of particles retained from 1000 m and deeper and N_{200} m: Number of particles retained from 200 m and deeper (including the deep-water region). The gray continuous line corresponds to the smoothed 200 m isobath, and the black line surrounding the 2 by 2-degree grid corresponds to the smoothed 1000 m isobath.

The percentage of particles that remained inside the BoC (Table 11) after 15 d of dispersal under HLC/low interaction condition was greater than under LLC/high interaction for all PD > 0.4, as well as for the BoC's null model. In addition, 100% of the particles dispersed from *Auxis* spp.'s and *B. atlanticus*' PD > 0.4 remained in the BoC under HLC/low interaction. This indicates a lower connectivity between the BoC and central GoM during the absence of interactions between mesoscale features in the southern GoM. However, after 30 d, while the percentage of particles dispersed outside the BoC decreased relative to what was calculated after 15 d, under LLC/high interaction more than 50 % of particles were dispersed outside the BoC.

For the species' PD > 0.4 outside the BoC, under LLC/high interaction, no particles entered the BoC after 15 d. However, after 30 d, 9 % of the released particles in the *B. atlanticus* PD > 0.4, north of the YS, reached the BoC under HLC/low interaction (vs. 6 % under LLC/high interaction). For *C. pauciradiatus* 12 % reached the BoC under LLC/high interaction (and 5 % under HLC/low interaction). This suggests there is some larval transport from north of the YS and the central GoM to the BoC.

	% Particles in the BoC at seeding (t = 0 d)		% Parti	cles retained or	% Particles retained or transported to the BoC		
Species habitat			transpor	ted into the BoC			
			(t = 15 d)		(t = 30 d)		
	HLC/low	LLC/high	HLC/low	LLC/high interact.	HLC/low	LLC/high interact	
	interact.	interact.	interact.	220,	interact.	220, <u>8</u> interdet.	
Auxis spp.	100	100	100	73	94	50	
B. atlanticus 1	100	100	100	64	87	48	
B. atlanticus 2	0	0	2	1	9	6	
C. pauciradiatus	0	0	7	5	5	12	
N. valdiviae	72	72	68	57	61	33	
BoC (null model)	100	100	84	74	73	44	

Table 11. Percentage of particles in the Bay of Campeche (BoC) at t = 0 d, at t = 15 d and t = 30 d for HLC/low interaction and LLC/high interaction. Bold values indicate the highest value for each comparison.

The differences in size and location of the PD > 0.4 in which particles were seeded led to differences in the connectivity among GoM's regions after 30 d (Figure 18) Overall, the particle dispersion and connectivity were largely limited to the BoC and the wGoM, except for the case of *B. atlanticus* PD > 0.4 off the northern
YS. This species had the greatest connectivity with particles dispersed outside the habitat's PD > 0.4 toward the sBoC and wGoM, as well as to the Florida Straits.

For the rest of the species, dispersion was mainly limited to the wGoM. *C. pauciradiatus* connectivity (the species with the PD > 0.4 located north of 22 °N) was observed with the north-central GoM mainly under LLC/high interaction, although the greatest percentage of particles remained in the wGoM, and few reached the southernmost BoC. For the BoC, dispersal was greater under LLC/high interaction, indicating greater connectivity when compared with HLC/low interaction. While *N. valdiviae* and the BoC's null model presented similar dispersal limited to the wGoM after 30 d, for *Auxis* spp. and *B. atlanticus* there was connectivity between sBoC and the deep waters of the nwGoM during LLC/high interaction. In contrast, under HLC/low interaction particle dispersal was limited to the GoM's western slope, and the level of connectivity with other areas of the Gulf was smaller.



Figure 18. Percentage matrix of particle dispersal under HLC/low interaction (top) and LLC/high interaction (bottom) experiments at t = 0 d, t =15 d and t = 30 d dispersion times. Each' row corresponds to a species or the BoC's null model. From top to bottom: BoC (Bay of Campeche), Not (*N. valdiviae*), Cub (*C. pauciradiatus*), Bre 1 (*B. atlanticus* in the sBoC) and Bre 2 (*B. atlanticus* off the northern YS) and Aux (*Auxis* spp.). Columns indicate quadrant numbers from figure 14. Red box corresponds with the wGoM (-98 to -92 °W), green to central GoM (-92 to 88 °W) and yellow to eastern GoM (-88 to 80 °W).

4.4 Discussion

Results highlight the importance of using a comparative approach centered on species with different potential habitats coupled with Lagrangian dispersion models to further understand the dispersal and connectivity of marine fish larvae. A general transport toward the north along the shelf from predicted habitat subset in the sBoC was observed. These results show that the size and distribution of the predicted habitat subset played a key role in dispersal patterns and connectivity between regions of the GoM's deepwater region. Larvae from habitat subsets that occupied the entire BoC were dispersed more homogenously toward the north, while larvae from habitats limited to the sBoC were more retained inside the BoC. Additionally, comparing the dispersal and connectivity between distinct circulation patterns (HLC/low interaction and LLC/high interaction) also indicated a strong influence in the dispersion paths from the predicted habitat subset, giving different connectivity patterns within the entire GoM such as dispersed larvae outside the GoM under HLC conditions and more retention with LLC.

4.4.1 Species-specific potential habitat predictions

The predicted potential habitat of *Auxis* spp. was in the sBoC near the continental slope. This agrees with studies that reported the presence of larvae of this species in this area during summer (Flores-Coto et al., 2009; Laura Sanvicente-Añorve et al., 2000). *Auxis* spp. larvae have also been caught beyond the slope in other regions of the GoM, such as the northern GoM during spring (Mendelssohn et al., 2017), off the western Florida Shelf (Houde et al., 1979) and in the region of influence of the LC (Lindo-Atichati et al., 2012). The presence of *Auxis* spp. larvae in offshore waters in the BoC could be due to (1) adult spawning in oceanic waters despite this being a mainly neritic species (see Collette and Nauen, 1983; Uchida, 1981) and/or (2) seasonal offshore cross-shelf transport in the south-eastern BoC (Martínez-López & Zavala-Hidalgo, 2009) coupled with high river runoff from the Grijalva-Usumacinta during periods of along-shelf convergence in the south-western BoC (Signoret et al., 2006). Although more in depth studies are needed since little is known about the distribution of larvae and adults of *Auxis* spp. in the GoM's deep-water region, Pruzinsky et al. (2020) indicated that *Auxis thazard* (among other neritic scombrids) in the northern GoM preferred areas with greater chl a concentrations, closer to the slope and with lower salinity. This might support the presence of larvae in the sGoM close to river runoff and upwelling areas due to cross-shelf transport in our study.

Potential habitats were also predicted for N. valdiviae and B. atlanticus in the sBoC, with varying spatial extent. The distribution of N. valdiviae's predicted potential habitat is consistent with its previously reported distribution (Rodríguez-Varela et al., 2001), since it is a cosmopolitan mesopelagic species found throughout the GoM's deep-water region (Conley & Gartner, 2009; Daudén-Bengoa et al., 2020; A. del C. Rodríguez-Varela et al., 2001). The highest larval densities were predicted for the BoC, which also agrees with previous studies for this and other mesopelagic species (Daudén-Bengoa et al., 2020; Flores-Coto et al., 2009; Laura Sanvicente-Añorve et al., 1998) and N. valdiviae's distribution observed in Chapter 1. The BoC has a higher nutrient concentration on the surface and higher zooplankton biomass than the central GoM (Färber-Lorda et al., 2019) and is considered more productive (Hidalgo-González & Álvarez-Borrego, 2008; Linacre et al., 2015). Hence, the higher densities could be attributed to the higher productivity in the BoC due to a shallowing of the pycnocline in the central BoC (Salas de León & Monreal Gómez, 2005), wind-driven upwellings (J. Zavala-Hidalgo et al., 2003) and river runoff from the Grijalva-Usumacinta river in the southeastern BoC (Signoret et al., 2006). In contrast, B. atlanticus has been described as both a neritic and mesopelagic species that mainly occupies the continental shelf's slope in the sGoM (Flores-Coto et al., 2009; L Sanvicente-Añorve et al., 2003; Zavala-García & Flores-Coto, 1994), southeastern BoC (Blas-Cabrera et al., 2006) and eastern GoM (Houde, 1981; Richards et al., 1993), which agrees with the potential habitat predictions. The potential habitat of B. atlanticus off the northern YS could be due to larval offshore transport toward deep waters caused by the easterly winds driving westward circulation over the shelf throughout the year (Jouanno et al., 2018; Ruiz-Castillo et al., 2016). Some studies have reported the presence of *B. atlanticus* larvae over the western Florida Shelf (Houde, 1981; Richards et al., 1993), and other Bregmaceros species in the sGoM's shelf (Flores-Coto et al., 2008; Zavala-García & Flores-Coto, 1994), however, little is known about B. atlanticus distribution in the GoM's deep-water region and further studies should be addressed.

The prediction of *C. pauciradiatus'* potential habitat spanning the deep waters of the northern BoC and the central GoM matches the description of the larval distribution in several GoM studies (Felder & Camp, 2006; Lamkin, 1998; McEachron, 2009), and is also consistent with their adult mesopelagic distribution (Bard et al., 2002; Froese & Pauly, 2021; Lespilette et al., 2003). Additionally, *C. pauciradiatus* has been described by Houde et al. (1979) as a species whose adults can be found at intermediate SSTs such as in environments like the interaction between AEs and CEs (Leben, 2005; Weisberg & Liu, 2017), which are found in the central GoM (Counillon & Bertino, 2009). Although our prediction encompasses larvae from all larval stages, the distribution of *C. pauciradiatus* predicted potential larval habitat in this region might indicate the presence of a near spawning habitat.

The agreement between the predictions of the potential habitats and the distribution described by other authors suggests that these habitats do reflect each species' environmental requirements, indicating that these areas are likely suitable for their growth and development and potential recruitment to adult populations. While using a 10-yr climatology does not allow for the characterization of each species' distribution over shorter times scales, grouping biological data from several cruises within a season allows for a broader view of the overall species distribution, and more robust predictions of the species potential habitats. Additionally, it provides a baseline for the comparison of dispersal patterns and connectivity under specific oceanographic conditions.

4.4.2 Simulation of larval transport

The spatial distribution of the PD > 0.4 strongly influenced the dispersion of virtual larvae in the GoM's deep-water region. Additionally, the location of mesoscale features and their interaction also controlled the retention and dispersion of the virtual larvae. Importantly, in natural populations, larvae can be dispersed toward areas with suitable conditions that favor growth and survival, or to unsuitable or disturbed areas where growth is limited and mortality is higher. However, over time, the spatial and temporal variability in dispersal patterns contributes to maintaining connectivity between areas with suitable conditions, which is key to larval development, survival and ultimately recruitment success (Cowen et al., 2006; N. B. Furey & Rooker, 2013; Munday et al., 2009).

Under a circulation pattern with HLC/low interaction, there was a northward transport from the BoC along the western slope as previously reported by Zavala-Hidalgo et al. (2003), and which is present from April to August. This northward transport was also observed in wBoC's continental shelf based on the analysis of surface drifters by Dubranna et al. (2011) and by Pérez-Brunius et al. (2013). In this study, the absence of LC-AC eddies under the HLC/low interaction condition led to the dispersion of the virtual larvae to the slope in the nwGoM (close to 26 °N). This is also observed from a 10-year simulation of monthly mean surface currents of the overall northward circulation in the wGoM's shelves the due to wind stress and the local currents described by Zavala-Hidalgo et al. (2003, 2006). The overall dispersion toward the nwGoM's slope may positively influence larvae of the neritic species *Auxis* spp., while the transport of mesopelagic species (*C. pauciradiatus*, *N. valdiviae*) to the continental shelf may affect survival.

With LLC/high interaction, there was also northward transport along the western slope. However, due to the slope's interaction with anticyclonic circulation, strong advection toward the deep-water region was

observed. This advection was also reported by Compaire et al. (2021) based on the analysis of chl a plumes in surface waters from the shelf near the Perdido region (close to 26 °N), and was accompanied by the transport of fish larvae of coastal and neritic species to the deep-water region. In addition, a northward transport from the central BoC was also observed under LLC/high interaction. This was previously described by Pérez-Brunius et al. (2013) and Hamilton et al. (2016), and was related to the intrusion of anticyclonic circulation into the BoC that interacted with semi-permanent CE.

The LC's high level of intrusion increased the connectivity along the northern GoM, as well as between the wGoM's and sGOM, and advected particles from the central gulf through the Florida Straits and to the Atlantic Ocean. In contrast, the limited intrusion of the LC into the GoM seems to limit the dispersion of particles to the Atlantic. Therefore, variation in the intrusion level of the LC might disperse or retain larvae closer to suitable development and survival conditions in which they were caught.

4.4.3 Retention, dispersion and connectivity of the BoC with the northern GoM

The species with PD > 0.4 in the southernmost BoC (*Auxis* spp. and *B. atlanticus*) had about ~50 % more particles within the Bay after 30 d of dispersion compared with species for which particles were seeded over the BoC's deep water region (*N. valdiviae* and the BoC's null model). This might indicate a greater retention of larvae with habitats limited to the sBoC. The greater retention after 30 d (HLC/low interaction: > 60 %) in the BoC under HLC/low interaction in all four species PD > 0.4 resembles to that described by Perez-Brunius et al. (2013) and Miron's et al. (2017). Under LLC/high interaction, our results also resemble Perez-Brunius et al. (2013), since the interaction of anticyclonic features with the BoC increased the dispersion toward the north (high interaction: < 50 % after 30 d). These results indicate that the interaction between mesoscale features from the central Gulf and those in the BoC tends to increase larval dispersion and thereby the connectivity with the nGoM.

N. valdiviae is considered a cosmopolitan species in the GoM's deep-water region (Rodríguez-Varela et al., 2001) and adults that occupy the GoM's mesopelagic waters might influence *N. valdiviae's* distribution. However, the dispersed particles (virtual larvae) from *N. valdiviae*'s PD > 0.4 in the nwGoM resembles that shown by Pérez-Brunius et al. (2013), where a greater proportion of surface drifters released closer to the nwBoC (~ 20 °N, -96 °W) were advected northward. Therefore, despite being a cosmopolitan species due to adult distribution, this connectivity with the nGoM might indicate that larvae dispersion is also a key factor that influences *N. valdiviae's* distribution in the GoM.

In this study, a high level of intrusion of LC transported virtual larvae from *C. pauciradiatus* PD > 0.4 to the wGoM's slope after 15 d, probably due to a westward circulation and low interaction with the BoC. This westward circulation has been reported by Olvera-Prado et al. (2022) after calculating the mean circulation and transport in the northern GoM under the influence of a high intrusion level of the LC. Additionally, 13 % of particles were dispersed further into neritic waters after 30 d, which will likely lead to the loss of those larvae since larvae of this species are not found over shelf waters, which may be due to the presence of unsuitable environmental conditions.

C. pauciradiatus is a mesopelagic species whose adult habitat preference is mainly near oceanic jets (Lamkin, 1998). These areas are of high productivity (Bakun, 2006; Counillon & Bertino, 2009), in contrast with the more oligotrophic areas of the deep water of the GoM (Hidalgo-González et al., 2005; Linacre et al., 2015). Under LLC/high interaction, the interaction of anticyclonic features from the nGoM near the 94 °W with the CE in the BoC increased the percentage of particles near PD > 0.4 and the BoC, leading to greater retention in the deep-water region (7 % more under LLC/high interaction than HLC/low interaction), thus increasing connectivity between the central GoM (approx. 23 °N, 94 °W) and the BoC (south of 22 °N). This transport between the central GoM and the BoC and the retention on oceanic waters was also observed Perez-Brunius et al.'s (2013) drifters. The greater percentage of particles in mesopelagic waters and the PD > 0.4 of suggests a greater survival and recruitment of a bigger proportion of *C. pauciradiatus* larvae.

4.4.4 Retention, dispersion and connectivity in the LC region

The variation in the intrusion level of the LC played a key role in the particle dispersion from *B. atlanticus* PD > 0.4 in the north. A higher level of intrusion of the LC dispersed more particles toward the western GoM as well as through the Florida Straits, suggesting the loss of some *B. atlanticus* larvae from the gulf ecosystem to the Atlantic. Clancey (1956) showed a high density of post-larval, juvenile and adult specimens of this species in the Florida Current throughout the year. Given that *B. atlanticus* is a cosmopolitan species distributed throughout the central Atlantic (Felder & Camp, 2006; Froese & Pauly, 2021), the intrusion of the LC may link populations within the GoM with those of the Atlantic if conditions in the Florida Current favor growth, survival and recruitment. The assessment of the implications of LC-driven connectivity of larval fish populations would have to be examined using chemical or genetic markers to examine population structure.

The lower LC intrusion showed a greater retention near the predicted habitat of *B. atlanticus* north of the YS, which may decrease the connectivity in contrast to particles advected toward the northern GoM during periods of high LC intrusion. Additionally, the presence of particles in the sBoC's *B. atlanticus* habitat's PD > 0.4 after 30 d of dispersion, could indicate an increase in the probability of survival due to the presence of more favorable conditions (as predicted with the potential habitat model). Similar connectivity patterns have been observed by Johnson et al. (2013) in red snapper (*Lutjanus campechanus*) larvae dispersion models, in which particles were dispersed from the YS toward the south reaches of the BoC. It was also found and in coral reef systems in the sGoM by Sanvicente-Añorve et al. (2014), particles tracked for 35 d traveled from the northern slope of the YS to the sBoC. These results might suggest that circulation between neritic and oceanic waters between the northern YS and the sBoC is connecting route for *B. atlanticus* habitat subsets.

4.5 Conclusions

The size and distribution of the species predicted potential habitats played a key role in the dispersion of particles and thus in the connectivity among regions in the deep-water region of the GoM.

High interaction between mesoscale features in the western and southern GoM led to greater dispersion and connectivity along the entire wGoM. In contrast, the absence of AEs interacting near the BoC led to greater retention and more limited connectivity between the sGOM and more northern waters.

The percentage of particles retained was greater in potential habitats with PD > 0.4 that were limited to the sBoC, which indicates low connectivity with the wGoM. Additionally, a low interaction between mesoscale features in the central and southern GoM increased the retention in the BoC.

Particles under the influence of high LC intrusion were advected outside the GoM through the Florida Straits. In contrast, a lower degree of intrusion particles remained close to the species potential habitat in the north off the YS which decreased connectivity.

Adult habitat and spawning seasonality played a key role in the larval distribution of oceanic species, which were broadly found throughout the deep-water region during both sampled seasons. Higher densities were found in more productive regions such as the BoC. This might indicate that adults spawn in areas with more suitable conditions in order to increase larvae survival.

Results indicate that the mesopelagic species *C. pauciradiatus* is distributed in the entire GoM deep-water region throughout the year with a spawning peak between August and September. This suggests that *C. pauciradiatus* is a cosmopolitan species in the deep-water region of the GoM, as has been reported previously.

As hypothesized, the density of fish larvae of oceanic species such as *C. pauciradiatus* and *N. valdiviae* were more closely related to the oceanographic conditions of the GoM's deep-water than species typical of neritic habitats.

Based on the GAM results, variables indicative of greater productivity such as higher surface chl a concentration, as well as lower stratification and greater wind speeds indicative of higher larval feeding success, correlated with higher species' densities, suggesting that either spawning or survival of larvae is higher in areas with greater food availability. This can ultimately increase survival and recruitment, and therefore warrants further research.

Neritic species (*Auxis* spp. and *C. crysos*) found in the deep-water region were distributed closer to the continental slope in comparison with the dominant oceanic species. This is likely explained by their cross-shelf and/or offshore advection by local currents. The presence of neritic species away from their original habitat might suggest that the larvae will not be recruited to adult populations.

My findings indicate that neritic species *Auxis* spp. and *C. crysos* are distributed beyond the 40 m isobath, mainly in the northeast of the Yucatan shelf, and that their spawning period is limited to the summer months.

The agreement between the potential habitat predictions and the species distribution patterns found in the literature suggests these areas were adequately characterized and are likely suitable for the survival and growth of each species. Results from the dispersion experiments show that the size and spatial distribution of species-specific predicted habitats played a key role in dispersal patterns and connectivity between regions in the deep-water region of the GoM. Smaller habitats in the sBoC had less connectivity with the northwestern GoM in comparison with those that occupied the entire BoC.

Additionally, a higher level of LC intrusion and a low interaction between the northern GoM and the BoC yielded greater retention of particles in the BoC, in comparison with the opposite conditions, the limited intrusion of the LC into the GoM and high interaction between mesoscale features in the vicinity of the BoC.

Dispersion from areas in the central GoM, such as the potential habitat of the mesopelagic species *C. pauciradiatus*, was strongly influenced by the level of intrusion of the LC and the interaction between mesoscale features in the northern GoM and the BoC. While advection toward the shelf might lead to the loss of the larvae of oceanic species as they would be transported to unsuitable habitat for recruitment, retention close to the original habitat may increase survival.

A greater retention of *B. atlanticus* virtual larvae was observed north of the YS during low LC intrusion, which suggests that a retracted LC decreases connectivity with other regions of the northern GoM.

A high intrusion of the LC led to dispersal of virtual larvae and their transport through the Florida Straight to outside the GoM. These conditions could increase connectivity between the northeastern GoM and the northwestern Atlantic Ocean.

This research contributes to the understanding of the importance of coupling ocean circulation models with ecological models (such as species habitat predictions) to further understand larval dispersion patterns and connectivity of marine fishes.

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Auxis spp.							
Family: Tweedie(p=1.368)		Link function: log					
	edf	Ref.df	F	p-value			
s(Stratification):seasonT1	1.73	1.92	1.14	0.31			
s(Stratification):seasonT2	1.00	1.00	10.73	0.001173 **			
s(SST):seasonT1	2.22	2.61	1.87	0.079772 .			
s(SST):seasonT2	1.00	1.00	8.02	0.004867 **			
s(SSH):seasonT1	1.00	1.00	4.08	0.044395 *			
s(SSH):seasonT2	1.00	1.00	0.47	0.49			
s(Chl):seasonT1	1.55	1.80	4.37	0.019704 *			
s(Chl):seasonT2	1.91	1.99	7.72	0.000885 ***			
s(wind_speed):seasonT1	1.50	1.74	8.43	0.000450 ***			
s(wind_speed):seasonT2	1.91	1.99	13.00	3.15e-06 ***			
Signif. codes: 0 '***' 0.001 '**' 0.0	0.0 (** 0.0)5 '.' 0.1 '	''1				
R-sq.(adj) = 0.282 Deviance explained = 39.9%							
-REML = 462.25 Scale est. = 9.5799 n = 326							
Benthosema suborbitale							
Family: Tweedie(p=1.331)		Link function: log					
	edf	Ref.df	F	p-value			
s(Stratification):seasonT1	1.31	1.53	6.33	0.020863 *			
s(Stratification):seasonT2	1.85	1.97	4.03	0.030785 *			
s(S_mean_0_200):seasonT1	1.84	1.97	5.86	0.002496 **			
s(S_mean_0_200):seasonT2	1.67	1.88	0.83	0.37			
s(SST):seasonT1	1.87	1.98	8.54	0.000478 ***			
s(SST):seasonT2	1.84	1.97	3.47	0.026782 *			
s(Chl):seasonT1	1.00	1.00	0.35	0.56			
s(Chl):seasonT2	2.55	2.85	9.13	2.66e-05 ***			
s(wind_speed):seasonT1	1.51	1.75	4.70	0.008301 **			
s(wind_speed):seasonT2	1.52	1.76	5.37	0.004629 **			
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1							
R-sq.(adj) = 0.202 Deviance explained = 27.1%							
-REML = 942.19 Scale est. = 6.7079 n = 326							
Bregmaceros atlanticus							
Family: Tweedie(p=1.338)		Link function: log					
	edf	Ref.df	F	p-value			
s(Stratification):seasonT1	1.00	1.00	13.11	0.000341 ***			
s(Stratification):seasonT2	1.00	1.00	0.00	0.97			
s(SST):seasonT1	1.00	1.00	16.06	7.66e-05 ***			
s(SST):seasonT2	1.00	1.00	1.57	0.21			
s(Chl):seasonT1	1.00	1.00	10.31	0.001462 **			

Table 12. GAMs using season as a categorical variable and as a categorical smoothing term. Season I (April-July) in red and season II (August-October) in blue.

s(Chl):seasonT2	1.86	1.98	4.92	0.013589 *			
s(wind_speed):seasonT1	1.00	1.00	1.90	0.17			
s(wind_speed):seasonT2	2.58	2.85	4.26	0.005362 **			
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1							
R-sq.(adj) = 0.104 Deviance explained = 17.3%							
-REML = 724.99 Scale est. = 6.4673 n = 326							
Cubiceps pauciradiatus							
Family: Tweedie(p=1.335)		Link function: log					
	edf	Ref.df	F	p-value			
s(Stratification):seasonT1	2.35	2.67	4.40	0.00436 **			
s(Stratification):seasonT2	2.40	2.75	3.10	0.07599 .			
s(S_mean_0_200):seasonT1	1.92	1.99	5.69	0.00289 **			
s(S_mean_0_200):seasonT2	1.66	1.87	2.94	0.03616 *			
s(SST):seasonT1	1.00	1.00	10.76	0.00116 **			
s(SST):seasonT2	1.80	1.97	6.88	0.00082 ***			
s(SSH):seasonT1	1.22	1.39	8.02	0.00238 **			
s(SSH):seasonT2	1.00	1.00	3.76	0.05335.			
s(Chl):seasonT1	1.65	1.88	4.73	0.02040 *			
s(Chl):seasonT2	1.64	1.86	0.81	0.47094			
s(wind_speed):seasonT1	2.08	2.46	2.80	0.07786 .			
s(wind_speed):seasonT2	2.10	2.46	18.09	< 2e-16 ***			
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1							
R-sq.(adj) = 0.217 Deviance explained = 49.6%							
-REML = 635.89 Scale est. = 9.6242 n = 326							
Notolychnus valdiviae							
Family: Tweedie(p=1.375)		Link function: log					
	edf	Ref.df	F	p-value			
s(Stratification):seasonT1	1.00	1.00	7.99	0.00498 **			
s(Stratification):seasonT2	1.00	1.00	0.28	0.5961			
s(SST):seasonT1	2.79	2.96	3.93	0.01023 *			
s(SST):seasonT2	1.00	1.00	0.23	0.63153			
s(wind_speed):seasonT1	2.57	2.86	7.84	5.98e-05 ***			
s(wind_speed):seasonT2	1.17	1.31	3.39	0.07211.			
s(Lon, Lat)	12.75	17.16	4.27	< 2e-16 ***			
Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1							
R-sq.(adj) = 0.23 Deviance explained = 32.8%							
-REML = 1186.6 Scale est. = 5.3505 n = 326							



Figure 19. Response plots of the oceanographic variables' additive effect on the density of target species. Season I (April-July) in red and season II (August-October) in blue. Smoothed values represented by a continuous line, and shaded color indicates 95% confidence intervals.

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Figure 20. Response plots of the oceanographic variables' additive effect on the density of target species. Season I (April-July) in red and season II (August-October) in blue. Smoothed values represented by a continuous line, and shaded color indicates 95% confidence intervals.



Figure 21. Scatterplots of species standardized abundance and oceanographic variables in the GoM's deep-water region. Red (blue) colors represent season I: April-July (season II: August-October).



Figure 22. Scatterplots of species standardized abundance and oceanographic variables on the Yucatan Shelf. Red (blue) colors represent season I: April-July (season II: August-October).



Figure 23. Species-specific larval potential habitats. Predicted fish larvae densities. A: *Auxis* spp., B: *B. atlanticus*, C: *C. pauciradiatus* and D: *N. valdiviae*. The red bold line indicates areas within which predicted densities > 0.4 are found (PD > 0.4) and which were used for particle seeding in tracking experiments. Two potential habitat areas with PD > 0.4 were predicted for *B. atlanticus* in the deep-water region. Dotted, dashed and continuous lines represent the 40, 200 and 1000 m isobaths.