



El Colegio de la Frontera Sur

Uso diferencial de hábitats por larvas de peces en el río
Grijalva, Tabasco

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Dedicatoria

A mi hijo Ivo Alessandro
a mis padres José Francisco y Petrona

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Resumen

Se realizaron cuatro estudios en torno a la hipótesis de Beck y colaboradores acerca del concepto de área de crianza para juveniles de peces. El primero es la revisión de las ventajas y desventajas de dicho concepto, concluyendo que los principales retos para probar esta hipótesis son: 1) la determinación de los factores ambientales y temporales que influyen en la obtención de datos precisos y confiables y 2) la determinación simultánea de los parámetros poblacionales requeridos en la prueba de la hipótesis (densidad, crecimiento, sobrevivencia y movimiento de los juveniles hacia los hábitats ocupados por adultos). Para el primer reto, se evaluaron los factores que afectan la riqueza y abundancia de larvas y juveniles de peces en diferentes ambientes estuarinos con diferente complejidad estructural, encontrando que la temporada y la hora del día son los que contribuyen más a la variación de estos parámetros. Para el segundo reto, se realizaron dos estudios en los que se prueba si la tasa de crecimiento puede ser indicador del valor de un hábitat como área de crianza. El primero consistió en confrontar las tasas de crecimiento con las densidades y tasas de mortalidad en diferentes ambientes estuarinos donde ocurre la guabina *Gobiomorus dormitor*. Se comprobó que la tasa de crecimiento es un buen indicador de la función de un hábitat como área de crianza, señalando el manglar como la mejor área de crianza para esta especie. Finalmente, se analizó la estructura de tallas de larvas en diferentes ambientes estuarinos como aproximación del valor de los hábitats como áreas de crianza, asumiendo que mayores tallas estarán relacionadas con hábitats de mejor calidad. Sin embargo, este último estudio no arrojó pruebas conclusivas. Estos estudios constituyen una base sólida sobre la cual es posible hacer inferencias que permitan la identificación de áreas de crianza valiosas y por ende, contar con argumentos que den soporte a estrategias de manejo y conservación de los hábitats estuarinos.

Palabras clave: áreas de crianza, estadios tempranos de peces, larvas, juveniles, estuarios tropicales, crecimiento, calidad de hábitat.

Abstract

Four studies were conducted based on Beck et al. (2001) hypothesis about the nursery role concept. First is a review of the advantages and disadvantages of this concept, concluding that the main challenges to test the hypothesis are: 1) the identification of environmental and temporal factors influencing the attainment of accurate and reliable data, and 2) determining simultaneous population parameters required to the hypothesis testing (density, growth, survival and movement of juveniles into habitats occupied by adults). For the first challenge, the factors affecting the richness and abundance of early stages of fishes in diverse estuarine environments with different structural complexity were evaluated, finding the season and time of day are the ones that contribute most to the variation of these parameters. For the second challenge, two studies that tested whether the growth rate can be an indicator of the value of a habitat and breeding area were performed. The first was to confront the growth rates densities and mortality rates in different estuarine environments where bigmouth sleeper *Gobiomorus dormitor* occurs. It was found that the growth rate is a good indicator of the habitat quality as nursery, being mangroves the nursery ground for this species. Finally, the size structure of larvae was analyzed in several estuarine environments as proxy of habitats nursery value, assuming that larger sizes will be related to higher quality habitats. However, the latter study did not produce conclusive evidence about it. These studies provide a solid basis on which it is possible to identify nursery habitats and therefore to have arguments that support conservation and management strategies of estuarine habitats.

Keywords: nursery, fish early stages, larvae, juvenile, tropical estuaries, growth, habitat quality.

Introducción general

Las zonas estuarinas proveen diversos servicios ecosistémicos como producción de alimento, protección contra erosión, captura de carbono, además de que contribuyen substancialmente a mitigar los efectos del cambio climático (Costanza et al., 1997; Nagelkerken et al., 2013) siendo por ello zonas prioritarias de conservación (Sheridan y Hays, 2003; Krumme, 2009; Blaber, 2013). Los hábitats asociados a las zonas estuarinas como marismas, manglares, playas arenosas, arrecifes, y/o vegetación sumergida, presentan una alta productividad y constituyen refugios naturales de una gran diversidad de organismos acuáticos, especialmente en sus fases tempranas como larvas y juveniles, funcionando como áreas de crianza y reclutamiento de muchas especies de importancia ecológica y comercial (Nagelkerken, 2009; Blaber, 2013).

En un principio, todas las zonas estuarinas eran consideradas como áreas de crianza y no se hacía distinción en las posibles diferencias que podía haber en el papel como áreas de crianza de los diversos hábitats que ahí se encuentran. A raíz de la identificación de este mosaico de ambientes estuarinos, los hábitats estructuralmente más complejos dentro del estuario (manglares y vegetación acuática sumergida) empezaron a ser designados como áreas de crianza debido a las altas abundancias y diversidad de juveniles que podían sostener en comparación con áreas de menor complejidad estructural (Heck et al., 2003; Able, 2005). Sin embargo, el uso exclusivo de la abundancia y diversidad para designar un área de crianza, no es suficiente, pues, se ignoran importantes atributos poblacionales que pueden indicar la función de un cierto hábitat como área de crianza para una especie determinada. A partir de este

vacío de información y definiciones más específicas para designar un área de crianza, Beck et al. (2001) proponen una hipótesis que trata de integrar estos atributos poblacionales al concepto de área de crianza: “un hábitat se considera área de crianza para juveniles de una especie si su contribución por unidad de área para la producción de individuos que se reclutan a las poblaciones adultas es mayor, en promedio, que la producción proveniente de otros hábitats ocupados por los juveniles”.

Para poder probar esta hipótesis es necesario determinar una serie de parámetros poblacionales como la densidad, tasa de crecimiento, sobrevivencia, y especialmente el movimiento de los juveniles de una especie hacia los hábitats ocupados por los adultos, en otras palabras la contribución relativa de reclutas de un determinado hábitat o área a las poblaciones adultas. Debido a la inherente complejidad para poder designar un área de crianza y sus parámetros asociados, la hipótesis de Beck resulta atractiva, pero al mismo tiempo difícil de probar. Sin embargo, esta hipótesis es la que mejor ha integrado los atributos que soportan el concepto de área de crianza, por lo que resulta indispensable su mención y aplicación en cualquier trabajo que pretenda demostrar la importancia de un hábitat o ambiente como área de crianza.

La hipótesis de Beck y colaboradores fue generada a partir de estudios en juveniles de peces. No obstante, es importante destacar que sus reglas y parámetros también pueden ser aplicados en otra parte importante del ciclo de vida de los peces, como es el estadio larvario, ya que de esta fase depende tanto la sobrevivencia de juveniles como el aporte de reclutas a las poblaciones adultas (Rose et al., 2001; James et al., 2003; Koenig et al., 2007; Houde, 2008).

Dado que la mayoría de estudios sobre áreas de crianza y de ecología de larvas en general han sido realizados en zonas subtropicales, donde la estacionalidad es muy

marcada (e.g. Heck et al., 2003; Le Pape et al., 2003; Sheridan y Hays, 2003; Vasconcelos et al., 2011), el estudio de este concepto en áreas tropicales resulta de gran relevancia, debido a que estas áreas albergan una mayor diversidad de especies y hábitats, en los que la influencia de factores ambientales propios de la región, como los cambios en los niveles y flujos de los ríos agregan mayores diferencias en el funcionamiento de estas zonas como áreas de crianza.

Basada en lo anterior, el objetivo general de esta investigación es determinar la importancia de los diferentes hábitats presentes en las zonas estuarinas tropicales (playas arenosas, manglares, río y vegetación acuática sumergida) como áreas de crianza para larvas y juveniles de peces. Para lograr dicho objetivo se eligió como área experimental a la Reserva de la Biosfera Pantanos de Centla (RBPC) y la zona costera adyacente (desembocaduras de los ríos Grijalva y San Pedro y San Pablo), debido a la diversidad de ambientes que presenta, incluyendo zonas con influencia marina y de agua dulce, lagunas costeras, manglares, zonas inundables y zonas con vegetación acuática sumergida. Debido a esto resulta un escenario ideal para la prueba de hipótesis relacionadas con la ecología de estadios tempranos en peces. A pesar de ser un área sobresaliente por su diversidad de hábitats y recursos bióticos y que está incluida dentro de un área natural protegida, el conocimiento de las larvas y juveniles de peces y aún de sus estadios adultos es muy limitado (e.g. Macossay-Cortez et al., 2011; Arévalo-Frías y Mendoza-Carranza, 2012; Sánchez et al., 2012).

De acuerdo a la problemática expuesta, el presente estudio se ha dividido en cuatro temas. El primero es una revisión crítica del concepto de las áreas de crianza en peces, abordando las ventajas y problemática que existe alrededor de los supuestos de esta hipótesis y sus limitaciones al aplicar dicho concepto en ambientes ecológicamente

dinámicos y en diversas escalas de tiempo. Esta revisión crítica da por resultado de que a pesar de las dificultades inherentes para aplicar la hipótesis de Beck, esta es a la fecha la que mejor integra en sus parámetros dicho concepto.

Debido a que la determinación de riqueza y abundancia de especies depende tanto del método de muestreo como su interacción con factores ambientales (hábitats) y temporales (ciclos circadianos, lunares, estaciones), la designación de un hábitat como área de crianza dependerá directamente del diseño muestral que se aplique y especialmente de los factores que se pueden considerar en dicho diseño, por lo que el objetivo del segundo capítulo de este trabajo fue la determinación de los factores que influyen en la riqueza y abundancia de larvas en diversos hábitats estuarinos. El diseño experimental fue basado en un muestreo jerárquico en diferentes escalas espaciales y temporales, incluyendo las principales fuentes de variación que actúan sobre la riqueza y abundancia de larvas planctónicas de peces (hábitat, temporada, fases lunares, y hora del día). El resultado más relevante de esta investigación se resume en que los dos factores que más afectan la riqueza y abundancia de larvas de peces son la estacionalidad y la hora del día. Pudiéndose concluir que la mayor riqueza y abundancia de especies está relacionada con épocas de secas durante muestreos nocturnos.

Siguiendo con los parámetros requeridos para identificar áreas de crianza, se incluyen dos estudios más. Por lo que en el Capítulo III, y debido a que uno de los factores fundamentales para la sobrevivencia en etapas tempranas es la velocidad de crecimiento (para evitar depredadores y competencia), se propuso probar la hipótesis de que la tasa de crecimiento puede ser un indicador de la calidad de los hábitats y por ende, del papel que tienen como áreas de crianza, confrontando las tasas de

crecimiento con la densidad y mortalidad de larvas y juveniles de guabina *Gobiomorus dormitor* Lacepède, 1800, en diferentes ambientes estuarinos. A través de este experimento de campo se pudo probar que las relaciones teóricas propuestas *a priori* por varios autores (Rose et al., 2001; Minello et al., 2003; Dower et al., 2009) se cumplen siendo que las mayores velocidades de crecimiento estuvieron relacionadas con densidades relativamente bajas y baja mortalidad, encontrando que la mejor área de crianza para la guabina se encuentra ubicada en el hábitat de manglar en el río Grijalva. Cabe mencionar que esto también abre la posibilidad de cuestionar si el concepto de área de crianza puede ser aplicado a nivel de comunidad o bien tiene que ser definido en forma específica.

Basado en la hipótesis anterior, acerca de la maximización de las tasas de sobrevivencia relacionadas con una mayor velocidad y talla de crecimiento, e indicando indirectamente una calidad de hábitat más alta y por tanto con áreas de reclutamiento adecuadas, en el capítulo IV, se presenta un análisis global de la estructura de tallas de larvas de peces para determinar cómo los diferentes hábitats muestreados (playas arenosas, manglares, río y vegetación acuática sumergida) actúan diferencialmente como áreas de crianza. El principal resultado de esta investigación fue que la estructura de tallas junto con la abundancia de cada especie ofrece una primera aproximación del valor de los hábitats como áreas de crianza. En este caso y agrupando las especies por río, se encontró que en el Grijalva ocurren larvas de mayor tamaño en comparación con el río San Pedro, sin embargo no se obtuvieron resultados concluyentes sobre la hipótesis planteada.

En forma global el presente trabajo es fundamental para entender el funcionamiento de los hábitats estuarinos como áreas de crianza, resultando un insumo

indispensable para definir estrategias de conservación y protección de los recursos acuáticos en áreas estuarinas tropicales.

Capítulo I. Revisión crítica del concepto de las áreas de crianza en peces

Introducción

Históricamente, el concepto de área de crianza se ha aplicado a peces e invertebrados con ciclos de vida complejos en los que las larvas se transportan a los estuarios, se transforman, crecen hasta ser subadultos y se mueven hacia los hábitats de los adultos (Beck et al., 2001). Este concepto originalmente proponía que todo el estuario cumplía con la función de zona de crianza y reclutamiento de larvas y juveniles para diversas especies de peces y crustáceos. Posteriormente, hábitats específicos y de alta complejidad estructural dentro de la zona estuarina (zonas de manglar y vegetación sumergida) empezaron a ser referidos como áreas de crianza debido a las altas abundancias de juveniles que potencialmente podían sostener (Heck et al., 2003; Able, 2005).

Desde su primera mención, el concepto de áreas de crianza ha sido utilizado indiscriminadamente dificultando la identificación de hábitats de crianza potencialmente valiosos (Beck et al., 2003b). Con base en este concepto, la importancia de algunos hábitats ha sido sobreestimada (e.g. vegetación sumergida, cuyo valor como área de crianza puede variar geográficamente), ignorando otros hábitats que pueden estar cumpliendo esta función, por ejemplo, los fondos arenosos (Beck et al., 2003b; Gratwicke et al., 2006).

Basados en esta controversia, Beck et al. (2001) proponen una definición y una hipótesis que ayude a la identificación de un área de crianza, definiéndola como un hábitat cuya contribución por unidad de área para el reclutamiento a las poblaciones adultas es mayor, en promedio, que la producción proveniente de otros hábitats

ocupados por los juveniles. Para determinar si un hábitat está cumpliendo la función de área de crianza ellos mencionan que es necesario tomar en cuenta los procesos o atributos ecológicos que operan en las áreas de crianza, como lo son la densidad, crecimiento, sobrevivencia y movimientos de los juveniles hacia los hábitats ocupados por los adultos; estos al ser comparados con otros hábitats deben aportar una mayor contribución al reclutamiento de adultos (Beck et al., 2001).

El desarrollo de la hipótesis de Beck et al. (2001) surge de la necesidad de enfocar esfuerzos y recursos en investigación, conservación, restauración y manejo, a través de un marco de trabajo que permita la identificación de áreas de crianza prioritarias. A este respecto (Brown, 2006), menciona que la identificación del área de crianza es relevante para comprender la función ecológica de diferentes hábitats empleados por los juveniles y para el manejo de poblaciones de peces explotadas y recursos costeros. Debido a la importancia en la conservación de recursos naturales que conlleva la determinación de áreas prioritarias y teniendo hasta el momento los conceptos de Beck et al. (2001) como base para esto, el objetivo del presente estudio es hacer una revisión de dicho concepto, discutiendo acerca de sus implicaciones tanto en aspectos metodológicos y especialmente enfatizando las capacidades que existen para aplicar ese concepto.

Determinación de áreas de crianza después de Beck et al. 2001.

Para probar la hipótesis de Beck et al. (2001) es necesario determinar la densidad, crecimiento, sobrevivencia y el movimiento de los juveniles hacia los hábitats que ocupan como adultos. La hipótesis se tiene que probar a nivel específico y la

especie objetivo debe cumplir con el requerimiento de ocupar hábitats diferentes en sus etapas juvenil y adulta. Sin embargo, no se da una explicación clara de este requerimiento o a que escala se debe de aplicar.

Una vez establecida la hipótesis de Beck et al. (2001), se esperaría que las investigaciones posteriores incorporaran los criterios propuestos, pero a la fecha, pocos trabajos lo han hecho. La tabla 1 muestra estudios en los que se identifica y evalúa la función de área de crianza, algunos señalan indicadores alternativos para identificar un área de crianza como son, las variables fisicoquímicas presentes en el área de mayor abundancia de juveniles de la especie, *e.g.* zona de máxima turbidez, abundancia de presas para larvas de peces, abundancia y riqueza de especies y la ausencia de depredadores. El estudio más completo a la fecha es el de (Vasconcelos et al., 2011) quienes presentan una evaluación de la función de áreas de crianza estuarinas para cuatro especies de importancia comercial. En este estudio los autores manejan los cuatro parámetros requeridos para indicar el valor del área de crianza, contrastando a su vez, el concepto de área de crianza y el de hábitat esencial para juveniles (Tabla 1).

Destacan también los trabajos de revisión del concepto que han compilado datos sobre densidad, crecimiento y sobrevivencia (*e.g.* Heck et al., 2003; Minello et al., 2003; Stoner, 2003; Gillanders, 2006). Sin embargo, estas revisiones sólo ofrecen detalles generales de los criterios empleados para la selección de los estudios incluidos en el análisis, incurriendo en la simplificación de detalles metodológicos importantes que podrían implicar errores o sesgos en la estimación de los parámetros medidos. Nagelkerken (2009) hace una evaluación crítica de la información que se ha generado con respecto a los manglares y vegetación acuática sumergida, y su valor como área de

crianza, basado en los parámetros establecidos por Beck et al. (2001). Además de esto, el autor incluye los procesos subyacentes que han derivado en paradigmas relacionados con el valor del área de crianza como son las hipótesis sobre la disponibilidad de alimento, riesgo de depredación, turbidez, heterogeneidad estructural del hábitat. Esto incrementa aún más la complejidad del concepto de área de crianza.

Tabla 1. Estudios realizados para la identificación y evaluación de áreas de crianza para peces.

Atributos determinados	Autor(es) y año	Especie objetivo	Hábitats evaluados	Resultados
No consideran la hipótesis de Beck et al. (2001) Abundancia de juveniles	Dulic et al. (2005)	Diversas especies	Aguas someras de hábitats con vegetación, fondos rocosos y fondos arenosos	Las áreas con sedimentos suaves sirven como áreas de crianza o refugio para especies de peces residentes y vicarias
	Pikitch et al. (2005)	Elasmobranchios	Arrecife y lagunas someras y profundas	El arrecife es empleado como zona de alumbramiento y de crianza
	Díaz-Ruiz et al. (2006)	Diversas especies	Lagunas rodeadas por pantanos de manglar, vegetación emergente y vegetación sumergida	Los juveniles emplean las zonas con vegetación sumergida como áreas de crianza y protección en condiciones de salinidad y temperatura bajas
	Franco et al. (2006)	Diversas especies	Hábitats con vegetación y sin vegetación	Hábitats con vegetación sumergida con diferente valor como área de crianza, variación latitudinal
	Gratwicke et al. (2006)	Diversas especies	Aguas someras con fondos rocosos, arenosos, con algas, con corales y manglares	Las zonas de lagunas son ocupadas por los juveniles como áreas de crianza
	Hajisamae et al. (2006)	Diversas especies	Manglares con fondos lodosos, y fondos cubiertos con cuatro distintas especies de pastos marinos	Uso preferencial de ciertos hábitats por algunas especies, mientras que otras ocupan todo el estuario. Detección de periodos de reclutamiento
	Pease et al. (2006)	Diversas especies	Márgen del canal principal del río, márgenes en canales laterales, lagunas aisladas	Las áreas de flujo lento en las zonas de inundación provee de importantes áreas de crianza para peces
	Félix et al. (2007)	Diversas especies	Playas arenosas	Asumen que las playas arenosas juegan el papel de áreas de crianza debido a que el 98% de los peces capturados fueron juveniles
	Martinho et al. (2007)	<i>Dicentrarchus labrax</i> <i>Platichthys flesus</i> <i>Solea solea</i>	Canales con diferentes características hidrológicas dentro del estuario	Uso diferencial del hábitat, los individuos de menor edad fueron más abundantes en las zonas de menor salinidad en el estuario
	Arceo-Carranza et al. (2010)	Diversas especies	Fondo con vegetación y fondo sin vegetación	La vegetación sumergida soporta un mayor número de especies, proveyendo alimento y protección
	Espino et al. (2011)	Diversas especies	Praderas de pastos marinos	Los prados de <i>Cymodocea nodosa</i> constituyen áreas de crianza en primavera y verano para juveniles de muchas especies entre ellas algunas de importancia comercial

Atributos determinados	Autor(es) y año	Especie objetivo	Hábitats evaluados	Resultados
Abundancia de juveniles	Rodríguez-Romero et al. (2011)	Diversas especies	Laguna costera rodeada por manglar	Mayor riqueza de especies en la temporada cálida, la mayor diversidad y riqueza de especies se obtuvo en la zona sur de la laguna costera. El tamaño de los peces confirma su papel como área de crianza
Abundancia de larvas y juveniles	Fujita et al. (2002)	Diversas especies	Aguas someras en las márgenes del estuario en zonas con vegetación y sin vegetación	Los fondos con vegetación sumergida sirven como áreas de crianza para peces costeros y eurihalinos
	Oliveira y Ferreira (2008)	Diversas especies	Playas, canales y canales lagunares	Identificación de áreas de desove y crianza para pimeióidos, esciéndidos y engráulidos con base en las altas abundancias de sus estadios tempranos
	Yagi et al. (2011)	Diversas especies	Aguas salobre marinas y agua dulce en tres estuarios	La alta abundancia de larvas y juveniles en aguas con mayor turbidez y menor salinidad indica el uso de la zona superior de los estuarios como área de crianza
Abundancia de larvas	Primo et al. (2013)	<i>Platichthys flesus</i> , <i>Solea solea</i> y <i>Solea senegalensis</i>	Zonas costeras del estuario y aguas interiores del estuario	Señala el uso diferencial de áreas dentro del estuario por las especies estudiadas y atribuyen las altas densidades de larvas y juveniles a la función de área de crianza
Abundancia de huevos y larvas	Mwaluma et al. (2011)	Diversas especies	Parques marinos en arrecifes	Relación positiva entre la abundancia de larvas y la abundancia de zooplankton y la temperatura
	Ooi y Chong (2011)	Diversas especies	Manglar y aguas costeras adyacentes	La salinidad, turbidez y el alimento, son los principales factores que estructuran la composición de especies
	Bustos et al. (2008)	<i>Engraulis ringens</i>	Mar interior de Chile austral y fiordos	Columnas de agua más estables
	Vacchi et al. (2012)	<i>Pleuragramma antarcticum</i>	Estuarios glaciares	Las altas abundancias de huevos y larvas recién eclosionadas en los embalses de los estuarios indican la importancia de la zona como área de crianza
Turbidez en el área de mayor abundancia de juveniles	Jaureguizar et al. (2003)	<i>Microgogonias furnieri</i>	Zona superior, media y baja del estuario	Distribución diferencial de clases de edad en el estuario, relacionada con los factores físicoquímicos. Clases de edad más jóvenes relacionadas con zonas de mayor turbidez

No consideran la hipótesis de Beck et al. (2011)

Atributos determinados	Autor(es) y año	Especie objetivo	Hábitats evaluados	Resultados
No consideran la hipótesis de Beck et al. (2001)	King (2004)	Diversas especies	Zonas de flujo lento y de flujo rápido en el canal principal del río	Asumen que las altas concentraciones de presas para larvas y peces pueden definir el potencial de un hábitat como área de crianza. Sus resultados no son concluyentes
	Courrat et al. (2009)	Diversas especies	Zonas de embalses a lo largo de la línea de costa	El impacto antropogénico afecta la función de área de crianza de los estuarios usando como indicador la abundancia de juveniles de especies migrantes marinas
	Horinouchi et al. (2012)	Diversas especies	Vegetación acuática sumergida (VAS)	Pocos piscivoros presentes en la zonas de VAS sugieren la importancia de este hábitat como área de crianza
	Ross (2003)	<i>Leiostomus xanthurus</i> <i>Micropogonias undulatus</i>	Estuario superior, medio e inferior	El área que presentó el crecimiento más alto y la menor mortalidad en ambas especies es la zona superior del estuario por lo que se señala como área de crianza
	Koenig et al. (2007)	<i>Epinephelus itajara</i>	Manglares de litoral, río y bahías poco profundas	Los factores fisicoquímicos (salinidad, oxígeno disuelto y otras variables de la calidad del agua afectan la aptitud de los manglares como área de crianza del mero
	Pasquaud et al. (2012)	Diversas especies	Estuario superior, medio e inferior	Organización espacial del estuario, los estadios larvarios ocupan la zona superior del estuario y los juveniles la zona media.
	Woodland et al. (2012)	Diversas especies	Zonas oligohalinas y polihalinas del estuario	Uso diferencial de las zonas del estuario de acuerdo con la historia de vida y requerimientos de las especies. Las tasas de crecimiento no difieren en los hábitats estudiados. El estuario en toda su extensión funciona como área de crianza.
	Able et al. (2011)	Diversas especies	Aguas interiores y zona estuarina adyacente	Uso diferencial de las zonas del estuario, los estadios más tempranos ocupan la zona superior del estuario y los juveniles la zona media. Conectividad entre los hábitats de aguas interiores y el estuario adyacente
Si consideran la hipótesis de Beck et al. (2001)	Vasconcelos et al. (2011)	<i>Solea solea</i> <i>Solea senegalensis</i> <i>Platichthys flesus</i> <i>Dicentrarchus labrax</i>	Zona estuarina y línea de costa	Identificación de las áreas de crianza de mejor calidad para lenguados de importancia comercial

Áreas de crianza y conceptos derivados

Los requerimientos para probar la hipótesis de Beck et al. (2001) conllevan una alta inversión en términos económicos, de tiempo y esfuerzo, siendo frecuentemente imposible establecer límites claros para las áreas de crianza de muchas especies. Levin y Stunz (2005) señalan que es preciso indicar la etapa en la que la especie es más vulnerable, debido a que todas las fases del desarrollo tienen su contribución a la población adulta. Para probar esto, ellos proponen un enfoque basado en tres pasos: 1) el desarrollo de modelos estructurados por edad e identificar las etapas sensibles de su historia de vida, 2) determinar cuáles hábitats, si es que los hay, son importantes para estas etapas y 3) identificar como importantes los sitios en los cuales las etapas más críticas ocurren en altas densidades. El enfoque propuesto por los autores es enriquecedor al arrojar cierta luz sobre las consideraciones que deben hacerse para incidir en la recuperación de las poblaciones basados en una etapa del ciclo de vida y en el hábitat esencial para asegurar la protección de dicha etapa. Sin embargo, los análisis realizados por ellos contienen supuestos que deben ser tomados con precaución para una posible aplicación del enfoque propuesto. Por ejemplo, la población modelo utilizada no está limitada por el reclutamiento, no incluyen densidad-dependencia, ni consideran los efectos de un cambio en el valor del hábitat en las demás etapas de la historia de vida de la especie, además de asumir que se trata de una población cerrada (Levin y Stunz, 2005).

Dentro de los supuestos de la hipótesis de Beck et al. (2001), los autores mencionan que, habrá excepciones en las que hábitats con baja densidad, bajo crecimiento y baja sobrevivencia sean hábitats importantes para juveniles, solamente porque ocupan un área extensa; indicando que no por ello son áreas de crianza *per se*.

Por el contrario, Dahlgren et al. (2006) indican que un hábitat es importante cuando contribuye con una proporción mayor de juveniles de una especie en particular, sin importar el área cubierta, esto es el hábitat juvenil esencial (HJE). Este concepto, al igual que el de área de crianza, tiene utilidad en la identificación de hábitats para conservación, restauración y manejo. Los autores enfatizan su importancia enfocada al manejo de recursos marinos (e.g. protección de los hábitats juveniles contra amenazas como, capturas incidentales y problemas de calidad de agua) (Dahlgren et al., 2006). Sheaves et al. (2006) hacen una evaluación crítica del concepto de áreas de crianza y HJE. Los autores concluyen que, debido al enfoque generalista del concepto de HJE, el sistema de clasificación de Dahlgren et al. (2006) no ofrece información que ayude a tomar decisiones de conservación y manejo. Sheaves et al. (2006) abunda en que los conceptos de HJE están dirigidos a la protección de recursos pesqueros ignorando el valor ecológico y evolutivo de estas áreas y los procesos que ocurren en ellas. A pesar que Sheaves et al. (2006) se enfocan en criticar el concepto de HJE, se puede considerar que esta crítica también es aplicable al concepto de Beck et al. (2001).

Heupel et al. (2007) reconocen que el concepto de área de crianza de Beck et al. (2001) es difícil de aplicar y hacen una revisión histórica del concepto de áreas de crianza para tiburones. A fin de identificar más fácilmente si una zona califica como área de crianza, ellos proponen tres criterios primarios para los juveniles del año: 1) que los tiburones se encuentran comúnmente y en mayor número en éstas áreas que en otras, 2) que los tiburones tienen una tendencia a permanecer o regresar por extensos periodos de tiempo y 3) que el área es repetidamente utilizada a través de los años. De acuerdo con estos criterios Norton et al. (2012) identifican hábitats críticos para la protección de *Pristis pectinata* en Florida. Aunque los datos fueron insuficientes para

cumplir con el segundo criterio de Heupel et al. (2007) consideran que el cumplimiento de los criterios restantes es un argumento suficiente para la protección de las áreas señaladas. Así como los criterios de Beck et al. (2001) los criterios propuestos por Heupel et al. (2007) son difíciles de probar en escalas cortas de tiempo y con muestreos de escala geográfica reducida y difícilmente se podría concluir que ciertas áreas son áreas de crianza, si no se comparan éstas con grandes áreas adyacentes. De esta forma, en la mayoría de los intentos de probar si un área es de crianza, generalmente se recurre a argumentos incompletos, precisamente por la dificultad que conlleva probar todas las hipótesis planteadas.

Consideraciones particulares sobre la hipótesis de Beck et al. (2001).

Conocimiento de la historia de vida de las especies

Un factor importante en la prueba de la hipótesis de áreas de crianza, es el conocimiento de la historia de vida de la especie. Si conocemos la historia de vida podemos discriminar las especies que si cumplen con el requisito de ocupar diferentes hábitats en su etapa juvenil y adulta. Si no la conocemos, es preciso dedicar más tiempo y esfuerzo para determinarla. Desafortunadamente, se desconoce el ciclo de vida completo de la mayoría de las especies, principalmente aquellas que no poseen importancia comercial (Able, 2005).

Esto es cierto para las especies que ocurren en la zonas estuarinas de la costa de Tabasco, ya que las especies que cuentan con mayor información acerca de su historia de vida son, *Centropomus undecimalis*, *Bagre marinus*, *Mugil curema*, *Mugil cephalus*, *Megalops atlanticus*, *Microponias undulatus*, *Gobiomorus dormitor* y

Dormitator maculatus. Del resto de las especies de importancia comercial sólo se conocen generalidades de su historia de vida por complejos de especies, tales como lo son, cíclidos, carángidos, y esciénidos.

Adicionalmente, la hipótesis de áreas de crianza tiene su aplicación en especies con ciclos de vida complejos (Beck et al., 2001). Estos ciclos incluyen movimientos como migración parcial, diadromía, catadromía, anadromía (McDowall, 2008). Aunque se conocen los patrones generales de migración de muchas especies, la dinámica de las migraciones no se conoce por completo (Albert, 2003). En algunos casos, puede haber una clasificación errónea o generalización excesiva de dichos patrones, por ejemplo, *G. dormitor*, *M. cephalus* y *M. curema*, han sido anteriormente clasificadas como catádromas, siendo que su comportamiento migratorio es más bien facultativo (Nordlie, 2011; Ibáñez et al., 2012). El uso alternativo de hábitats en diferentes temporadas agrega un grado más de complejidad en la identificación del área de crianza, como es el caso de *M. cephalus* y *M. curema* (Ibáñez et al., 2012).

Diseño del muestreo

El diseño del muestreo es fundamental para la determinación de la importancia de los hábitats como áreas de crianza. El diseño debe incluir todos los hábitats en los que los juveniles de la especie objetivo se distribuyen y debe a su vez, incorporar las posibles fuentes de variación que pueden afectar la densidad de la especie (e.g. variación nictemeral, fases lunares, variaciones estacionales e interanuales). Por último, es primordial que las metodologías de muestreo sean estandarizadas, i.e. horarios, equipo de colecta, para minimizar errores de medición. Para la identificación de áreas de crianza, es preciso que se realicen monitoreos continuos, para incluir el posible uso

alternativo de hábitats y la variabilidad en el reclutamiento de las especies a lo largo del tiempo. Como ya se discutió en secciones anteriores la mayoría de los trabajos basan sus conclusiones en diseños muestrales incompletos.

Movimiento de juveniles hacia los hábitats de adultos

Muy pocos estudios incluyen el movimiento de los juveniles hacia los hábitats adultos (e.g. Kraus y Secor, 2005; Vasconcelos et al., 2008; Vasconcelos et al., 2011) a través del uso de marcas químicas en otolitos de adultos para identificar dónde pasaron su etapa juvenil. Esta técnica es útil para el marcaje de individuos y determinar el hábitat de origen de los mismos de una manera general. Sin embargo, no puede emplearse para medir la contribución de los hábitats juveniles a los hábitats adultos.

El movimiento de los juveniles a hábitats de adultos es el más difícil de medir de los cuatro factores considerados (Sheaves et al., 2006; Vasconcelos et al., 2011). Paradójicamente, dicho factor es el más importante puesto que exhibe el éxito de un hábitat como área de crianza, pues es precisamente el que podrá señalar la contribución de cierta área a la dotación de organismos adultos. A pesar de todos los esfuerzos hechos hasta la fecha este proceso, aún no ha podido ser medido de manera directa (Caley et al., 1996).

Se han llevado a cabo análisis sensibles y modelos de simulación para medir dicha contribución pero los resultados sólo brindan inferencias y predicciones que deben tomarse con precaución pues en general los supuestos son difíciles de cumplir en realidad (Caley et al., 1996; Halpern et al., 2005). Los modelos generados con el objetivo de medir la contribución de las áreas de crianza a las poblaciones adultas

deben tomar en consideración los mecanismos independientes y dependientes de la densidad que actúan sobre la variabilidad del reclutamiento (Martinho et al., 2012).

Consideraciones subyacentes al concepto de áreas de crianza

El área de crianza para una especie se presenta como un concepto cuyo valor es fijo, tanto espacial como temporalmente e intentando establecer límites geográficos relacionados a diferentes hábitats. Un área de crianza debe concebirse como un paisaje dinámico, que alberga un mosaico de hábitats que una especie puede emplear en una misma etapa de su ciclo de vida o teniendo cambios de acuerdo a los requerimientos ontogénicos de sus poblaciones.

Proteger un “área de crianza” *sensu* Beck et al. (2001) ignora el hecho de que muchas veces el mosaico de hábitats contribuye más al valor del área de crianza, pues se aumentan las posibilidades de los juveniles de reclutarse a diversos hábitats, en vez de pensar en proteger solo el área que aparentemente y en un momento determinado tiene las supuestas características de un área de crianza (Sheaves et al., 2006). El enfoque no debe limitarse a la protección de hábitats en los que ocurren las especies, también deben protegerse los procesos ecológicos que permiten a las poblaciones persistir y que muchos de los cuales se encuentran fuera del área misma (Levin y Stunz, 2005). Por tanto, el área de crianza debe entenderse como un proceso dinámico relacionado con las historias de vida de las especies y los mecanismos que han desarrollado para hacer frente a los cambios ambientales y a condiciones adversas para su mantenimiento a lo largo del tiempo.

El uso de hábitats puede variar entre cohortes, agregando complejidad a la identificación de áreas de crianza (Dahlgren et al., 2006; Sheaves et al., 2006; Able et al., 2012). Por ejemplo, las especies de peces que tienen alta fecundidad, baja sobrevivencia en estadios tempranos y traslape de generaciones de adultos, por lo general, exhiben clases de edad abundantes y poco frecuentes (Winemiller y Rose, 1992; Kraus y Secor, 2005), por lo tanto, su ocurrencia y abundancia presentará variación interanual dificultando la identificación de sus áreas de crianza.

Diversos factores pueden hacer que el valor de un área de crianza varíe a lo largo del tiempo y en el espacio, por ejemplo, debido a cambios en el régimen hidrológico de los estuarios, sequías y lluvias extremas, inundaciones, inclusive el incremento en el nivel medio del mar, entre otros. De acuerdo con esto, el tercer criterio de Heupel et al. (2007), *el área es repetidamente utilizada a través de los años*, es rebatible, siendo que si las condiciones ideales de estas áreas han cambiado, su potencial como áreas de crianza disminuirá, teniendo un valor más bajo que las áreas que fueron designadas como áreas de crianza.

El objetivo de ambos conceptos (Beck et al., 2001 y Heupel et al., 2007) es identificar áreas de crianza, pero no consideran que ese valor puede variar a lo largo de tiempo y por tanto no proponen la medición constante de su valor o su revalidación. Así mismo, ambas hipótesis sólo pueden ser probadas en términos de comparaciones. Los datos derivados de muestreos puntuales, difícilmente contienen todos los elementos que proponen Beck et al. (2001), y tampoco cumplen los criterios de Heupel et al. (2007), quienes enfatizan la facilidad de su aplicación.

Áreas de crianza y protección de recursos acuáticos

La encomienda impuesta por el acta de manejo y conservación pesquera Magnuson-Stevens (NOAA, 1996) de identificar el hábitat esencial para peces, es decir, “aquellas aguas o sustrato necesario para que los peces se reproduzcan, críen, alimenten y/o crezcan hasta alcanzar la madurez”, resulta en la designación de grandes extensiones de aguas estuarinas y marinas (Levin y Stunz, 2005), dificultando el establecimiento de áreas marinas protegidas (Kinney y Simpfendorfer, 2009). De ahí la necesidad de identificar áreas prioritarias a proteger para el mantenimiento y/o la recuperación de recursos acuáticos, objetivo principal de la designación de áreas de crianza. Sin embargo, la protección de los recursos acuáticos basada en la conservación de áreas de crianza no puede tomarse como la única acción que conducirá a la sostenibilidad de las poblaciones, en este caso, de peces. Si el recurso, además de ser afectado en sus etapas tempranas de vida, es objeto de explotación, los esfuerzos de protección deben dirigirse de manera conjunta hacia la conservación de áreas de crianza así como hacia medidas de manejo pesquero que protejan a los reproductores y reclutas.

La pertinencia de la aplicación del concepto de áreas de crianza, ya sea para el establecimiento de áreas marinas protegidas, para asegurar la recuperación de las poblaciones, o para la sobrevivencia de las mismas, debe ser analizada con base en la historia de vida de las especies. Kinney y Simpfendorfer (2009), en su revisión sobre áreas de crianza enfatizan que, el efecto positivo de la protección de áreas de crianza sólo sea para especies con ciclos de vida cortos y que, en el caso de los tiburones, este enfoque no beneficiaría las clases de edad más importantes (subadultos y adultos) en términos de estabilidad y recuperación de la población. Esto se debe a que cualquier

remoción de la población reproductora tiene un efecto proporcionalmente mayor y más duradero sobre el tamaño de la población que el que tendría una remoción similar en una población de teleósteos (Kinney y Simpfendorfer, 2009). Esta afirmación subestima la gran variedad de historias de vida que presentan los teleósteos, ya que los efectos serían en una especie de teleósteo muy longeva con madurez tardía y reclutamiento esporádico, como en el caso de epinefélidos y escorpénidos (Winemiller y Rose, 1992; Sadovy, 2001). Además, aunque un reclutamiento bajo no contribuya al colapso de la población, la poca abundancia de reclutas en años específicos puede tener un efecto inhibitorio al grado en que las poblaciones no pueden recuperarse (Myers et al., 1997).

Las estrategias de conservación y manejo deben enfocarse a todas las etapas del ciclo de vida de las especies, ya que la contribución de cada una de ellas depende de manera directa de la contribución de la etapa precedente. Aun cuando no se ha podido medir directamente la contribución del reclutamiento en la tasa intrínseca de crecimiento de una población, debe considerarse el efecto compensatorio de los mecanismos denso-dependientes (Rose et al., 2001) y la variabilidad de la importancia de los hábitats juveniles en el mantenimiento de las poblaciones en función del grado de explotación de los adultos (Halpern et al., 2005). En algunos casos, como en el de *Carcharhinus obscurus* y *Carcharhinus plumbeus* es urgente el desarrollo de medidas alternativas de manejo pesquero debido al decremento de sus poblaciones (McAuley et al., 2007, Romine et al., 2009).

Estudio de caso: Reserva de la Biosfera Pantanos de Centla (RBPC)

Con base en las mayores abundancias y la amplia ocurrencia espacial y temporal de *Gobiomorus dormitor* Lacepède, 1800 (catádrroma); *Elops saurus* Linnaeus, 1766 (anádroma), y una *Achirus lineatus* Linnaeus, 1758 (estuarino-residente) en la RBPC (Arévalo-Frías y Mendoza-Carranza, 2012), se planteó la prueba de hipótesis de las áreas de crianza de Beck et al. (2001) empleando tres de los cuatro atributos ecológicos que operan en las áreas de crianza: densidad, crecimiento y mortalidad de larvas y juveniles de las especies antes mencionadas.

Así mismo, fueron tomados en cuenta las posibles fuentes de variación de la densidad de larvas y juveniles y se diseñó un muestreo que incluyera diferentes hábitats (costa, manglar, río y vegetación acuática sumergida), diferentes temporadas (secas y lluvias), fases lunares (luna nueva, cuarto creciente, luna llena y cuarto menguante) y por último la variación nictemeral. Estas variaciones en el enfoque del muestreo permite analizar la dinámica de la comunidad a diferente escala permitiendo visualizar patrones no perceptibles a escalas mayores (escala mensual) (Krumme et al., 2003; Pepin y Helbig, 2011). Este diseño experimental se aplicó en una campaña de muestreo realizada de abril a agosto de 2010.

Comparando los muestreos de 2004-2005 y 2010, la riqueza y composición de especies, y sus abundancias variaron de manera dramática de uno a otro. En los muestreos de 2004-2005, se colectaron 31 especies de larvas y en el 2010, 44 especies. A pesar del intenso esfuerzo de muestreo realizado en 2010, solamente se obtuvieron muestras suficientes de *G. dormitor*. *E. saurus* y *A. lineatus* ocurrieron en muy bajas densidades ($n= 125$ y $n= 58$) y en longitudes muy pequeñas.

Los principales filtros en la selección de especies con las cuales se puede probar la hipótesis de Beck et al. (2001) son, el conocimiento de la historia de vida de la especie, que ocurra por lo menos en dos hábitats y que sean lo suficientemente abundantes para determinar sus tasas de crecimiento y mortalidad en cada hábitat. Además, el concepto de área de crianza solamente se ha aplicado a especies marinas y a especies que visitan el estuario con fines reproductivos, lo que reduce dramáticamente las posibilidades de prueba de la hipótesis de área de crianza.

De estas 31 especies (muestreo de 2004-2005) solamente 10 presentaron altas densidades de juveniles. Estas especies ocurren principalmente en el ambiente costero (en orden de abundancia: *Mugil cephalus*, *Mugil curema*, *Achirus lineatus*, *Harengula jaguana*, *Elops saurus*, *Oligoplites saurus*, *Trachinotus falcatus*, *Trachinotus carolinus* y *Megalops atlanticus*), y en el ambiente de manglar y río, *Gobiomorus dormitor* fue la más abundante. Durante la campaña de muestreo de 2010, el ensamblaje de especies y sus densidades fue muy diferente que en la campaña previa. Las especies que se presentaron en altas densidades fueron *G. dormitor*, *A. mitchilli*, *Anchoa hepsetus*, *Pterygoplichthys* sp. y *Dormitator maculatus*.

De las 10 especies más abundantes, *G. dormitor* fue la única especie susceptible para probar la hipótesis de Beck et al. (2001) a través de la medición de tres de los cuatro parámetros requeridos. Con base en los resultados obtenidos de la prueba de la hipótesis para *G. dormitor*, se concluyó que los hábitats de manglar y río son importantes áreas de crianza de esta especie.

Este ejemplo demuestra por un lado cuanto puede cambiar la supuesta importancia de un hábitat para ciertas especies en un periodo de tiempo y al mismo

tiempo prueba la dificultad que se tiene al momento de aplicar el concepto de área de crianza suponiendo condiciones estables a lo largo del tiempo.

Consideraciones finales

El concepto de área de crianza debe abordarse desde dos enfoques principales: 1) a nivel específico, para describir la historia de vida de la especie e identificar los patrones de uso de hábitats y su conectividad; y 2) por grupos de especies: este enfoque tiene implicaciones para el manejo y el establecimiento de núcleos de protección, además la presencia de muchas especies de importancia comercial convergiendo en un espacio común, es un poderoso argumento para justificar la protección de áreas de crianza.

Las estrategias de conservación deben incluir además, la protección de corredores para garantizar el movimiento de las cohortes desde un hábitat hacia otro en función de sus requerimientos ontogénicos (Mumby, 2006). La disponibilidad de múltiples áreas de crianza puede promover la estabilidad y la persistencia de poblaciones y comunidades o sostener remanentes de poblaciones (Hilborn et al., 2003; Kraus y Secor, 2005).

Mientras no se desarrolle una metodología capaz de medir la contribución real de una potencial área de crianza a la población adulta, el objetivo de identificar las áreas de crianza de “mayor calidad” y/o el hábitat esencial para los juveniles como herramienta de manejo y argumento para la protección y conservación de recursos dista mucho de ser logrado. Además, el etiquetar un hábitat como más valioso o de mayor calidad implica por fuerza que otro(s) sea(n) catalogado(s) como de poco valor,

el riesgo inherente a esto es, que el valor de áreas poco o no estudiadas puede ser pasado por alto. Si las áreas de crianza actualmente no contribuyen con suficientes adultos para sostener las poblaciones (e.g. (Romine et al., 2009), entonces categorizar ciertas áreas como importantes sólo priorizará la reducción de la producción de las áreas de crianza en su totalidad, sean “eficientes” o no (Sheaves et al., 2006).

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**Capítulo II. Influence of temporal and spatial factors on abundance and richness
of fish early stages in shallow tropical estuaries**

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Influence of Temporal and Spatial Factors on Abundance and Richness of Fish Early Stages in Shallow Tropical Estuaries

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Abstract

Accurate determination of abundance and richness of fish early stages in estuarine zones is critical to support management and protection plans; it is therefore necessary to consider all influential factors. Habitat diversity, seasonality, moon phase and diel variations, and their interactions are factors that can affect richness and abundance estimations. Appropriate spatial and temporal scales in sampling design are important to understand the assemblage dynamics of fish early stages. The objective of this research is to test how temporal and spatial scales influence the determination of abundance and

richness of fish early stages based on a hierarchical sampling design considering season (dry and rainy), moon phase (new, crescent, full, and waning), day period (sunrise, midday, sunset, and night), habitat (coastal, riverine, mangrove, and *Vallisneria americana* beds), and their interactions. Samples were collected using a conical zooplankton net and towed horizontally for 5 minutes at a depth of 50 cm. A variance component analyses model showed that day period, season, and their interactions were the main factors determining variations in fish early stage abundances and richness (26.68, 10.78, and 12.82%, respectively). The highest abundance and richness occurred at night, with significant seasonal variations related to the runoff from the Grijalva-Usumacinta basin. Abundance and richness were higher in the dry season, which were related to higher dissolved oxygen and water transparency. Presented findings can be generalized to tropical and subtropical estuaries with shallow waters.

Keywords: variance components, diel variation, moon phase, larvae, tropical estuary

Introduction

Shallow estuarine zones are important for recruitment and refuge areas in larval and juvenile fishes (Martinho et al. 2007; Day et al. 2012). In tropical regions, estuarine areas present a diversity of habitats (marsh, submerged aquatic vegetation, and mangroves among the most conspicuous) that provide abundant food as well as refuge against predators, thus acting as nursery grounds during early stages for many fish species (Beck et al. 2001; Elliott and McLusky 2002; Beck et al. 2003). The appropriate determination of ecological attributes in estuarine areas is a global concern. It is the basis for proposing areas as priorities for conservation, management, and protection,

highlighting their importance as biodiversity reservoirs and supporting the survival of high quantities of commercially important species (Miller 2002; Beck et al. 2003; Pepin and Helbig 2012).

The abundance and richness of fish early stages in estuarine areas depend on several factors, from the life cycle of a species (e.g., spawning patterns) to ecological (e.g., predators and food availability) and environmental interactions (Miller 2002; Ramos et al. 2006a; Primo et al. 2011a;). Among the most important physical factors identified as influencing the abundance and richness of fish early stages in estuarine areas are habitat diversity, seasonality, circadian rhythm, and moon phase (D'Alessandro et al. 2010; Primo et al. 2011b; Specziár et al. 2013). However, their interactions and effects on richness and abundance are not well understood (DiBacco et al. 2001; Hatcher 2006; Pepin and Helbig 2012).

Factors that influence larval settlement and recruitment, especially effects of moon phases and diel variations in coral reef environments, have been explored. For example, higher richness and abundance have been found during new and full moon phases (Wantiez et al. 2007; Hernández-León 2008; D'Alessandro et al. 2010). However, inconclusive results were observed when diel variations were not incorporated into the sampling design (Pepin and Helbig 2012). In addition to lunar effects, other authors have concluded that the highest abundance of fish larvae occur at night (Araujo-Lima et al. 2001; Castro et al. 2011). In contrast, a lack of circadian variations was related to the shallow depth and strong tidal currents in the Taperaçu estuary in northern Brazil (Magalhães et al. 2011). This difference in outcomes may be related to incomplete sampling designs that considered partial factors while neglecting the interactions between factors (Wantiez et al. 2007).

A sampling design including proper spatial and temporal scales is the main challenge to understanding the assemblage dynamics of fish early stages (Sanvicente-Añorve et al. 2000; Miller 2002; Ramos et al. 2006b). Since the zooplankton net is the most commonly used gear for abundance and richness determinations (e.g. Able et al. 2011; da Silva et al. 2012; Kent et al. 2013), the present research focused on its use, disregarding the possible bias derived from the avoidance, extrusion, and patchiness of larvae (Johnson and Morse 1994; Suthers et al. 2009). Additionally, shallow waters and the structural complexity of estuarine areas impede the use of traditional sampling strategies, such as oblique tows (Ooi and Chong 2011). In the present study, these conditions require the use of a special steel structure that was designed specifically to make horizontal zooplankton tows in shallow areas and channels, allowing for a more homogeneous sampling process during the survey (Zavala-García and Flores-Coto 2005).

Tropical estuarine diversity is well represented in the Centla Wetland Biosphere Reserve (CWBR), which was identified as a world conservation area by Ramsar in 1992 (Instituto Nacional de Ecología 2000; Novelo-Retana 2006). The diversity of the aquatic environments and fish fauna (46 larvae and 96 juvenile fish species) in the CWBR (Arévalo-Frías and Mendoza-Carranza 2012) make the experimental test designs suitable to assess richness and density variations in fish early stages.

The objective of the present paper is to measure the effects of season, moon phase, diel variations, and their interactions on the abundance and richness of fish early stage assemblages in the estuarine environments within the CWBR. Therefore, we used four tropical estuarine habitats (coastal zone, mangroves, river, and submerged aquatic

vegetation) of the CWBR as a model, considering the influential physicochemical parameters.

Methods

Study area

The sampling survey was undertaken at the lower basin of the Grijalva-Usumacinta riverine system in Centla, Tabasco, Mexico. This lower basin is a complex wetland ecosystem that was identified as an area of conservation concern, declared as a Biosphere Reserve by the federal government of Mexico in 1992, and noted by the Ramsar Convention of 1995 as a wetland area of international importance. The Grijalva-Usumacinta basin is the second-most important contributor of freshwater to the Gulf of Mexico after the Mississippi basin (Toledo 2003).

This area features two tidal cycles per day, with a small difference between high and low water levels, ranging from 35–50 cm (Thom 1967; Ponce Vélez 1991). Moreover, a strong seasonal freshwater runoff that comes from the most plentiful rivers in Mexico dominates this area (Toledo 2003).

Sampling areas were distributed as follows: the Grijalva-Usumacinta river mouth (18°36'03"N 92°41'46"W), characterized by brackish-marine environments and sandy beaches (GRC); Isla del Buey (18°30'00"N 92°39'05"W), in a zone characterized by mangroves, mainly *Rhizophora mangle* (GRM), located 7 km from the river mouth; the union of the Grijalva and Usumacinta rivers (18°24'22"N 92°38'56"W), a riverine environment lacking submerged vegetation and margins surrounded by modified vegetation, mainly livestock forage (GRR), located 20 km from the river mouth; and the San Pedrito lagoon (18°21'58"N 92°35'02"W), characterized by dense eelgrass

(*Vallisneria americana*) beds and surrounded by reeds and swamp vegetation (GRV), located 26 km from the river mouth (Fig. 1).

Sample collection

Sample collections were made during April and May (dry season) and July and August (rainy season) of 2010, using a conical zooplankton net (150-cm length, 50-cm mouth diameter, and 500- μ m mesh), supported on a special steel structure designed specifically to make horizontal tows in shallow areas and channels (Zavala García and Coto 2005). This structure was attached to the side of a fiberglass boat (7-m length) with a 40 HP outboard motor, towed from 1.5 to 2 knots (2.7 to 4 km/h). Horizontal tows of 5 minutes each were made at a fixed depth of 50 cm. The sampled habitats present shallow water and the structural complexity (mangrove roots, mud layers, and aquatic submerged vegetation such as *V. americana*) that impede the use of other common zooplankton sampling strategies such as oblique tows (Ooi and Chong 2011). Samples were preserved in a 4% formaldehyde solution using sodium borate as buffer. Dissolved oxygen (mg/l), salinity (PSU), water temperature ($^{\circ}$ C), pH, and water transparency (cm) were recorded at the beginning and end of each replicate ichthyoplankton sample series. Water samples were obtained with a 5 l van Dorn bottle at a depth of 50 cm. Dissolved oxygen and water temperature ($^{\circ}$ C) were measured with an YSI $\text{\textcircled{R}}$ Oximeter model 55, salinity was measured with an Atago $\text{\textcircled{R}}$ refractometer, and pH was measured with an Oakton 35423-10 pH Tester EcoTestr pH 2 $\text{\textcircled{R}}$. The transparency of the water was recorded using a 20 cm-diameter Secchi disc tied to a rope marked in centimeters.

Sample processing

All ichthyoplankton and early juveniles from the zooplankton net samples were separated and counted under a stereomicroscope. All fish early stages were identified to the lowest possible taxonomic level using the identification keys of Álvarez and Flores-Coto (1981), Flores-Coto and Méndez-Vargas (1982), Richards (2005), and Fahay (2007), using the serial method. This method involves the comparison of older stages and progressively associates them to smaller specimens through a sequence of shared characteristics (Powles and Markle 1984). For each habitat sampled, abundances were compared by estimating species density (organisms number·100/m³, Smith and Richardson 1977). Richness was expressed as the species number (Krebs 1999).

Experimental sampling design

A multilevel sampling design was performed to test the influence of the major factors on the abundance and richness of estuarine fish early stages. Four estuarine habitats (coast, mangrove, riverine, and submerged aquatic vegetation) were chosen, based on their importance as nursery areas (Beck et al. 2001; Arévalo-Frías and Mendoza-Carranza 2012). These four habitats composed the first level (Fig. 2). The second level comprised the dry (April and May 2010) and rainy seasons (July and August 2010). The third level involved moon phases (new, crescent, full, and waning moon), and the fourth level comprised the day period (sunrise, midday, sunset, and night; Fig. 2). Two replicates, composed of three zooplankton samples each, were collected per condition, comprising a total of 768 samples.

Data analysis

To determine the importance of the factors considered in the experimental design on richness and abundance of fish early stage variations, a variance component analysis was performed (Searle, Casella and McCulloch 2009). Variance component analysis is based on ANOVA for synthesized errors with degrees of freedom calculated by Satterthwaite's method (Satterthwaite 1946). To meet the ANOVA assumptions, the data were transformed using the $\log_{10}(n+1)$ equation (Anderson et al. 2011; Zar 2010).

Three models were tested: 1) using the variance components only (season, moon phase, habitat, and day period; 2) using the variance components plus environmental variables as covariates (water temperature, dissolved oxygen, salinity, and pH), and 3) adding water transparency as a covariate to the second model. These models resulted from different arrangements among experimental levels and environmental variables, noticing *a priori* that transparency is a determinant variable that strongly influences abundance and richness of fish larvae. For each physicochemical parameter, an ANOVA was performed to assess differences between habitats and seasons sampled (Zar 2010). Lastly, a Spearman rank correlation analysis was performed to determine the main correlations among larval abundance and physicochemical parameters (Zar 2010).

Results

Communities of fish early stages and physicochemical parameters

We collected a total of 35,095 fish early stages distributed into 29 families, 37 genera, and 46 species. During the dry and rainy seasons, 39% and 13% of total species occurred, respectively, and 48% of total species occurred in both seasons. Although the

dry season featured the occurrence of species associated with marine and brackish-marine water, the most abundant species during this period were *Gobiomorus dormitor* (n=19,540), unidentified gobiids (n=4,273), *Anchoa mitchilli* (n=1,225), and *Anchoa hepsetus* (n=671). The rainy season was characterized by the occurrence of brackish and freshwater species. Most abundant species during this period were *G. dormitor* (n=5,581), unidentified gobioids (n=503), early stages of the non-native suckermouth armored catfish *Pterygoplichthys* spp (n=423, Fig. 3), and *Anchoa mitchilli* (n=313).

Highest abundances and richness occurred during the night in both dry and rainy seasons (27,951 individuals/44 species and 7,144 individuals/27 species, respectively). Species richness was similar in all habitats sampled, with 30 species occurring in coastal habitat, 24 in mangrove, 28 in river, and 25 in SAV habitat (Table 1).

Gobiomorus dormitor was the species with the highest densities of early stages. Highest abundances of *G. dormitor* occurred at night during the dry season (218.7 ± 476.5 org·100/m³) and at midday during the rainy season (224 ± 555 org·100/m³, Table 1). The larvae of Gobiidae were the most abundant at sunset and night in the dry season (29.4 ± 38.7 and 52.5 ± 105 org·100/m³, respectively), and larvae of Gobioidae were abundant at sunset in the rainy season (14.6 ± 21.6 org·100/m³).

The coastal habitat showed the highest values of salinity and dissolved oxygen during the dry season (5.6 ± 2.6 and 6.5 ± 1.1 , respectively). Salinity, dissolved oxygen, pH, and transparency decreased during the rainy season (Table 2). The decreases in these parameters, particularly dissolved oxygen and transparency, were associated with the strong river runoff that increased water turbidity produced by downstream material transport. Spearman rank correlation analysis showed a positive correlation between

abundance and both dissolved oxygen and transparency ($r_s=0.29$ and 0.16 , respectively, $p<0.05$); also, a strong correlation was found between abundance and dissolved oxygen plus transparency ($r_s=0.79$, $p<0.05$). All physicochemical parameters differed significantly between habitats and seasons (Table 3).

Variance components of the early stage abundance and richness

The first variance component model showed that the day period was the most important factor to explain variations in the abundance and richness of fish early stages (26.68 and 33.63%, respectively). Season was the second contributor to explain this variance (10.78 and 16.37%, respectively, Table 4). The interaction between these two factors (day period and season) most significantly explained the variation in abundance (12.82%); nevertheless, this interaction could not explain the variation in richness (Table 4). The calculated errors of the first model for abundance and richness were 17.31 and 20.11%, respectively. Despite the fact that the day period was the main contributor to the explained variance, the ANOVA did not show significant differences for abundance and richness ($F=4.185$, $p=0.105$ and $F=13.367$, $p=0.053$, respectively).

With the addition of the environmental variables as covariates (second model), the importance of the variance components remained, as in the first model. However, the error slightly decreased in relation to the first model (16.89 for abundance and 19.56% for richness). In this second model, significant differences ($F=12.159$, $p=0.038$) were only observed for richness in the day period (Table 4). When transparency was added as a covariate in the third model, season becomes the principal contributor of the explained variance (37.85% for abundance and 46.19% for richness), showing significant differences for both variables ($F=12.321$, $p=0.023$ and $F=28.543$, $p=0.010$,

respectively) but also increased the unexplained variance for abundance and richness (20.7 and 25.3%, respectively) and concealing the effects of the other factors (mainly day period, Table 4). It is important to note that habitat has little importance on the variation of abundance and richness, compared to day period and season. Nevertheless, some interaction values where this variable is present are significant (Table 4).

Abundance peaks of *G. dormitor* (1.2% of the total samples) were detected and related to the rearrangement of data; thus, abundance variation was analyzed in two ways: considering all species, and omitting the abundance of *G. dormitor*. In the first analysis, a peak was observed during midday in the rainy season (31.1 org·100/m³). This result does not confirm the general pattern displayed by previous analyses. The presence of two samples with an extreme number of *G. dormitor* (3,636 and 1,128 individuals) caused this abundance peak. In the three other cases, the peaks in early stages occurred during the night, from a minimum of 12.2 org·100/m³ during the rainy season to a maximum of 252.6 org·100/m³ during the dry season (Fig. 4). A two-way ANOVA on variations in abundance using only season and day period as factors and excluding the abundance peaks of *G. dormitor* showed significant differences ($p < 0.001$) between all factors (Table 5).

Discussion

Appropriate sampling design is crucial to obtain accurate data for reliable estimations of larval abundance and richness, revealing natural patterns (Wolff et al. 1999; Miller 2002; Krumme 2003). Additionally, standardization of sampling methodology, environmental conditions, and habitat configuration are critical aspects to consider in the design protocols of

aquatic research (Ramos et al. 2006a; Ramos et al. 2006b; Sanvicente-Añorve et al. 2000). Classic analyses used to explain larval assemblages, such as cluster analysis and ordination techniques, fit the dataset according to their similarity or displaying them in function of “components” to improve the explanation of the model (Miller 2002; López-Sanz et al. 2011). Such analyses produce a loss of accuracy in determining the actual effect of a determinant factor, which should be considered at different time and geographic scales. In contrast, variance component analysis, supported by a complete sampling design, is an optimal analytical tool when the primary purpose of the research is to determine the influence of factors involved in abundance and species composition changes (e.g., Ysebaert and Herman 2002; Méthot et al. 2012; Drolet et al. 2013; Specziár et al. 2013;).

Furthermore, variance component analysis shows its robustness, since isolated peaks in the abundance of certain species (e.g., *G. dormitor*) do not affect the overall results. The accuracy of variance component analysis is increased when using large samples, as occurred during this research (Searle, Casella and McCulloch 2009; Liv et al. 2012). Despite the use of mixtures of taxonomic levels inside the analysis, it is important to highlight that individuals identified at the family level represent only the 14% of the total number of identified individuals. Results accurately indicate the effects of several parameters on abundance and richness for fish early stages in estuarine environments. However, these results represent important implications for future studies on species diversity in the study area.

The dynamics of fish communities in this important estuarine area are not well known. While Macossay-Cortez et al. (2011) and Sánchez et al. (2012) reported 46 fish species from a 10-year sampling survey (2000–2010) in which poecilids and cichlids

dominated the abundance, Arévalo-Frías and Mendoza-Carranza (2012) reported 96 fish species during year-round sampling (2004–2005) with *A. mitchilli*, *Mugil curema*, and *Mugil cephalus* as the most abundant species. Although both studies were made in shallow water ecosystems in the Centla Wetlands Biosphere Reserve, they only shared 27 fish species. These differences indicate the need for more studies to explain the dynamics and ecology of the fish communities within this important Biosphere Reserve, emphasizing commercially important species (Mendoza-Carranza et al. 2010). The presence of the suckermouth armoured catfish *Pterygoplichthys* as a component of the ichthyofauna of the Centla Wetlands has been already reported (Wakida-Kusonoki et al. 2007). Ecological implications of the presence of *Pterygoplichthys* (larvae and adults) in the Grijalva-Usumacinta basin were discussed by Mendoza-Carranza et al. (2010) and Capps et al. (2011), indicating the potential threat for fish estuarine communities.

The present results show an increase of 33% in species richness compared to previous species list presented by Arévalo-Frías and Mendoza-Carranza (2012) on study area. *A. mitchilli*, *A. hepsetus*, and *G. dormitor* were the most abundant species in these studies, varying only in their densities. The differences in fish community composition and species abundance can be attributed to the sampling design, since the studies were performed with identical zooplankton nets. While we performed a complete sampling survey, including all possible factors that would affect fish early stage richness and abundance, our former study (Arévalo-Frías and Mendoza-Carranza 2012) was conducted following a diurnal eulerian sampling design, ignoring potential sources of variation (Sommer and Lewandowska 2011; Ohman 2012). Diurnal and eulerian sampling surveys allow us to obtain general patterns on a broader scale, mainly in space, where high-resolution sampling is not possible in terms of cost and effort, but

they undergo loss of information about the abundance and presence of species over a shorter period (Grioche et al. 2000).

Despite the bias produced by the sampling design, the life cycle and reproductive peaks of species play important roles in larval abundance (Houde 2008; Takemura et al. 2010; Breheny et al. 2012). The highest densities of *G. dormitor* are closely related to their reproductive and spawning season (Bacheler et al. 2004; Hernández-Saavedra et al. 2004; Harris et al. 2011). Moreover, it is possible that massive spawning occurs in *G. dormitor* as a strategy to ensure food availability and minimize predation (Hernández-León 2008). The occurrence of high densities of fish early stages at midday during the rainy season may be due to the low transparency of water, thus increasing total abundance. In *G. dormitor*, a pattern of distribution, structured by size and age, was also recognized. Larvae are found in large amounts closer to the coast, whereas juvenile abundance increased upriver (Arévalo-Frías and Mendoza-Carranza 2012). A similar pattern occurs with *G. dormitor* adults, where fish size increases upstream from the river mouth (personal observation).

As in other estuarine areas dominated by large riverine systems, the Grijalva-Usumacinta estuarine area is strongly influenced by seasonal runoff; this fact has important implications on the physicochemical conditions of the sampled areas (Shuiwang et al. 2000; Toledo 2003; Li et al. 2007; Primo et al. 2011b). In the dry season, marine-estuarine waters rich in dissolved oxygen and high transparency dominate the estuarine zone; during the rainy season, the estuary is dominated by freshwater with low levels of dissolved oxygen and high quantities of diluted nonorganic and organic materials (Dai et al. 2006; da Costa et al. 2011; Salcedo et al. 2012). These two contrasting conditions have a strong influence on the fish early stage richness and

abundance; during dry season, the estuarine conditions facilitate the presence of marine, estuarine, and freshwater larvae, thus increasing richness and abundance (Matos et al. 2011). Conversely, during the rainy season, the marine and estuarine larvae are flushed from the estuarine areas, resulting in a diminution of larval richness and abundance (Baptista et al. 2010; Primo et al. 2011a; Garcia et al. 2012;). Moreover, turbidity has a negative influence on estuarine fauna, especially in plankton species (González-Ortegón et al. 2010). High turbidity increases larval mortality and reduces the physiological health of the individuals (Griffin et al. 2009).

In addition, our study indicates that the diel cycle was the second most-relevant factor to explain variations in abundance and richness of fish early stages. Such variations are frequently linked to tidal variations and vertical migration (Grioche et al. 2000; Primo et al. 2011b; Meerhoff et al. 2013). However, in the Gulf of Mexico tidal variations are of little importance, with a slight variation (c.a. 45 cm) in the Tabasco coast (Thom 1967; Ponce-Vélez 1991; Sanvicente-Añorve et al. 2011); being the phototactic behavior of larvae potentially related to the observed pattern (Chícharo et al. 2009; Colton and Hurst 2010).

Regarding lunar influence, although some authors have related highest fish catches to nights closer to a full or new moon, their results are inconclusive, since not all species follow this pattern (Reyier and Shenker 2007; Hernández-León 2008; D'Alessandro et al. 2010; Lecchini et al. 2013;). In the present experimental design, moon phases could not explain variations in abundance and richness, nor did they have significant interactions with other factors. Possible causes for these findings could be related to the low tides and shallow depths in the sampled area (Ramos et al. 2011; Becker et al. 2012).

The lack of significant differences in abundance and species number related to habitat is due to the presence of a similar number of different species. Furthermore, the relative distances between these habitats are insufficient for the detection of significant changes in physicochemical parameters. Only closer habitats would allow the most abundant larvae species to have the same opportunities to colonize these different locations (Barletta and Barletta-Bergan 2009; Winston 2012). Despite this similarity of abundant species, differences between species assemblages by habitat were observed in the Centla Wetlands, with marine-estuarine species (e.g., *Elops saurus*, *Myrophis punctatus*, *Dorosoma* spp, *Harengula jaguana*, *Oligoplites saurus*, *Trachinotus carolinus*, *Gobiesox strumosus*, *Porichthys porosissimus*, and *Microdesmus longipinnis*) dominating the coastal habitat and freshwater species (e.g., *Atherinella* spp, *Rivulus* spp, *Hyporhamphus* spp, and the Cichlidae family) dominating upriver habitats, a pattern also observed in diurnal eulerian samples in the same area (Arévalo-Frías and Mendoza-Carranza 2012).

Our methodological approach, from using a hierarchical sampling design to applied data analyses, is a valuable tool to determine the effects of the principal factors and their interactions on the abundance and richness of communities of fish early stages. We revealed that the most influential factors were day period and season. Our findings can be generalized to tropical and subtropical environments, where the presence of shallow waters and complex structured habitats, such as coral reefs, mangroves, and submerged aquatic vegetation, obligates the use of horizontal tows (Chew and Chong 2011; Ooi and Chong 2011). Future research focusing on the determination of the abundance of ichthyoplankton should consider that greatest abundance and numbers of species of fish early stages occur at night.

Both cost and effort are high in our sampling design, but we take into account most of the factors that can explain the variability in richness and abundance of fish early life stages. The current results can be used to generate abundance adjustment models from studies based on classic ichthyoplankton sampling design (diurnal and eulerian surveys) using conical ichthyoplankton nets. This adjustment is necessary to obtain accurate and reliable data on the richness and abundance required for habitat assessment, management, protection plans, and evaluation of nursery area functions.

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Figure Captions

Fig. 1 Sampling points at the estuarine habitats of the Grijalva river, Tabasco, Mexico. GRC: Grijalva coast, GRM: Grijalva mangrove, GRR: Grijalva river, GRV: Grijalva submerged vegetation

Fig. 2 Multilevel sampling scheme. SAV: submerged aquatic vegetation, s: sample, s': sample replicate

Fig. 3 Dorsal, lateral, and ventral views of larvae of the suckermouth armored catfish *Pterygoplichthys*

Fig. 4 Seasonal (dry season, circles; rainy season, triangles) and diel fish early stage abundance variations and standard deviation (SD) with (open symbols) or without *G. dormitor* (closed symbols) at the estuarine habitats of the Centla Wetlands Biosphere Reserve

Table 1 Richness and mean density (organisms·100/m³) of fish early stages during the dry and rainy seasons in the estuarine habitats of the Centla Wetlands Biosphere Reserve

Family	Species	n	Size range (mm)	Dry				Rainy					
				Sunrise	Midday	Sunset	Night	Sunrise	Midday	Sunset	Night		
Elopiidae	<i>Elops saurus</i> ^{c,m,r,s}	125	21–57		1.1±0.4				3.5±4				
Megalopidae	<i>Megalops atlanticus</i> ^c	12	16–28				0.8±0.3				0.8±0.3	3±0.3	
Ophichthidae	<i>Myrophis punctatus</i> ^{c,m}	3	36–67						1.2 ^a				0.9±0.1
Clupeidae	<i>Dorosoma</i> spp. ^{c,m,r,s}	31	10–17				0.8±0.3		2.1±1.8		0.8±0.3	0.9±0.3	1.6±1.2
	<i>Dorosoma petenense</i> ^{n,r}	2	13–71						0.8 ^a				0.9 ^a
	<i>Harengula jaguana</i> ^{c,m}	3	31–39						1.1±0.3				
	Clupeidae ^{c,m,r,s}	83	6–31						1.3±0.7		0.9±0.4	1.3±0.5	3.1±4.3
Engraulidae	<i>Anchoa hepsetus</i> ^{c,m,r,s}	720	3–56	2.5±1.8	0.9 ^a	2.7±1.9		16.1±18.7					9.8±5
	<i>Anchoa mitchilli</i> ^{c,m,r,s}	1538	3–73	7.9±5.9	2.8±1.4	7.3±9.2		5.9±8.6					
	<i>Anchoa</i> spp. ^{c,m,r,s}	167	8–13	12.5±7	5.6±3.3	7.7±6.5		13.5±11.5		4.6±5.7	1.3±0.5	0.8±0.1	9.9±16.1
Characidae	<i>Astyanax</i> spp. ^{c,m,r}	6	28–35									0.8±0.4	
Loricariidae	<i>Pterygoplichthys</i> spp. ^{c,m,r,s}	423	13–47							4.3 a	0.5±0	6.5±9.2	7.4±8.1
Batrachoididae	<i>Porichthys porosissimus</i> ^{c,m,r}	70	14–21						5.9±8.3				
	<i>Opsanus beta</i> ^m	1	23						1.1 ^a				
Gobiesocidae	<i>Gobiesox strumosus</i> ^c	1	21						0.9 ^a				
Atherinopsidae	<i>Atherinella alvarezii</i> ^s	81	21–27	4.6±4.7	2.6±2.9	1.9±0.9		9.5±10.1					1.4±0.6
Rivulidae	<i>Rivulus</i> spp. ^{n,r}	2	23–26						1.8 ^a			1.2 ^a	
Belontiidae	<i>Strongylura</i> spp. ^{c,r,s}	3	34–42	1.1 ^a					0.9 ^a		0.5 ^a		
Hemirhamphidae	<i>Hyporhamphus</i> spp. ^r	1	17										1.3 ^a
Syngnathidae	Syngnathidae ^{c,m,r,s}	84	4–43	2±1.5	1.9±1.4	1.5±0.6		1.3±0.5		2.1 ^a			1.2±0.4

Synbranchidae	<i>Ophistemon</i> spp. ^{f,s}	8	67–98						1.4±0.9		
Triglidae	<i>Prionotus</i> spp. ^c	1	12						1 ^a		
Carangidae	<i>Caranx</i> spp. ^c	1	11						0.8 ^a		
	<i>Oligoplites saurus</i> ^c	1	16						1.2 ^a		
	<i>Trachinotus carolinus</i> ^c	3	12–15						1.1 ^a		
Gerreidae	Gerreidae ^{c,m,r,s}	517	5–10	2.8±2.3	5.6±9.9	2.5±3.3	7.3±17.8	6±5.5	3.6±2.1		1±0.2
Sparidae	Sparidae ^{c,m,r}	10	3–10	1.4±0.3	0±0	0.8 ^a	1.3±0.5				
Sciaenidae	<i>Bairdiella</i> spp. ^f	1	14				1.4 ^a				
	Sciaenidae ^{c,m,r,s}	154	3–14	1.2±0.3	0.8±0.1	1.4±0.8	3.1±3.4		0.5 ^a		
Cichlidae	<i>Cichlasoma urophthalmus</i> ^{f,s}	2	14–19				0.9 ^a		1.5 ^a		
	<i>Petenia splendida</i> ^a	4	18				4.5 ^a				
	Cichlidae ^{c,m,r,s}	23	14–20		1.1±0.5	1.9 ^a	1.6±1.4	1±0.2	0.8 ^a	1.5 ^a	0.9±0.1
Blenniidae	<i>Hypsoblennius</i> spp. ^{c,m,r,s}	8	3–12	0.9 ^a	0.8±0.1	0.9±0	0.7 ^a				
Eleotridae	<i>Dormitator maculatus</i> ^{m,r,s}	229	9–16		1.4 ^a		8.8±10.7	1.4±0.6	0.8 ^a		1.8±0.9
	<i>Gobiomorus dormitor</i> ^{c,m,r,s}	25121	9–35	54.2±179	5.1±5.5	3.5±3.4	219±476	36.8±33.2	224±555	5.9±4.8	0.9±0
	Eleotridae ^{f,s}	8	2–8				1.2±0.5				1 ^a
Gobiidae	<i>Gobiosoma</i> spp. ^{f,s}	11	2–12								1.3±0.6
	Gobiidae ^{c,m,r,s}	4340	3–11	1±0.6	5.6±15.1	29.4±38.7	52.5±105	2.6±2.5	2.2±2		
	Gobioidei ^{c,m,r,s}	503	2–5					2.5±1.0	2.2±1.6	14.6±21.6	9.7±14.8
Microdesmidae	<i>Microdesmus longipinnis</i> ^{c,f,s}	7	20–31				1±0.3				1 ^a
Ephippidae	<i>Chaetodipterus faber</i> ^f	1	8	0.9 ^a							
Paralichthyidae	<i>Eitropus crossotus</i> ^c	1	13				0.9 ^a				1 ^a
	Paralichthyidae ^{c,m,r}	44	8–13				2.6±1.3				
Achiiridae	<i>Achirus lineatus</i> ^{c,m,r,s}	58	1.5–5	3.6±3.7	0.9±0.1	1.1±0.3	1.8±1.1				
	<i>Trinectes maculatus</i> ^a	4	3–5				1.2 ^a				1±0.5

Individuals (n)	1577	460	523	25479	377	5316	250	1177
Species (n)	14	16	13	39	10	13	11	22

[°]Coast, [™]Mangrove, [†]River, [§]Submerged aquatic vegetation, [‡]Individuals in only one sample, ^bIncludes unidentified gobies with a low-quality conservation state

Table 2 Physicochemical parameters in estuarine habitats of the Centla Wetlands Biosphere Reserve

Dry season						
Habitat	D.O. ^d (mg/L)	Salinity (PSU)	Temp (°C)	pH	Transp. ^t (cm)	Depth (cm)
Coast	6.5 ± 1.1	5.6 ± 2.6	29.4 ± 1.0	7.9 ± 0.5	92.2 ± 18.9	390 ± 90
Mangrove	5.2 ± 1.4	4.7 ± 2.8	29.5 ± 1.2	7.9 ± 0.4	103.7 ± 20.5	190 ± 30
River	5.3 ± 1.0	1.6 ± 1.6	30.0 ± 0.9	7.9 ± 0.4	100.2 ± 35.9	340 ± 40
SAV	5.5 ± 0.9	2.8 ± 2.0	30.1 ± 1.0	8.0 ± 0.4	64.7 ± 15.0	130 ± 10
Rainy season						
Coast	4.0 ± 0.5	2.1 ± 1.8	29.2 ± 1.8	7.2 ± 0.2	23.7 ± 8.9	440 ± 120
Mangrove	4.0 ± 0.5	2.0 ± 1.6	29.1 ± 0.6	7.1 ± 0.3	21.4 ± 9.5	210 ± 40
River	4.6 ± 0.4	2.2 ± 1.8	28.9 ± 0.9	7.3 ± 0.1	22.4 ± 8.0	350 ± 50
SAV ^s	4.9 ± 0.3	2.4 ± 1.9	31.0 ± 1.4	7.6 ± 0.2	57.4 ± 10.9	150 ± 20

^dDissolved oxygen, ^tTransparency, ^sSubmerged aquatic vegetation

Table 3 ANOVA results for physicochemical parameters from the estuarine habitats of the Centla Wetlands Biosphere Reserve

Physicochemical parameters	Habitat		Season	
	F	p	F	p
Salinity	22.944	<0.001	59.287	<0.001
Water temperature	74	<0.001	7	0.009
Dissolved oxygen	11.6	<0.001	1199.6	<0.001
pH	23	<0.001	696	<0.001
Transparency ^a	14.48	<0.001	745.77	<0.001
Depth	111.24	<0.001	2.70	0.103

^aOnly daylight samples

Table 4 Relative variance components (percentages) of the models to explain variabilities of abundance and richness of fish early stages within the Centla Wetlands Biosphere Reserve

Component	Without covariates		With covariates ^a		With covariates ^b	
	Abundance	Richness	Abundance	Richness	Abundance	Richness
Season (1)	10.78	16.37	13.84	19.44	37.85*	46.19*
Lunar phase (2)	2.37	2.89	2.33	2.84	3.33	3.78
Habitat (3)	0	0	1.38	0.53	0.14	0
Day period (4)	26.68	33.63	26.24	33.81*	0	0
1*2	0	0	1.04	2.28	0.09	1.75
1*3	7.80*	6.71*	2.48	1.96	1.17	1.56
1*4	12.82*	3.97	13.26*	4.18	7.93*	1.00
2*3	0	0	0	0	0	0
2*4	0	0	0	0	0	0
3*4	4.74*	0.66	5.15*	0.94	7.24*	2.73
1*2*3	2.80*	0.51	3.04*	0	3.98*	0.09
1*2*4	5.28*	4.65*	4.77*	3.82*	6.15*	4.63
1*3*4	0.16	1.13	0.18	0.53	0	0
2*3*4	4.62*	3.70	4.60*	3.59	5.32*	4.12
1*2*3*4	4.58*	5.60	4.73*	6.45	6.02*	8.80*
Error	17.31	20.11*	16.89	19.56*	20.73	25.30

^aCovariates: Dissolved oxygen, salinity, water temperature, and pH

^bCovariates: Dissolved oxygen, salinity, water temperature, and transparency

*Significant differences in ANOVA for synthesized errors with degrees of freedom

Table 5 ANOVA results for season and day period to determine fish early stage abundance from the estuarine habitats of the Centla Wetlands Biosphere Reserve

Source	d.f. ^a	SS ^b	MS ^c	F	p
Season	1	6.59	6.59	25.65	<0.001
Day period	3	54.82	18.27	71.15	<0.001
Season × day period	3	8.97	2.99	11.65	<0.001
Error	412	105.82	0.26		
Total	419	192.13			

^aDegrees of freedom, ^bSums of squares, ^cMean squares

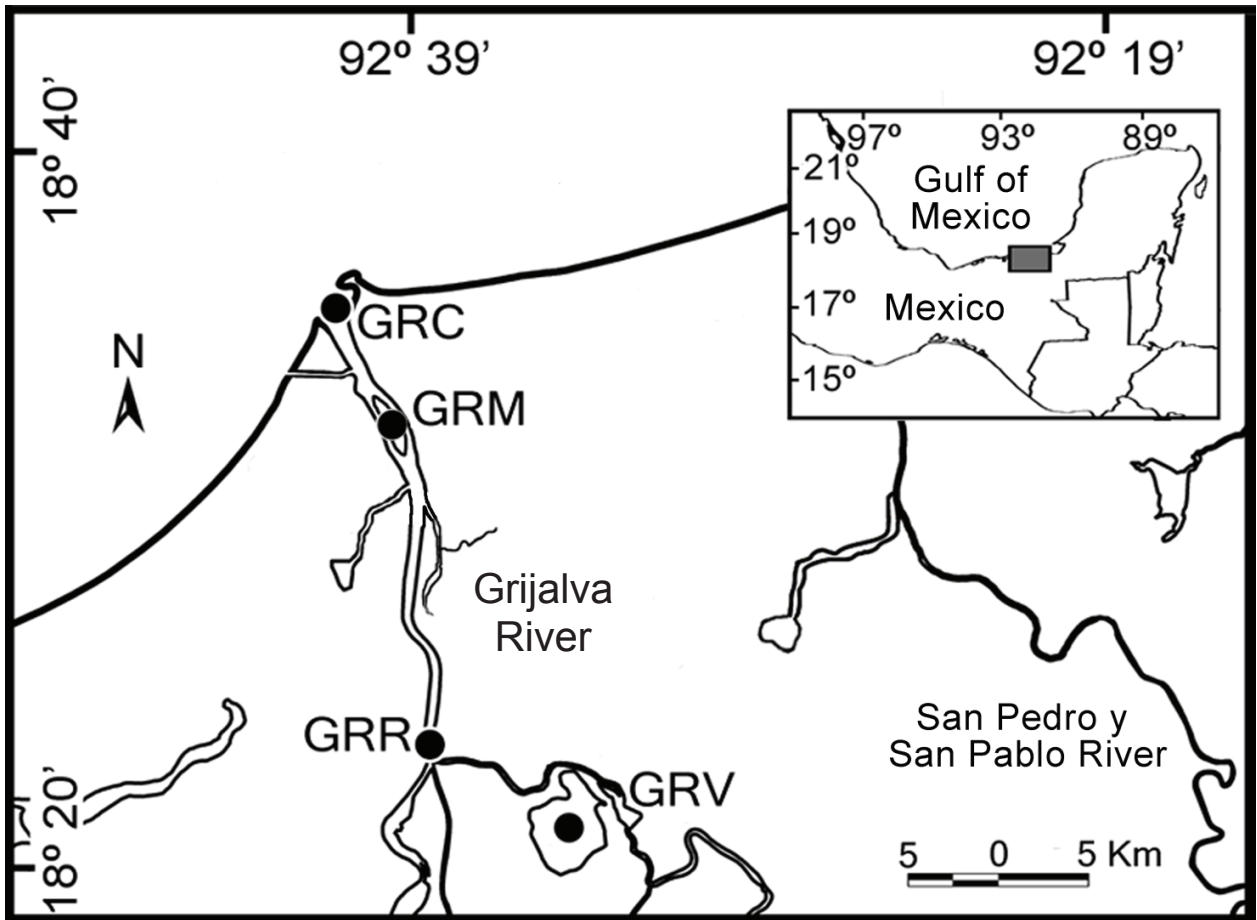


Figure 1

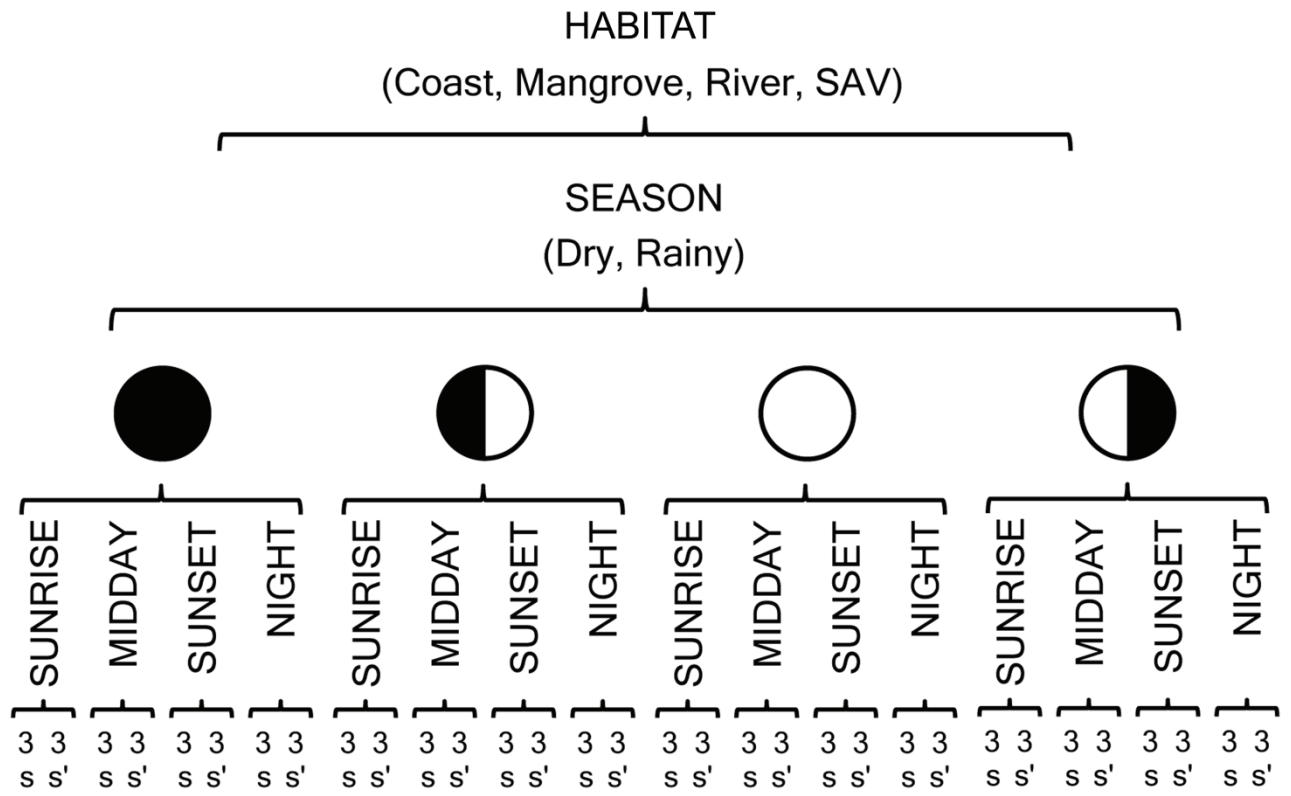


Figure 2



Figure 3

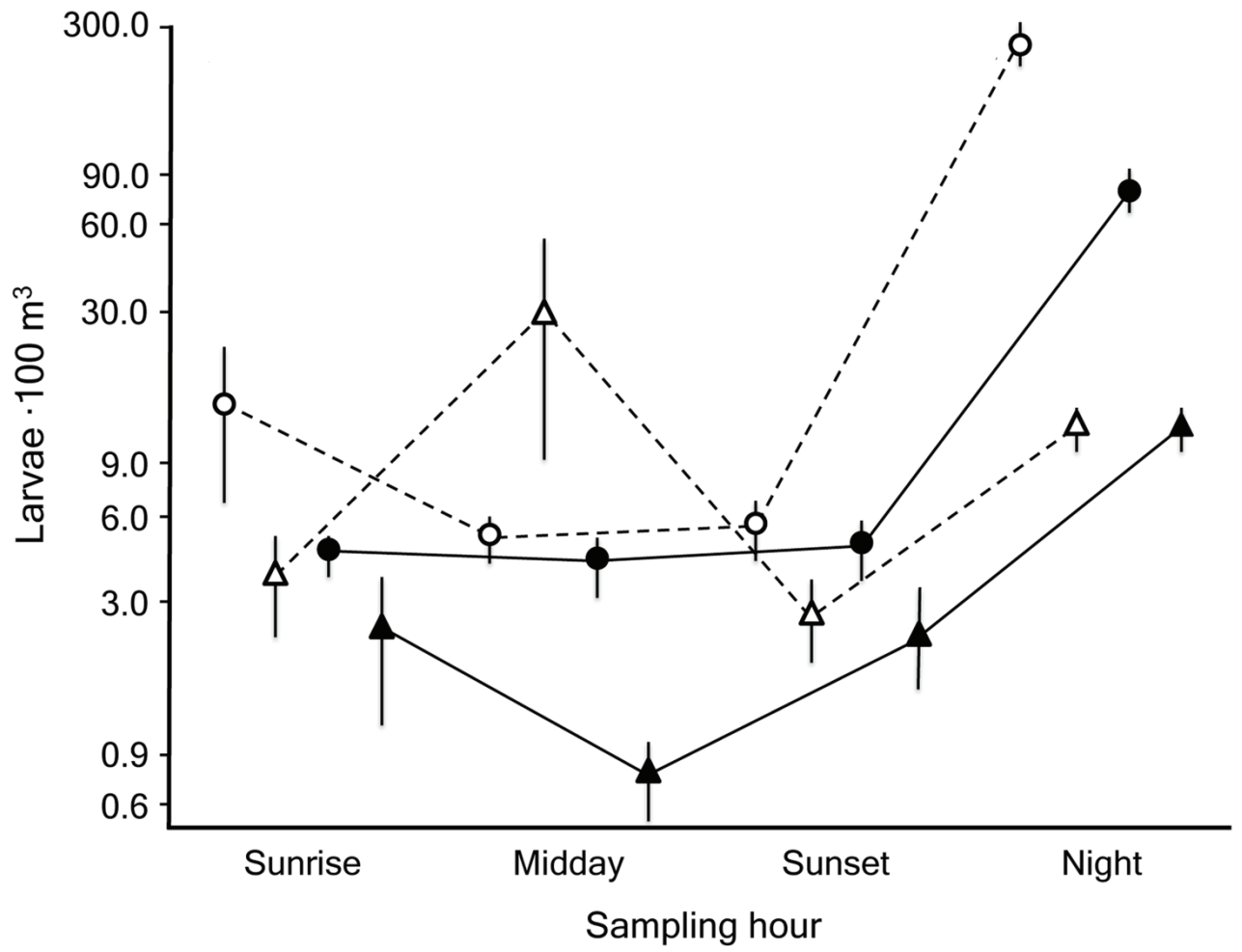


Figure 4

Capítulo III. Growth rate as indicator of nursery value for fish early stages in shallow water tropical estuaries.

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Growth Rate as an Indicator of Nursery Value for Fish Early Stages in Shallow Water Tropical Estuaries

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Abstract

The assessment of the nursery role of certain habitats for a species it is a complex task to accomplish and proven difficult to apply. Since fish growth rates are related to habitat attributes (food availability, predation, environmental stress), we proposed them as an indicator of nursery value for fish early stages. Growth rates were compared for early stages of bigmouth sleeper *Gobiomorus dormitor* occurring in estuarine environments (coastal zone, mangroves, non-vegetated riverine areas and eelgrass beds) at Centla Wetlands Biosphere Reserve, Tabasco, Mexico, considering their physicochemical conditions (dissolved oxygen, temperature, pH, transparency). Coastal environments at Grijalva and San Pedro y San Pablo rivers presented high fish densities (19.86 ± 37.78 and 22.74 ± 48.15 ind/100m³) and mortalities (3.43 ± 1.39 and 3.55 ± 1.44 year⁻¹). Faster growth rate (1.43 ± 0.29) and low mortality rates were observed in habitats with low salinity (0) and medium-high dissolved oxygen concentration (5.2–5.9 mg/L) in Grijalva riverine and mangrove areas. Our results show that early stages growth rates are related with the nursery quality. In addition to growth rates determination, comparison and monitoring of abundances and spatial-temporal patterns of age/size classes are highly recommended towards the understanding ecological dynamics relying on habitat nursery function.

Resumen

La designación de hábitats como área de crianza para una especie es una tarea compleja y ha probado ser difícil demostrar. Siendo que las tasas de crecimiento están relacionadas directamente con los atributos del hábitat (disponibilidad de alimento, depredación y estrés ambiental), en esta investigación se propone que las tasas de crecimiento pueden ser un indicador del valor de hábitats como área de crianza para estadios tempranos de peces. Para demostrar esta hipótesis fueron comparadas las tasas de crecimiento de juveniles de la

guabina *Gobiomorus dormitor*, que ocurre en hábitats estuarinos (zonas costeras, manglares, ríos y vegetación acuática sumergida) de la Reserva de la Biosfera Pantanos de Centla, Tabasco, México, tomando en cuenta los parámetros fisicoquímicos de cada lugar (oxígeno disuelto, temperatura, pH, transparencia). Los ambientes costeros de los ríos Grijalva y San Pedro y San Pablo presentaron las mayores densidades (19.86 ± 37.78 and 22.74 ± 48.15 ind/100m³) y mortalidades (3.43 ± 1.39 and 3.55 ± 1.44 year⁻¹) de *G. dormitor*. Altas tasas de crecimiento y bajas tasas de mortalidad fueron relacionados con bajas salinidades (0) y concentraciones medias y altas de oxígeno disuelto (5.2-5.9 mg/L) especialmente en la zona riverense y manglares del río Grijalva. Nuestros resultados demuestran que la determinación y comparación de las tasas de crecimiento se pueden relacionar con la calidad ambiental de un área de crianza. El monitoreo de los patrones espacio temporales de la abundancia de las clases de edad y talla son altamente recomendables para entender la dinámica ecológica de los hábitats designados como áreas de crianza.

Keywords: juvenile fish, recruitment, density, natural mortality, age.

Introduction

Tropical estuarine environments support a great abundance and diversity of juvenile fishes and invertebrates, being designated as nursery areas (Beck et al., 2003a). Within these ecosystems, some habitats as seagrasses and mangroves have been identified as critical nursery areas based on the relative abundance, species diversity and habitat complexity (Beck et al., 2001). Nevertheless, this approach has been applied indiscriminately for all the environments where species are found as larvae and juvenile, despite important differences among species life cycles and differential habitat uses (Beck et al., 2001; Secor y Rooker, 2005; Nagelkerken, 2009).

Conversely, the designation of a nursery area should be made at a species level and based on life history type characteristics. Furthermore, if the nursery-role hypothesis is considered, it is necessary to test if the habitats where early stages are found fulfill the nursery function, comparing attributes as species growth rate, density, survival and their contribution of recruits to the adult population (Beck et al., 2001; Minello et al., 2003). Nursery role hypothesis and its attributes have proven difficult to apply and to test at the same time (Kraus y Secor, 2005; Heupel et al., 2007). Nevertheless, the possible relation between these attributes is susceptible to be tested.

Since fish growth depends on the environmental conditions, food abundance, intra and inter-specific competition and predation (Rose et al., 2001; Bone y Moore, 2008), then, it is possible to establish an empirical relation between growth rates and some physicochemical characteristics to look for the best combination of environmental conditions in a diversity of habitats designated as potential nursery grounds (Tonkin et al., 2011). In addition, a fast growth rate is critical to the survival of larvae and juvenile fishes, leaving these vulnerable stages faster and ensuring a good recruitment to the adult population (Minello et al., 2003; Dower et al., 2009). However, few works have been performed in order to compare juvenile growth rates and other attributes (mortality and density) in habitats with differences in environmental conditions, but nominally designated as nursery grounds (Stunz et al., 2002; Beck et al., 2003a; Heck et al., 2003; Minello et al., 2003; Kraus y Secor, 2005).

The Centla Wetlands Biosphere Reserve (CWBR) brings together coastal, mangrove, riverine and eelgrass beds environments, making it a proper zone for testing the importance of several habitats for the growth of early stages of fishes that occupied it as a nursery area. In CWBR has been reported the occurrence of almost 46 larvae and 96 juvenile fish species (Arévalo-Frías y Mendoza-Carranza, 2012). Inside these fish species, larvae and juvenile of bigmouth sleeper *Gobiomorus dormitor* Lacepède, 1800 has been found abundantly in almost all the estuarine areas of CWBR (Arévalo-Frías y Mendoza-Carranza, 2012). The life cycle of bigmouth sleeper depends on the estuarine habitats, first for spawning in freshwater near of the coastal zone, posteriorly for development of eggs in the marine coastal zone and finally for the development of larvae and juvenile at estuarine habitats (Nordlie, 2011). Bigmouth sleeper is an amphidromous species with commercial and game fish importance (Bacheler et al., 2004; Harris et al., 2011). The habitat characteristics of CWBR and the life cycle and habitat utilization of the bigmouth sleeper allow using it to test the possible relation between growth rates and the role of diverse habitats as nursery ground.

Considering the life cycle and requirements for *G. dormitor* (Bacheler et al., 2004) it is possible to hypothesize that a habitat with good environmental quality (high dissolved oxygen concentrations and low salinity) could allow high growth rates for early stages of this species (Nordlie, 2011). Additionally, if the referred habitat present a complex structure (e.g. mangrove or submerged vegetation) predation and intra and interspecific competition rates could decrease (Bone y Moore, 2008).

Based on the raised hypothesis, the aim of this study is to test and to compare the growth rates of bigmouth sleeper in several habitats of the CWBR (coastal zone, mangroves, non-vegetated

riverine areas and eelgrass beds), supported by the assumption that environmental quality of the habitat influence growth rates (Houde, 1997; Hixon y Jones, 2005). Additionally, larvae and juvenile densities as well as mortality rates were estimated and compared, in order to contrast our results with the conventional parameters required to designate a habitat as nursery ground for a species.

Material And Methods

Study area

Centla Wetland Biosphere Reserve is located at 18° 35' N, 92° 42' W and 18° 28' N, 92° 26' W, at the lower basin of the Grijalva-Usumacinta riverine system, in Tabasco, Mexico. This riverine system is considered as the second wetland zone in importance at North America and seventh worldwide (Toledo, 2003). Based on its exceptional ecological features it was declared as biosphere zone in 1992 and subscribed in the RAMSAR convention of 1995 as wetland area of international importance (INE, 2000).

Juvenile of bigmouth sleeper were obtained in monthly sampling surveys from June 2004 to May 2005, covering four habitats in the Grijalva River and three in the San Pedro y San Pablo river, Tabasco, Mexico (Fig. 1). The habitats sampled in Grijalva river were: coastal area (GRC) located in the adjacent marine area of Grijalva river mouth at (18°35'08"N 92°42'22"W) characterized by brackish-marine environments and sandy beaches; mangroves (GRM) located at Polo stream, (18°30'00"N 92°39'05"W), approximately 15 km from Grijalva river mouth, characterized by the presence of *Rhizophora mangle* L. (1753) forest; riverine environment (GRR) located near to the place named Tres Brazos, (18°24'22"N 92°38'56"W), approximately 29 km from coast, characterized by a riparian environment surrounded by modified vegetation, mainly livestock forage; and eelgrass beds (VAM) located at San Pedrito lagoon (18°24'22"N 92°38'56"W), 35 km from coast, characterized by dense eelgrass *Vallisneria americana* Michx. beds surrounded by reeds and swamp vegetation (Fig. 1). In San Pedro y San Pablo river the habitats sampled were: Coastal area (SPC) located adjacent to the river mouth 18°38'46"N 92°28'02"W to 18°40'40"N 92°25'16"W, characterized by sandy beaches and brackish-marine environments; riverine environment (SPR, 18°35'35"N 92°26'53"W), 12 km from coast, distinguished as riparian areas with modified vegetation on its banks, mainly livestock forage; and mangroves (ECM) located at El Cometa lagoon (18°28'7"N 92°27'13"W), 25 km from coast, characterized mainly by the presence of *R. mangle* and high contents of organic matter at the bottom (Fig. 1).

Collection methods

Fish early stages were collected using one zooplankton conical net (150 cm length, 50 cm of diameter in mouth and 500 μm mesh). The zooplankton net was supported in a side of the boat by a special structure of steel designed to make horizontal tows in shallow areas and channels (Zavala García y Coto, 2005). Tows were circular of five minutes each, with a fiberglass boat (25 ft. length) with 40 hp outboard motor 1,5 to 2 knots (2,7 to 4 km/h^{-1}) of speed. Samples were fixed in of 4% formaldehyde solution with sodium borate as buffer (Smith y Richardson, 1977). Additional samples of fish early stages were collected using a 9 m beach seine (13 mm bar mesh in the wings and 0.5 mm in the center 3 m section) that was pulled by two people covering an approximate area of 63 m^2 . The haul of this seine was semi circular (1/4 of a circle). Four hauls were made monthly at each location. Collected fishes were stored in labeled plastic bags with 10% formaldehyde inside. Before and after the fish samplings physicochemical parameters were recorded. The transparency of the water was recorded using a 20 cm diameter Secchi disc tied to a rope marked in centimeters; salinity was measured with an Atago $\text{\textcircled{R}}$ refractometer; water temperature ($^{\circ}\text{C}$) and dissolved oxygen (mg/L) were measured with an YSI $\text{\textcircled{R}}$ Oximeter model 55. The pH was measured with an Oakton 35423-10 pH Tester EcoTestr pH 2 $\text{\textcircled{R}}$. Water samples to determine the above-mentioned parameters were obtained with a 5 l van Dorn bottle at an approximate depth of 50 cm.

Bigmouth sleeper identification

Bigmouth sleeper larvae and juveniles were identified and measured at the nearest 1mm of total length (TL). Larvae were separated and examined in search of signs of transition to juvenile stage. Bigmouth sleeper shares estuarine habitats with other eleotrid species morphologically very similar in its early life stages. At CWBR and nearby habitats, it has been documented the presence of *Dormitor maculatus* (Bloch, 1792) and *Eleotris perniger* (Cope, 1871) (Arévalo-Frías y Mendoza-Carranza, 2012). These species present high resemblance at the larval stage; *D. maculatus* is distinguishable from the other two species at 10 mm TL. *G. dormitor* and *Eleotris sp.* are distinguishable at prejuvenile and juvenile stages from 14 mm TL.

Age determination

From each juvenile of bigmouth sleeper collected were taken nine scales from one side of the body: three on the anterior, medium and posterior sections. The scales were cleaned and

mounted on slides and fixed with Cytoseal 60®. The *circuli* of 1728 scales were counted, this scales corresponding to 192 individuals within a TL rank from 15 to 285 mm. Two independent readers counted growth rings (*circuli*) at each scale using an optical microscope. Scales were taken because the morphology of bigmouth sleeper otoliths does not allow the observation of growth marks.

Potential regressions from length at age data of four habitats sampled were performed in order to compare differential growth rates at each habitat sampled. *Circuli* number and total length values were log transformed and regressions were compared using a covariance analysis (ANCOVA) (Bedarf et al., 2001; Zhu et al., 2009).

Age validation

An additional sampling survey in November 2011 was done at riverine habitat in Grijalva River, using a beach seine in order to collect live organisms to validate age-scale rings numbers relation. Twenty-four bigmouth sleeper juveniles from 54 ± 20 mm TL, were collected alive and transported in a plastic container with aeration. In the laboratory fishes were placed in two aquariums (60 L). Aquariums were kept at 27 °C, dissolved oxygen (DO) 5.0 ± 0.5 mg/L, pH 8.0 ± 0.2 conditions and daily water turnover rate of 20%. Fish were fed three times per day with Wardley® basic flakes for tropical fish.

Posteriorly to the individual collection and aquarium adaptation (five days), juveniles were measured (TL mm) and five scales from lateral line, proximal to caudal fin were removed from left side of fish. This procedure was repeated 15 days later extracting scales from right side of fish. Scales were cleaned and mounted on slides and fixed with Cytoseal 60®. Previously to measurement and scale extraction juvenile fish were anesthetized individually in a 2 l container adding a 0.05 ml/L dose of clove oil (Durville y Collet, 2001). Only 8 individuals survived at the end of experiment. Periodicity of growth increments formation was calculated as the average difference in *circuli* before and after the experimental period and expressed as *circuli* by day. Statistical differences between *circuli* numbers were analyzed using a Student's T test of dependent samples (Zar, 2010).

Data analyses

Gobiomorus dormitor density from zooplankton collection was estimated for every habitat sampled following Smith and Richardson (1977), expressed as individual/100m³. The *G. dormitor* density from beach seine collections was transformed to individual number/100m³ by multiplication of sampling area (63m²) by sampling depth.

Mortality rates (year⁻¹) at each sampled environment was estimated using the Lorenzen (1996) model as a power function of weight:

$$M_w = M_u W^b$$

where: M_w is the natural mortality at weight W (dry weight) and b is the allometric scaling factor. Mortality-weight model parameters were based on the estimation for natural tropical ecosystems (Lorenzen, 1996). Additionally, a random function obeying normal distribution was used to bigmouth sleeper early stages mortality estimations considering the 90% confidence intervals provided by Lorenzen (1996).

Since only one growth curve and therefore, only one b value can be determinate for bigmouth sleeper at each environment, we ran a bootstrap routine to estimate probabilistic growth rates for each individual sampled by environment. The interval used in the bootstrap procedure was based in the 95% confidence interval estimated by the non-linear regression using Levenberg-Marquardt's algorithm between the size and determined age by ring counts (Saila et al., 1988; Sparre y Venema, 1997; Rico et al., 2001). The predicted values of b were used to run a principal components analysis (PCA) to estimate the relation between abiotic characteristics of sampled habitats (temperature, dissolved oxygen, salinity and water transparency) and biological parameters of the species (growth rates, density and mortality) (Lepš y Šmilauer, 2003).

Results

Physicochemical parameters

Coastal habitats (GRC and SPC) showed the highest salinity values (11.2 ± 5.9 and 24.4 ± 8.5 respectively), minor salinity values occurred in GRR (0) during all sampling period. VAM presented the highest values of DO (5.9 ± 0.8 mg/L) while ECM showed the lowest (4.5 ± 1.0 mg/L). pH showed a slight variation among habitats, the highest value was showed by VAM (8.4 ± 0.2) and the minor by ECM (7.8 ± 0.2). The temperature were from a minimum of 27.6 ± 1.6 °C in GRC to a maximum of 29.3 ± 2.3 °C (Table 1). The transparency was highest in SPM with 93.2 ± 28.2 cm and the minimum was observed in SPC with 50.1 ± 17.0 cm (Table 1).

(Table 1 here)

Bigmouth sleeper biological parameters

Coastal environments presented high densities of bigmouth sleeper (GRC: 19.86 ± 37.78 ind/100m³ and SPC: 22.74 ± 48.15 ind/100m³ sum up 48.7% of total bigmouth sleeper collected). Remaining habitats show low densities from 0.67 ± 0.47 in GRM to 12.96 ± 36.29 ind/100m³ in SPM (Table 2). Natural mortality pattern present a similar behavior as density being observed highest values at coastal zones of Grijalva (GRC= 3.43 ± 1.39 year⁻¹) and San Pedro y San Pablo rivers (SPC= 3.55 ± 1.44 year⁻¹, Table 2).

Bigmouth sleeper size and age distribution presented gradient from coast to the freshwater environments. Smaller average sizes and ages were observed in SPC (12.18 ± 2.48 mm, 6.26 ± 0.83 days) and biggest sizes and ages were observed at GRM (54.09 ± 54.72 cm, 22.73 ± 32.29 days; Table 2). Growth rates (b) show similar behavior as age-sizes; lower values were observed at coastal environments of both rivers (0.66), higher values were observed at GRM (1.43 ± 0.29) and GRR (1.36 ± 0.71 ; Table 2).

Slopes homogeneity test for growth rates of bigmouth sleeper separated habitats into three groups. The first group consisted of Grijalva River mangrove habitat (GRM) and riverine habitat (GRR) showing a faster growth ($b= 1.43 \pm 0.29$ and 1.36 ± 0.71 respectively).

ANCOVA showed no significant differences between growth curves of these habitats ($F= 1.44$, $p= 0.252$). The second group consisted eelgrass beds habitat (VAM) and San Pedro y San Pablo River habitat (SPR) showing a medium growth rate ($b= 1.30 \pm 0.22$ and 1.22 ± 0.18 respectively), ANCOVA showed no significant differences between growth curves of these habitats ($F= 0.072$, $p= 0.788$). Lowest growth rates were observed in mangrove habitat at El Cometa lagoon (SPM, $b= 0.47 \pm 0.04$) being statistically different ($F= 3.82$, $p=0.000$) from the other habitats with lowest b values as GRC and SPC (Table 2).

(Table 2 here)

Age and growth validation

Scale formation in bigmouth sleeper starts at 15 mm TL and initiates with the scale embossment printed on the skin surface. This engraving begins longitudinally in the lateral line from the posterior to the anterior section of the body and transversally from lateral line to the upper and lower margins. Scales of the posterior part are fully formed when individuals reach 15.5 mm TL. Bigmouth sleeper with complete squamation were found from 16 mm TL. Pigmentation begins in the head and caudal peduncle around 15-16 mm.

The TL-*circuli* number relation were fitted to the potential regressions $TL=a \cdot (\text{circuli number})$

^b. The average periodicity of increments formation is 0.74 increments per day (assuming one

circuli per day). Average initial *circuli* number readings was 67.92 ± 10.44 and average final readings was 79.06 ± 17.07 . Average size increment was $0.7 \pm \square \square \square \square$ mm per day. Despite the increment in *circuli* number, experimental period was too short to detect significant differences between initial and final *circuli* numbers. Student's T test showed no difference between increments formation within sample ($t = -1.64$, $p = 0.14$).

Relation between physicochemical and biological parameters

The first two axes of the PCA accounted for 56.82% (axis 1 38.01% and axis 2 18.81%) of the accumulated variance explaining the relation among physicochemical and biological parameters of bigmouth sleeper (Fig. 2). The best nursery areas for *G. dormitor*, for instance the higher *b* values are associated to low salinity and higher temperature periods, especially in GRM during February, March and May, and in GRR during April, June and July (Fig. 2). High *G. dormitor* density values were associated to high mortality rates under high salinity conditions and were inversely related to growth rate values. Low size and young *G. dormitor* larvae recruited in massive form in the coastal zone, especially in the Grijalva mouth (GRC) during November and December and in San Pedro y San Pablo river mouth (SPC) during December. The relative importance of *V. americana* as nursery is observed since this habitat were associate to relative high growth rate values, however with low *G. dormitor* densities (Fig. 2).

El Cometa mangrove was excluded of the principal PCA, since it presented contrasting conditions between growth rate values against mortality and density values. Despite the high variation in the abundance along the year the *b* values remain low. Then, when the data of this sampling point is included inside the PCA, the inverse relation between growth rate with density and mortality is not observed (Fig. 2).

Discussion

The identification of a nursery is based on the test and comparison of several attributes of these potential nurseries (growth rates, survival and production of recruits to adult population from a designated nursery place). Some of these attributes are difficult to test, specially the contribution of recruits of determinate habitat to the adult population a (Beck et al., 2001). However, in this research we show that growth rate can provide an indirect indicator of the quality of a potential nursery as contributor of recruits. Since the growth rate is increasing, survivorship increases, then the probability that more individuals can recruit to the adult population also increases (Rose et al., 2001; Minello et al., 2003; Bone y Moore, 2008).

A faster growth rate implies some advantageous conditions as abundant food supply, low intra and interspecific competition and predation rates, and a suitable environmental condition (Bakun, 1989; Hare y Cowen, 1997; Houde, 1997; Hixon y Jones, 2005). On the other hand, low growth rates result from low quality habitat conditions as low levels of dissolved oxygen (Phelan et al., 2000), low food intake caused by high inter and intraspecific competition related with high densities (Hixon y Jones, 2005; Shoji et al., 2005; Bone y Moore, 2008). As our PCA shows, high growth rates and low mortality rates of juvenile of bigmouth sleeper are related with freshwater environments with relative high concentration of dissolved oxygen, being these conditions specific for juvenile and larvae of bigmouth sleeper (Nordlie, 2011).

Despite the little knowledge about life cycle of bigmouth sleeper is known that mature females breeding near or in the marine zone (Bacheler et al., 2004; Nordlie, 2011). Since potentially hatching of larvae is in the coastal marine zone, bigmouth sleeper larvae need to travel along estuary to reach a desirable nursery habitat occurring high mortality rates during this process. Then, another critical factor that determines the importance of a habitat as nursery area is the distance from the origin of larvae to potential nursery habitats (Beck et al., 2001). As other species, the production of large broods is a tactic of bigmouth sleeper uses to face this mortality, increasing the probability of the larvae to reach optimal nursery grounds (Winemiller y Rose, 1993; Winemiller, 2005). As was observed in our results, an additional cost of this tactic is that some larvae reaching suboptimal habitats, being reflected as slower growth rates and low probabilities of survival (Rose et al., 2001; Barletta y Saint-Paul, 2010). The relation between time and energy required to reach optimal nursery areas is poorly understood, larval stages depending on passive drifting and relying on rheotaxis could experiment high mortality rates (Hinch et al., 2006; Bone y Moore, 2008).

Low abundances and low growth rates showed by bigmouth sleeper at some environments near from the brooding areas indicate that are not suitable for a good larval development. For the contrary, the distance that larvae of bigmouth sleeper have to travel to reach a desirable nursery habitat as *V. americana* beds in San Pedrito lagoon and El Cometa lagoon, exceeds dispersion by larval drift. In fact, the total larvae abundance at this habitat is low all year round, and the juvenile fish found are principally cichlids, clupeids, engraulids and gerreids (Arévalo-Frías y Mendoza-Carranza, 2012). Habitats with less structural complexity, nearer to coastal zone could be more important as nursery since are easily reached by larvae. A similar trend was observed by (Kopp et al., 2010) when comparing fish assemblages and their size structure between mangrove and seagrass beds habitats near to coral reef, noticing that

assemblages of seagrass-mangrove areas consisted of early juveniles and seagrass reef areas are shelter juvenile of bigger sizes. Also Nakamura *et al.* (2012) found that early juveniles of Pacific yellowtail emperor (*Lethrinus atkinsoni* Seale, 1910) use as nursery seagrass beds next to their spawning site. Although this habitat is used for food and shelter, 90% of natural mortality occurs there while older juveniles move to coral reefs where mortality decreases.

The mangrove ecosystem with high structural complexity, can be appointed as an important nursery area, however el Cometa lagoon with a well conserved mangrove habitat, do not reach the expected conditions as a nursery area; this is reflected in the low growth rates exhibited by juveniles at this place despite the higher or lower abundances presented along year. Abnormal daily ring increments, impairment and disruptions in scales of *G. dormitor* collected at El Cometa Lagoon indicate adverse environmental conditions that influence the growing process (lowest dissolved oxygen concentration, lowest pH and highest transparency). Similar effects are observed in juvenile of the red drum *Sciaenops ocellatus* (Linnaeus, 1766) for food deprivation and in the medaka *Oryzias melastigma* (McClelland, 1839) juveniles exposed to long-term hypoxia (Cheung *et al.*, 2007). Conversely Grijalva river mangrove and riverine habitats are suitable nursery grounds for bigmouth sleeper, offering a combination of abiotic factors (low values of salinity, medium values of dissolved oxygen concentration and a relative short distance from the hypothetical breeding zones) related to highest growth rates, high densities and highest survival rates. The differential importance between similar and potentially important habitat (mangrove) as suitable nursery areas, could be attributed to differences in distance from the brooding areas of bigmouth sleeper (Beck *et al.*, 2001; Beck *et al.*, 2003a; Nordlie, 2011). While Grijalva Mangrove (Polo stream) is 15 km from the coastal zone, El Cometa lagoon is 25 from coast, being, being more difficult to the larvae reach this last habitat.

Continuous monitoring of abundances and distribution patterns (age/size classes) complementary to growth rates determination are highly recommended towards the understanding ecological dynamics relying on habitat nursery function since nursery importance is a dynamic concept where species and habitats present changes along time (Beck *et al.*, 2001; Gillanders *et al.*, 2003; Minello *et al.*, 2003). Additionally, a detailed knowledge of the life cycle of the species and fish assemblages dynamics are fundamental to understand the relative importance as nursery grounds of habitats occupied by larvae and juveniles fishes (Secor y Rooker, 2005).

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Figures

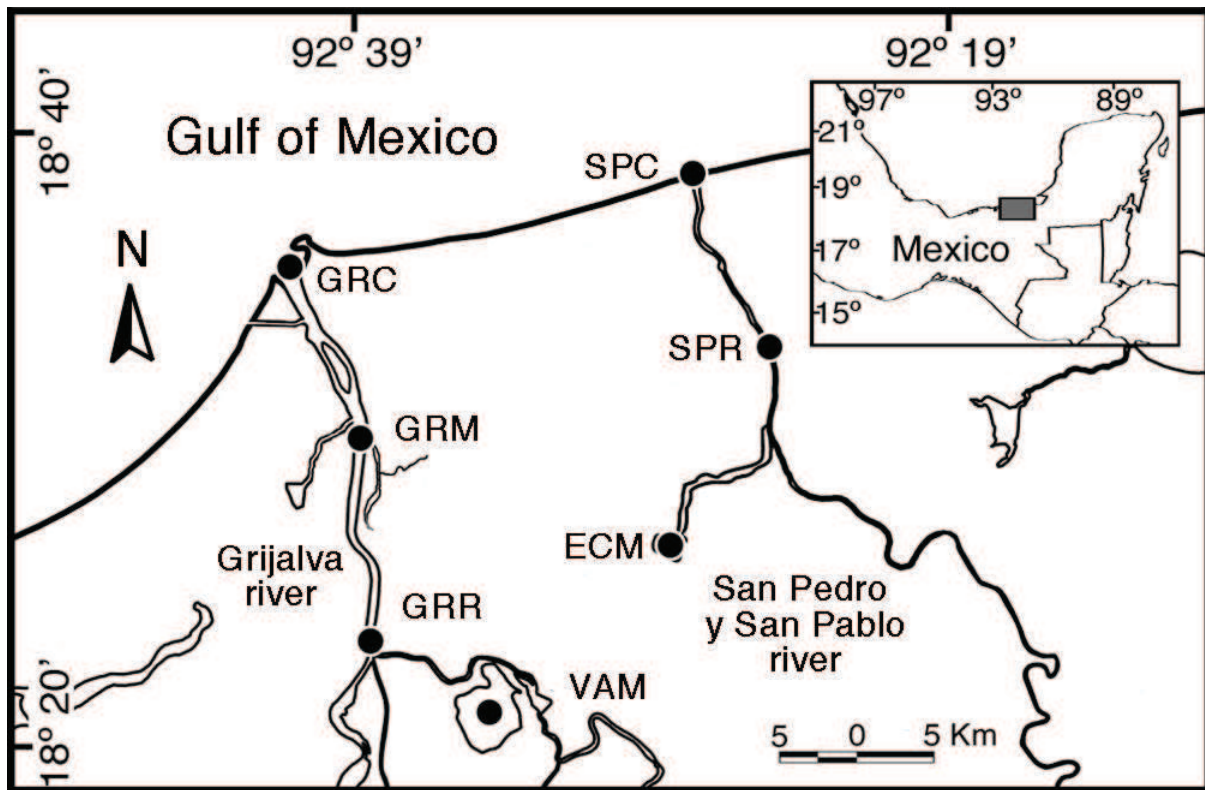


Fig. 1. Sampling points at Centla Wetlands Biosphere Reserve (dots), GRC= Grijalva coast, GRM= Grijalva mangrove, GRR= Grijalva river, VAM= *Vallisneria americana* beds, SPC= San Pedro y San Pablo coast, SPR= San Pedro y San Pablo river and ECM= El Cometa mangrove.

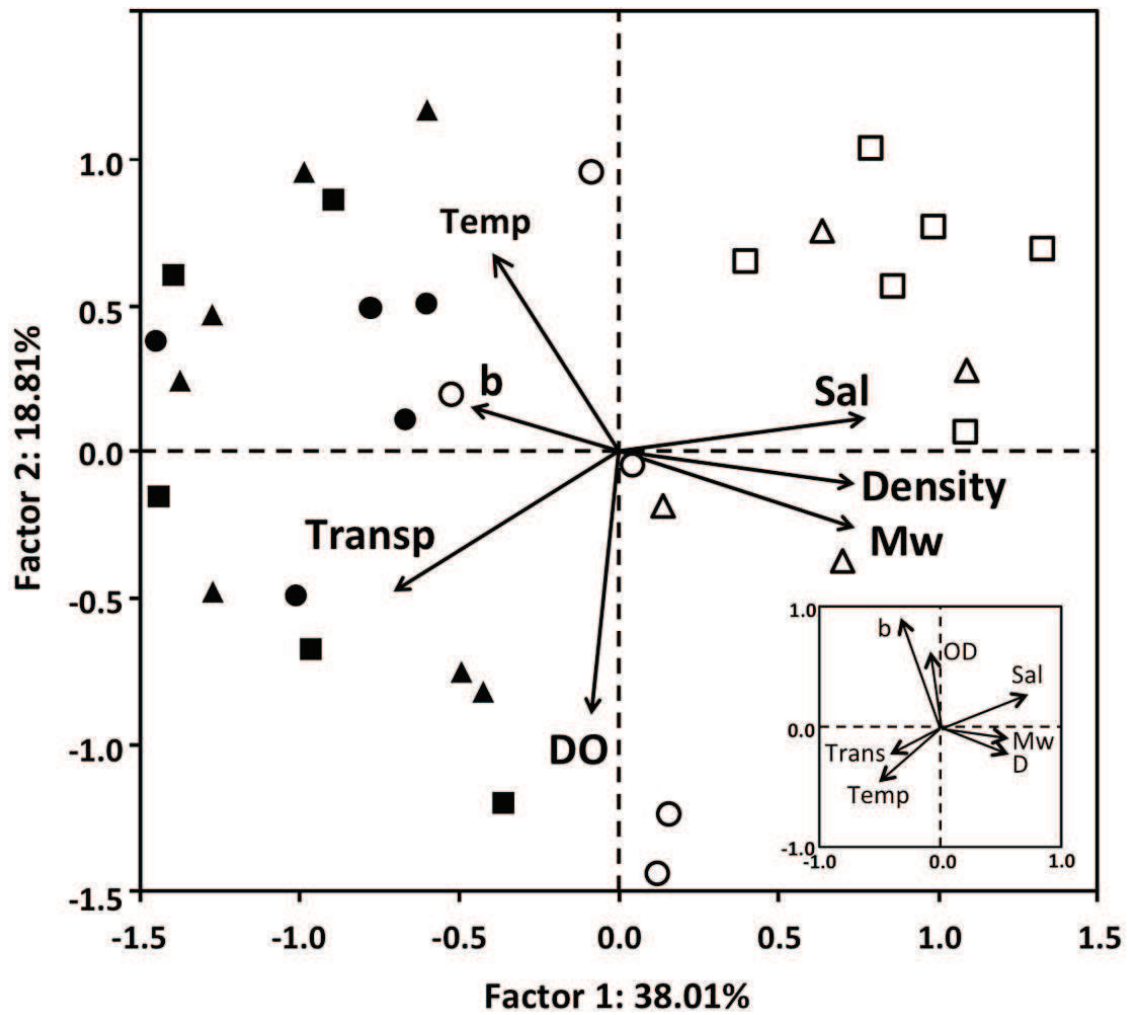


Fig. 2. PCA ordination plot for environmental and biological parameters of juvenile *Gobiomorus dormitor* in Centla Wetlands Biosphere Reserve. Grijalva mangrove = closed squares, Grijalva river = closed circles, *Vallisneria americana* beds = closed triangle, San Pedro river = open circles, Grijalva coast = open triangles, San Pedro coast = open squares. Right down PCA ordination plot including El Cometa mangrove (D=density).

Table 1. Environmental parameters at estuarine habitats from CWBR. GRC: Grijalva coast, GRM: Grijalva mangrove, GRR, Grijalva river, VAM: *Vallisneria americana* beds SPC: San Pedro y San Pablo coast, SPM: San Pedro y San Pablo mangrove and SPR: San Pedro y San Pablo river.

Habitat	Salinity (ups)	Dissolved oxygen (mg/l)	pH	Temperature (°C)	Transparency (m)
GRC	11.2 ± 5.9	5.3 ± 0.6	8.0 ± 0.0	27.6 ± 1.6	69.2 ± 16.5
GRM	0.4 ± 0.7	5.2 ± 1.0	8.0 ± 0.2	28.3 ± 2.4	67.0 ± 23.1
GRR	0.0 ± 0.0	5.4 ± 0.8	8.1 ± 0.1	29.3 ± 2.3	57.5 ± 20.7
VAM	0.1 ± 0.2	5.9 ± 0.8	8.4 ± 0.2	29.2 ± 2.8	73.5 ± 26.2
SPC	24.4 ± 8.5	5.3 ± 0.7	8.1 ± 0.1	28.2 ± 2.5	50.1 ± 17.0
SPM	1.8 ± 2.6	4.5 ± 1.0	7.8 ± 0.2	28.9 ± 3.1	93.2 ± 28.2
SPR	0.4 ± 1.3	5.2 ± 0.9	8.0 ± 0.2	29.1 ± 2.7	63.2 ± 27.8

Table 2. Biological parameters of *Gobiomorus dormitor* from estuarine habitats at CWBR. GRC: Grijalva coast, GRM: Grijalva mangrove, GRR, Grijalva river, VAM: *Vallisneria americana* beds, SPC San Pedro y San Pablo coast, SPM: San Pedro y San Pablo mangrove, and SPR: San Pedro y San Pablo river.

Habitat	Density ± SD	Mortality	Total length	Age	Length at age parameter equation	
	Ind·100 m ⁻³	Year ⁻¹ ±95%CI	mm ± SD	Days ± SD	a± 95%CI	b± 95%CI
GRC	19.86 ± 37.78	3.43 ± 1.39	12.23 ± 6.57	12.40 ± 3.59	2.43 ± 0.20	0.66 ± 0.25
GRM	0.67 ± 0.47	1.91 ± 1.19	54.09 ± 54.72	22.73 ± 32.29	0.06 ± 0.03	1.43 ± 0.29
GRR	3.24 ± 3.65	0.11 ± 0.09	24.14 ± 31.80	6.84 ± 13.37	0.07 ± 0.27	1.36 ± 0.71
VAM	0.96 ± 0.64	2.05 ± 1.10	36.78 ± 32.01	15.77 ± 18.47	0.13 ± 0.14	1.30 ± 0.22
SPC	22.74 ± 48.15	3.55 ± 1.44	12.18 ± 2.48	6.26 ± 0.83	1.21 ± 0.10	0.66 ± 0.27
SPM	12.96 ± 36.29	3.02 ± 1.57	18.87 ± 8.67	16.27 ± 3.59	4.20 ± 1.06	0.47 ± 0.04
SPR	3.18 ± 6.66	2.21 ± 1.11	26.04 ± 15.50	10.70 ± 8.47	0.19 ± 0.15	1.22 ± 0.18

Capítulo IV. Larval fish size comparison in tropical estuarine environments.

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Larval fish size structure comparison in tropical estuarine environments

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Abstract

The size structure of fish larvae in estuarine environments was analyzed to assess indirectly different habitats quality as nursery. A total of 432 zooplankton samples were collected (June 2004 to May 2005) with horizontal tows using a 500 µm mesh size conical net, in sandy beach, mangrove, river and submerged aquatic vegetation (*Vallisneria americana*) of the Grijalva and San Pedro y San Pablo Rivers, Mexico. A total of 32 species were found, 14 occurred in both riverine systems, 10 occurred only in Grijalva River and 9 species in San Pedro y San Pablo River. Fish larvae lengths indicated that most species from Grijalva River are larger than San Pedro y San Pablo River ones. Maximum median larvae sizes were observed in *Sinodus foetens* (51 mm) in the Grijalva coast and *Elops saurus* (39 mm) in Grijalva and San Pedro y San Pablo coasts (39 mm). Only *Anchoa hepsetus* and *Gobiomorus dormitor* were present in all estuarine environments. Significant differences of the species lengths shared in both rivers indicated better growth conditions in Grijalva River system (Kruskal-Wallis and Mann-Whitney tests). Described differences in size of larvae could be related to differences in feeding and environmental conditions for fish larvae development.

Key words: body size, larval assemblage, nursery grounds, mangrove, coastal zone, estuaries.

Comparación de la estructura de tallas de larvas de peces en ambientes estuarinos tropicales.

Resumen

La estructura de tallas de larvas de peces en ambientes estuarinos fue analizada con el objetivo de determinar diferencias en la calidad de los hábitat como áreas de crianza. Un total de 432 muestras de zooplancton fueron colectadas (junio 2004- mayo 2005) con ayuda de una red cónica de zooplancton de 500 µm de luz de malla en zonas de playas, manglar, margen de río y sobre vegetación acuática sumergida (*Vallisneria americana*) en los ríos Grijalva y San Pedro y San Pablo en el sureste de México. Se identificó un total de 32 especies de larvas de peces, 14 ocurrieron en ambos ríos, 10 ocurrieron solo en el Grijalva y 9 en el rio San Pedro y San Pablo. Las máximas medianas de tallas fueron observadas en *Sinodus foetens* (51 mm) en la zona costera del Grijalva y *Elops saurus* (39 mm) en la zona costera de ambos ríos. Solamente *Anchoa hepsetus* y *Gobiomorus dormitor* estuvieron presentes en todos los hábitat muestreados. Se detectaron diferencias significativas (Kruskal-Wallis y Mann-Whitney) entre los tamaños de larvas de ambos ríos y ambientes. Las diferencias observadas pueden estar relacionadas a diferencias en abundancia de alimentos y condiciones ambientales.

Palabras clave: estructura de tallas, áreas de crianza, manglares, zonas costeras, estuarios

Introduction

Estuarine environments support great abundance of juvenile fishes and invertebrates, including highly importance commercial species (Able 2005, Nagelkerken 2009), being considered as conservation priority zones (Heck *et al.* 2003, Sheridan and Hays 2003). These environments have been indicated as important nursery areas for juvenile fish, however few studies had been focused to compare the relative importance of different sites in broad estuarine areas (Kraus and Secor 2005). Most of this research has been focused in the diversity and abundance of larvae species analyses (e.g. Arceo-Carranza *et al.* 2010, Espino *et al.* 2011, Mwaluma *et al.* 2011, Ooi and Chong 2011, Rodríguez-Romero *et al.* 2011, Yagi *et al.* 2011, Vacchi *et al.* 2012, Kent *et al.* 2013) leaving aside other important population attributes related to the habitat quality, such as the condition of the organisms that occupy specific habitats which is closely related to the larvae survival (Minello *et al.* 2003, Booth and Beretta 2004, Houde 2008a).

The access of fish larvae to optimal nursery habitats is critical for their survival, and it mainly depends on biological processes, such as adult breeding areas selection and the coupling of physical processes, as the flow currents and tides for the subsequent dispersion of larvae to potential nursery habitats (Peterson *et al.* 2000, Sheridan and Hays 2003, Strydom and Wooldridge 2005). Once these larvae occupy certain environments, its survivors will depend on the quality of habitat (e.g. dissolved oxygen, salinity, currents) (Phelan *et al.* 2000), and especially of the food availability (Wootton 1999, Houde 2008). Since growth rates are associated to habitat quality then is possible to use the size of larvae as indirect indicator of environment quality (Stunz *et al.* 2002). However, scarce information is provided regarding specific size structure from larval assemblages (Hermosilla *et al.* 2012).

In addition to the above mentioned, an important technical issue in relation to the comparison of the larvae size among several estuarine environments is the collection method, since this will determine the collected size distribution of larvae (Johnson *et al.* 2012), also a homogeneous collection method is critical to avoid bias (Pepin and Helbig 2012, Johnson and Fogarty 2013). There are several methods for zooplankton collection, however the most extensively used is the conical zooplankton net (Johnson *et al.* 2012). For this reason this study aims to test for differences in the body size distribution of larval fish among several environments (coast, river, mangrove and eelgrass beds areas) in a tropical estuarine zone, focusing on the use of conical zooplankton net and additionally introducing a modification that allow homogeneous tows among shallow aquatic environments. A structure designed to make horizontal tows in shallow areas (Zavala García and Coto 2005).

Materials and methods

Study site

Monthly zooplankton samples were obtained in estuarine environments during a year (June 2004 to May 2005). The Grijalva River system: 1) Coastal area (18°35'08"N 92°42'22"W), characterized by brackish-marine environments and sandy beaches; 2) Mangrove Environment (18°30'00"N 92°39'05"W) dominated by riparian mangrove forest mainly *Rhizophora mangle* L.; 3) Riverine Environment (18°24'22"N 92°38'56"W) characterized by soft muddy bottoms without submerged aquatic vegetation; and 4) Eelgrass Beds (18°24'22"N 92°38'56"W), characterized by the presence of dense beds of eelgrass *Vallisneria americana* Michx. surrounded by reeds and swamp vegetation (Fig. 1). In the San Pedro y San Pablo River systems the sampled habitats were: 5) Coastal Area (18°38'46"N 92°28'02"W), characterized by sandy beaches and brackish-marine environments; 6) Riverine environment (18°35'35"N 92°26'53"W), characterized by riparian modified vegetation on its banks, mainly livestock forage; and 7) Mangrove Environment (18°28'7"N 92°27'13"W), characterized by the presence of *R. mangle* and high contents of organic matter at the bottom (Fig. 1).

Sample collection and process

A total of 432 samples (three samples per site per month) were obtained using one zooplankton conical net (150 cm length, 50 cm of diameter in mouth and 500 μ m mesh). The zooplankton net was attached to the side of a boat (with a 25 ft length fiberglass boat with a 40 hp outboard motor) by a special designed steel structure to make horizontal tows in shallow areas and channels (Zavala-García and Flores-Coto, 2005). Each sample was collected with circular tows of five minutes each at 1,5 to 2 knots (2,7 to 4 $\text{km}\cdot\text{h}^{-1}$) of speed. Samples were fixed in of 4% formaldehyde solution with sodium borate as buffer (Smith and Richardson 1977). Fish larvae and juveniles were separated and identified to the lowest taxonomic level. Only organisms identified to species level were included in the analyses.

Data analysis

The frequency distribution of fish larvae total length median (interquartile range) values was assessed for the different estuarine habitats from Grijalva River and San Pedro y San Pablo River systems. Median sizes of fish larvae of the species shared by both rivers were statistically compared using the Kruskal-Wallis test to compare samples sites when more than two of samples were available, and the Mann-Whitney test when only one pair of data was present (Zar 2010, Sokal and Rohlf 2012).

Results

A total of 32 species were found in the estuarine habitats of Grijalva River and San Pedro y San Pablo River systems. From the total 10 species were found exclusively in the Grijalva River system and 9 species in the San Pedro y San Pablo River system, and 14 species were found in both systems (Table I) Higher total number of larvae were collected at San Pedro and San Pablo River, specifically in the coastal (5) and riverine (6) environments (Table I, Fig. 1).

Maximum median larvae sizes were observed in *Sinodus foetens* (51 mm) in the Grijalva coastal zone and *Elops saurus* in Grijalva y San Pedro y San Pablo coast (39 mm). *Achirus linneatus* and *Sinodus foetens* larvae were the littlest (3 mm). Higher size ranges were observed in *Gobiomorus dormitor* (37 mm), *Elops saurus* (36 mm) and *Anchoa mitchilli* (36 mm, Table I). Fish larvae were most abundant at the coastal zone, and only *Anchoa hepsetus* and *Gobiomorus dormitor* were present in all estuarine environments (Table I). Kruskal-Wallis and Mann-Whitney tests showed significant differences in total length of fish larvae species between environments (Table I).

When the size species data are grouped by river is observed that median size from *A. hepsetus* (25% quartile= 7 mm, median= 10 mm, 75% quartile= 16 mm), *Chaetodipterus faber* (9 -9.5- 10), *Chloroscombrus chrysurus* (17 -27.5- 31), *Elops saurus* (37 -39- 41), *Etropus crossotus* (11.5 -12.5- 13), *G. dormitor* (-10-), *Megalops atlanticus* (24 -25- 26), *Micropogonias furnieri* (10 -17- 20), *Mugil curema* (29 -31- 32) and *Synodus foetens* (38 -51- 64) were significantly larger in Grijalva River environments than in San Pedro y San Pablo River environments. Only *Achirus lineatus* (-3-) and *Spherooides maculatus* (10 -12- 15) were larger in San Pedro y San Pablo River environments than those collected in the Grijalva River system (Fig. 2).

Discussion

Since Beck et al. (2001) presented their hypothesis about nursery importance determination; several researches have been focused on solving or testing this hypothesis (Heck et al. 2003, Minello et al. 2003, Sheridan and Hays 2003). The most commonly argument to test the hypothesis of Beck et al. (2001), is the abundance and diversity comparison among habitats or regions (Heck et al. 2003, Dahlgren et al. 2006, Nagelkerken 2009), and rarely growth rates, survival and movement to adult habitat has been applied (Gillanders et al. 2003, Dahlgren et al. 2006, Nakamura et al. 2008).

Size distribution is a common and useful tool to assess commercial fish stocks (Genner et al. 2010, King 2013, Sundblad et al. 2013). However, is barely used to describe and to compare larval fish communities (e.g. Machado et al. 2011). Hermosilla et al. (2012) propose size structure of fish larvae as a convenient way to assess the quality of habitats for development and successful recruitment of fish. According to the former, this study suggests that size structure analysis, in addition to abundance determination, is a viable approach to compare the potential of habitats as nursery grounds.

Few researches on larval fish have been focused on size structure analysis, some authors have related body size to competition (Nakayama and Fuiman, 2010, Wasserman 2012), habitat loss (Wilson et al. 2010) and ontogenic habitat shift (Nakamura et al. 2012). The differences found on the size of fish larvae community, and specially in those shared species in both systems (Grijalva River and San Pedro y San Pablo River) could indicate suitability differences of each system as nursery grounds enhancing a faster growth. A faster growth rate (for instance big sizes) is critical to the survival of the individuals, the reduction of the time that a fish live as larvae will increase the possibilities to reach the juvenile stage diminishing the mortality probabilities (Beyer et al. 1999, Houde 2008). Since

growth rates are difficult to evaluate at field, then an indirect indicator of the quality of habitat on the larval growth could be the comparison of the size frequency distribution at similar times, though some assumptions are required a) that larvae groups come from the same spawning event, population and species, b) the comparison has to be done on the same period of time and c) the collection method has to be homogeneous (Johnson and Fogarty 2013). Within this framework, differences in larvae sizes among environments can be related the influence of external factor as physicochemical conditions, food availability and predators abundance.

More studies should be focused to understand how environmental and biological conditions (and coupled physical-biological processes) particularly affect larval development and survival in the zone. This has been already observed in fish eggs (Brooks *et al.* 1997) and in the survival and growth of larvae (Sabo *et al.* 1991). Also, long-term monitoring surveys are suggested to understand fish larvae habitat use dynamics, and to detect changes in community composition and size structure related the impact of multiannual processes as the ENSO (El Niño Southern Oscillation), and global climate change in tropical estuarine systems (Lo Yat *et al.* 2011, Acha *et al.* 2012).

Size structure is a good indicator of health of a population, being important to include as an indirect comparative parameter of quality of habitats when is designated as nursery grounds. Big organism could indicates abundant food sources, low competition and predation (Beck *et al.* 2001, Wasserman 2012). Additionally, it is necessary to perform comparative studies about larval age and growth rates at different habitats occupied by the one species during its early life stages, this could be a good indicator of the contribution of determinate habitat to recruits to adult populations therefore indicating high quality nursery grounds (Beck *et al.* 2001, Beck *et al.* 2003, Houde 2008).

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Table I. Minimum > 25% quartile – median – 75% quartile < maximum total length and individual numbers of fish larvae in estuarine environments of Centla Wetlands Biosphere Reserve, Tabasco, Mexico.

Species	Grijalva River		San Pedro y San Pablo River	
	Coast ^a	Mangrove ^b River ^c SAV ^d	Coast ^e	Mangrove ^f River ^g
<i>Achirus lineatus</i>	2 > 3-3-4 < 4 (388) ^e		2 > 3-3-3 < 5 (315)	4 (2)
<i>Anchoa hepsetus</i>	5 > 10-14-18 < 38 (302) ^{b,c,e}	2 > 5-5-7 < 15 (76) ^{sg} 5 > 7-8-9 < 10 (36) ^{sg} 7 > 8-9-14 < 19 (11) ^e	3 > 13-16-20 < 34 (6845)	8 > 8-16-17 < 17 (3) 8 > 10-13-15 < 17 (21)
<i>Anchoa mitchilli</i>	8 > 18-21-22 < 36 (3536)		3 > 15-20-24 < 39 (684)	7 > 17-18-21 < 36 (895) 9 > 18-21-24 < 38 (2392) ^{ef}
<i>Archosargus probatocephalus</i>			3 > 5-6-6 < 7 (28)	9 > 9-9.5-10 < 10 (2)
<i>Archosargus rhomboidalis</i>	7 (1)			
<i>Atherinella alvarezi</i>			22 (3)	
<i>Chaetodipterus faber</i>	7 > 9-9.5-10 < 14 (6) ^e		5 > 6-6-8 < 13 (19)	
<i>Chloroscombrus chrysurus</i>	15 > 17-27.5-31 < 35 (10) ^e		6 > 10-11-28 < 37 (119)	
<i>Cynoscion arenarius</i>	3 > 3-3-4 < 15 (9) ^e		3 > 4-5-6 < 7 (24)	
<i>Diapterus rhombeus</i>			5 > 8-8-9 < 10 (48)	
<i>Dorosoma petenense</i>				13 > 22-23-25 < 30 (21)
<i>Elops saurus</i>	21 > 37-39-41 < 57 (2958)	36 (1) SAV	27 > 37-39-40 < 56 (559)	31 > 34-35-37 < 39 (42) ^{ac}
<i>Eitropus crossotus</i>	11 > 12-13-13 < 13 (7) ^e	10 (1) SAV	9 > 10-10-11 < 12 (179)	
<i>Eugerres plumieri</i>	7 > 7-7.5-8 < 8 (2)			
<i>Gobiomorus dormitor</i>	6 > 10-10-10 < 34 (1410) ^{ef,sg}	9 > 10-10-11 < 23 (7) 9 > 10-10-11 < 23 (103)	1 > 10-10-11 < 18 [2207]	2 > 10-10-11 < 16 (980) 2 > 10-11-13 < 39 (427) ^{cef}
<i>Gobionellus oceanicus</i>		10 (2)	8 > 13-14-17 < 19 (346)	15 > 15-16-17 < 17 (3) 13 (1)

<i>Gobiox strumosus</i>		11(1)	
<i>Harengula jaguana</i>	31 >32- 33 -39< 39 (7)		
<i>Hyporhamphus mexicanus</i>			17(1)
<i>Lutjanus griseus</i>	10 >12- 13 -14< 15 (23)		
<i>Lutjanus synagris</i>	15 >18- 20 -21< 22 (6)		
<i>Megalops atlanticus</i>	22 >24- 25 -26< 28 (76) ^e	16 >23- 25 -25< 28 (62)	23(1)
<i>Menicirrhus americanus</i>	24 >24- 24 -26< 26 (3)		
<i>Micropogonias furnieri</i>	2 >10- 17 -20< 37 (133) ^e	14 (3)	
<i>Stephanolepis hispidus</i>	120(1)		
<i>Mugil curema</i>	23 >29- 31 -32< 32 (12) ^e	14 >20- 21 -23< 35 (109)	
<i>Opisthonema oglinum</i>	19 >32- 34 -35< 36 (9)		
<i>Selene vomer</i>	40(1)		
<i>Sphoeroides maculatus</i>	7 >7.5- 8 -9< 10 (4)	3 >10- 12 -15< 19 (6)	
<i>Synodus foetens</i>	38 >38- 51 -64< 64 (6) ^e	29 >32- 35 -35.5< 38 (14)	
<i>Trachinotus falcatus</i>		12(1)	
<i>Trichiurus lepturus</i>		20 >24- 27 -29< 31 (30)	

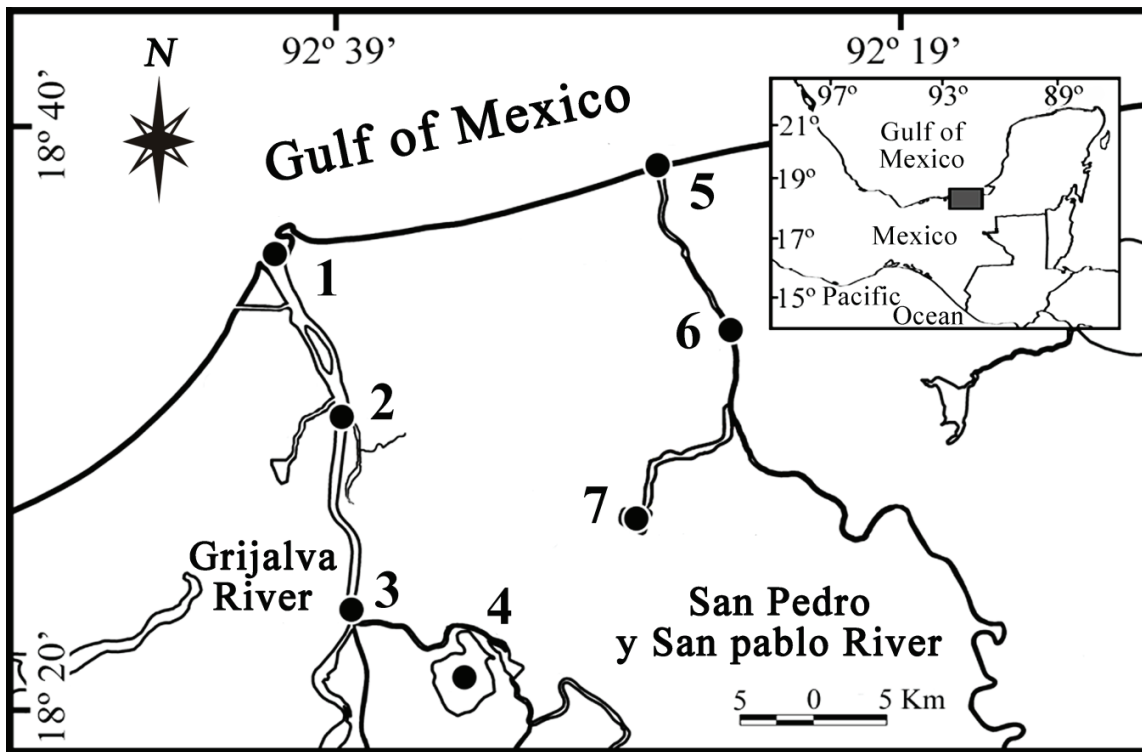


Figure 1. Sampling points at estuarine environments at Grijalva-Usumacinta lower basin, Tabasco Mexico. 1) Grijalva coast, 2) Grijalva mangrove, 3) Grijalva river, 4) Submerged aquatic vegetation (*Vallineria americana*), 5) San Pedro y San Pablo coast, 6) San Pedro y San Pablo river, 7) San Pedro y San Pablo mangrove.

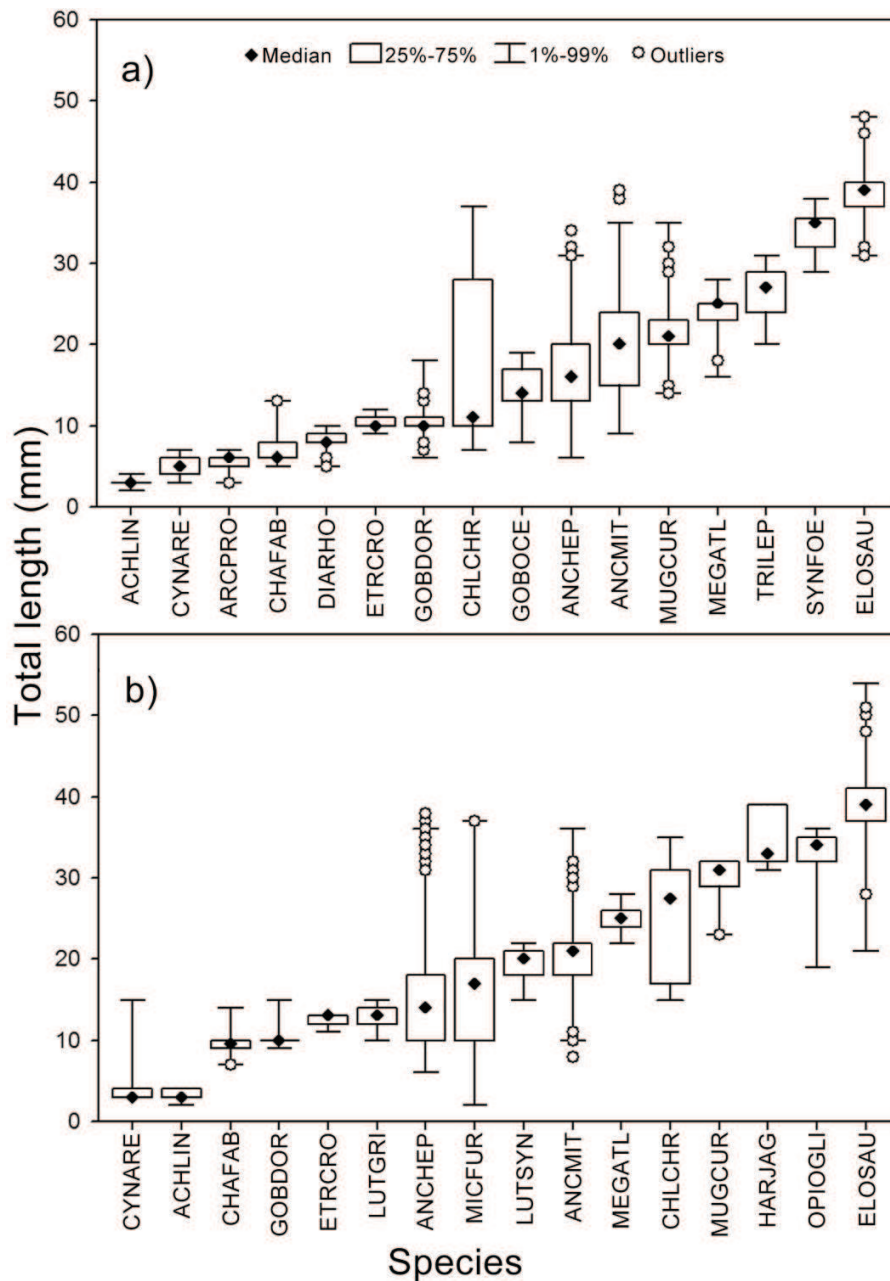


Figure 2. Size frequency distribution of the larvae species occurring in both Grijalva River (a) and San Pedro y San Pablor River (b). ACHLIN= *Achirus linneatus*, CYNARE= *Cinocion arenarius*, ARCPRO= *Archosargus probatocephalus*, CHAFAB= *Chaetodipterus faber*, DIARHO= *Diapterus rhombeus*, ETRCRO= *Etropus crossotus*, GOBDOR= *Gobiomurus dormitor*, ANCHEP= *Anchoa hepsetus*, ANCMIT= *A. mitchilli*, MUGCUR= *Mugil curema*, MEGATL= *Megalops atlanticus*, TRILEP= *Trichiurus lepturus*, SYNFOE= *Synodus foetens*, ELOSAU= *Elops saurus*.

Consideraciones finales

La información generada en esta investigación proporciona una línea base para el conocimiento acerca de larvas de peces en Tabasco. Su contribución al conocimiento de la diversidad ictiofaunística es alta en relación con trabajos previos realizados en la región, debiéndose principalmente a las diferentes estrategias e intensidades de muestreo y al número de ambientes estudiados. Sin embargo, es necesaria la incorporación de otras técnicas que permitan la colecta de especímenes en hábitats de difícil acceso, como lo son las raíces adventicias y neumatóforos de los mangles y la parte inferior de los mantos de *Vallisneria americana*. Además es importante incluir dentro de estos estudios el análisis de la distribución vertical de la comunidad de larvas pues muchos de sus movimientos entre las áreas de desove y las áreas de crianza se relacionan directamente con las corrientes de entrada y salida en las zonas estuarinas (Ellis et al., 2012; Ospina-Álvarez et al., 2012; El-Regal, 2013).

Nagelkerken (2009) menciona que, para fines de conservación, la importancia de un ambiente como área de crianza también debe determinarse a través del número de especies de importancia comercial cuyos juveniles ocurren en altas abundancias en la zona. En nuestro caso fueron identificadas 17 especies de larvas y 42 especies de juveniles de peces con importancia comercial, lo cual refuerza la importancia de las áreas costeras de la RBPC para el desarrollo y reclutamiento de especies explotadas en la zona. A pesar del elevado número de especies encontradas es importante considerar que muchas de ellas presentan historias de vida diferentes y por tanto el uso de áreas de crianza difiere en relación a su desarrollo ontogénico.

La identificación de la hora del día y la temporada como los principales factores que determinan la variación de la riqueza y abundancia de larvas de peces, permite la

optimización de los esfuerzos y costos de muestreo, además de proveer datos útiles para la elaboración de un modelo de ajuste de abundancias que permita corregir datos provenientes de muestreos diurnos. Este estudio es novedoso ya que incorpora las principales fuentes de variación que afectan las estimaciones de abundancia y riqueza, a diferencia de trabajos que abordan de manera parcial esta problemática (e.g. Wantiez et al., 2007; Hernández-León, 2008; D'Alessandro et al., 2010). Los estudios futuros en los que se cuantifique la abundancia de larvas de peces deberán considerar que las mayores abundancias ocurren en la noche y en temporada de secas en estuarios tropicales y subtropicales. Adicionalmente, el desarrollo de esta investigación proporcionó nuevos datos sobre la ocurrencia de estadios larvarios de la especie invasora *Pterygoplichthys sp.* en ambientes salobres de la desembocadura del río Grijalva.

Otro resultado importante de esta investigación es que el análisis de las tasas de crecimiento constituye una valiosa herramienta que nos permite realizar una evaluación rápida del valor del hábitat para una especie en particular; siendo posible determinar que altas tasas de crecimiento se relacionan con hábitats óptimos confirmados de forma independiente por medio de agrupamientos a través del análisis canónico de correspondencia. Dentro de este planteamiento es necesario considerar las características de la especie objetivo y el método por el cual se establecerá la edad. En este caso, la determinación de la edad en *G. dormitor* se pudo determinar a través del conteo de incrementos diarios en las escamas debido a que la morfología del otolito aunado al tamaño del mismo no permite que se puedan distinguir incrementos diarios. La validación de su crecimiento a través de estudios de laboratorio fue muy satisfactorios, teniendo de esta forma una base sólida en la determinación de edad de

individuos de vida silvestre. Así mismo, la combinación de los valores de densidad y edad de larvas y juveniles de la especie permitió el cálculo de la mortalidad natural en los diferentes ambientes muestreados, confirmando que el crecimiento y la mortalidad son procesos estrechamente relacionados (Houde, 2008).

El análisis de la estructura de tallas de larvas de peces como aproximación de la calidad de hábitat propuesto para evaluar su función como áreas de crianza, no arrojó resultados concluyentes, a pesar de que el tamaño es un indicador del crecimiento y representa la calidad intrínseca de los hábitats (Le Pape et al. 2003).

Esta evaluación de las áreas de crianza proporciona información crítica necesaria como fundamento para la toma de decisiones sobre conservación y protección de los recursos naturales. Sin embargo, es preciso llevar a cabo estudios complementarios, como la determinación del ingreso de los juveniles a los hábitats ocupados por los adultos, lo cual puede lograrse por medio de diversas técnicas de marcaje y estudios moleculares (Gillanders et al., 2003; Vasconcelos et al., 2011), así como la realización de monitoreos continuos que incorporen las variaciones espaciales y temporales que pueden afectar en la ocurrencia y abundancia de las diferentes especies de peces que se distribuyen en la región, además de integrar medidas de productividad del ambiente, condición nutricional de larvas y juveniles y cambios en los regímenes del ecosistema. La identificación de hábitats de alta calidad para la conservación, restauración y manejo, permitirá establecer estrategias efectivas para asegurar la permanencia de las poblaciones adultas de especies que sostienen la actividad pesquera, así como para reforzar y justificar aún más la necesidad de la conservación estos importantes hábitats, protegiendo así los servicios ecosistémicos que estos prestan.

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