UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA

ECOLOGÍA

EVALUACIÓN DEL FLUJO ENERGÉTICO Y DE LA ESTRUCTURA TRÓFICA DE DOS SISTEMAS LAGUNARES-ESTUARINOS DEL SUR DEL PACÍFICO MEXICANO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

JESÚS MANUEL LÓPEZ VILA

TUTOR PRINCIPAL: **DR. ERNESTO VELÁZQUEZ VELÁZQUEZ**
INSTITUTO DE CIENCIAS BIOLÓGICAS, UNICACH
COTUTOR: **DR. ISAÍAS HAZARMABETH SALGADO UGARTE**
FACULTAD DE ESTUDIOS SUPERIORES ZARAGOZA, UNAM
COMITÉ TUTOR: **DR. JUAN JACOBO SCHMITTER SOTO**
DEPARTAMENTO DE SISTEMÁTICA Y ECOLOGÍA ACUÁTICA, ECOSUR

MÉXICO, CD. MX.   OCTUBRE, 2019.

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OFICIO CPCB/1046/2019

Asunto: Oficio de Jurado para Examen de Grado.

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología, Manejo Integral de Ecosistemas, Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 29 de julio de 2019, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **LÓPEZ VILA JESÚS MANUEL** con número de cuenta **515016143** con la tesis titulada: **"Evaluación del flujo energético y de la estructura trófica de dos sistemas lagunares-estuarinos del sur del Pacífico mexicano"**, realizada bajo la dirección del **DR. ERNESTO VELÁZQUEZ VELÁZQUEZ**:

Presidente:	DR. ALFREDO LAGUARDA FIGUERAS
Vocal:	DRA. DENI CLAUDIA RODRÍGUEZ VARGAS
Secretario:	DR. JUAN JACOBO SCHMITTER SOTO
Suplente:	DRA. GABRIELA VÁZQUEZ HURTADO
Suplente	DR. JAIRO ANDRÉS ARROYAVE GUTIÉRREZ

Sin otro particular, me es grato enviarle un cordial saludo.

A T E N T A M E N T E
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx., a 30 de septiembre de 2019.

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

POSGRADO EN CIENCIAS BIOLOGICAS
COORDINACIÓN

c.c.p. Expediente del (la) interesado (a).

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Con mucho amor a la vida y obra de **Adán Enrique Gómez González**

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ÍNDICE

RESUMEN

Los modelos tróficos son herramientas para identificar propiedades holísticas de los ecosistemas, no evidentes a partir de observaciones directas. Estos modelos son primordiales si se desea analizar el funcionamiento y estructura de ecosistemas complejos y altamente cambiantes, como las lagunas costeras. La confluencia de dos masas de aguas distintas (marina y dulceacuícola) origina un gradiente físico-químico que propicia una heterogeneidad ambiental, la cual alberga una biodiversidad adaptada a este mosaico abiótico. Además de la diversidad biológica, las lagunas costeras brindan bienes y servicios ambientales, como regulación hídrica, recreación, y provisión de alimentos. Por otra parte, también son ecosistemas altamente amenazados por la ganadería, desarrollos inmobiliarios, contaminación, sobrepesca y modificación del cauce de los ríos. En la costa de Chiapas existen aproximadamente 20 lagunas costeras, agrupadas en varios sistemas lagunares; de éstos, destacan por su diversidad biológica los de Chantuto-Panzacola y Carretas-Pereyra, ambos dentro del polígono de la Reserva de la Biosfera La Encrucijada. Estos sistemas surgieron apenas dentro de los últimos 5,000 años, considerándose jóvenes en términos geológicos. El objetivo de esta tesis fue construir un modelo trófico para cada uno de los sistemas lagunares costeros de esta área protegida, con el fin de probar si sistemas estuarinos de reciente aparición pueden ser estables o no en términos de sus características ecológicas. Además, se determinó el papel de cada grupo funcional en la trama trófica y se evaluó el efecto de la conectividad del sistema (boca permanente en Chantuto-Panzacola vs. temporal en Carretas-Pereyra) en dichas características. De acuerdo con los resultados, el detritus fue el grupo más importante en ambos sistemas en términos de biomasa y flujos energéticos, y en segundo plano estuvieron los invertebrados, los cuales actuaron como intermediarios energéticos entre el detritus y niveles tróficos superiores. Respecto a la resiliencia y energía de reserva (i.e. energía disponible para recuperarse después de una perturbación), los grupos funcionales que más participan en estas propiedades fueron el detritus, fitoplancton y zooplancton. Las características ecológicas de ambos complejos lagunares revelaron que son ecosistemas que se han desarrollado en un 30% y que

presentaron características propias de este nivel de desarrollo como: dominancia de organismos juveniles, preponderancia de omnivoría en la trama trófica, abundancia de vías energéticas paralelas, elevada producción primaria respecto a la respiración del sistema, y poco reciclaje de nutrientes. Sin embargo, también se detectaron ciertas características relacionados a etapas de mayor grado de desarrollo, como una alta riqueza de especies y una trama trófica en forma de red basada en el detritus. A pesar de su juventud geológica y su grado de desarrollo, los dos sistemas lagunares presentan una serie de mecanismos que les permiten mantenerse estables, pese a los cambios ambientales drásticos y a la conectividad temporal. Paradójicamente, el poco desarrollo presente en estas lagunas es un elemento importante en la estabilidad del ecosistema. La capacidad osmorregulatoria de las especies, así como el recambio de éstas, junto con las interacciones débiles en la red trófica, la omnivoría y la acumulación de energía de reserva, brindan estabilidad al sistema. Los efectos del cierre temporal de Carretas-Pereyra se reflejaron en un aumento en la biomasa de varios grupos funcionales, como el detritus, algunos invertebrados y varios grupos de peces con afinidades estuarinas y dulceacuícolas secundarias. Esto indicaría que Carretas-Pereyra se mantuvo cerrado por un tiempo prolongado y que las aperturas de su boca duraron poco. La principal diferencia entre Chantuto-Panzacola y Carretas-Pereyra, derivada de la conectividad y considerando la suma de los flujos de energía, se encontró en el desarrollo del sistema. En contraste con la diferencia de superficie de cada sistema (37 km^2 en Carretas-Pereyra vs. 180 km^2 en Chantuto-Panzacola), Carretas-Pereyra tuvo un aumento mayor de la biomasa que la de su sistema vecino. Los hallazgos en este estudio se observaron dentro de lo reportado para en otros sistemas lagunares estuarinos. En conclusión, ambos sistemas poseen elementos que les brindan estabilidad a pesar de su juventud geológica y ecológica. Estos mecanismos permiten que el funcionamiento del sistema no colapse y que pueda recuperarse a pesar de los cambios drásticos ambientales, incluido el cierre temporal del sistema.

ABSTRACT

Trophic models are tools to identify holistic properties of ecosystems, not evident from direct observations. These models are fundamental if one wants to analyze the functioning and structure of complex and highly changing ecosystems, such as coastal lagoons. The confluence of two different water masses (marine and freshwater) originates a physicochemical gradient that favors an environmental heterogeneity, which shelters a biodiversity adapted to this abiotic mosaic. In addition to biological diversity, coastal lagoons provide environmental goods and services, such as water regulation, recreation, and food provision. On the other hand, they are also highly threatened by cattle ranching, real estate developments, pollution, overfishing, and modification of the river beds. In the coast of Chiapas there are approximately 20 coastal lagoons, grouped in several lagoon systems, of which the Chantuto-Panzacola and Carretas-Pereyra, both within the polygon of the La Encrucijada Biosphere Reserve, stand out for their biological diversity. These systems emerged just 5,000 years ago, so they are young in geological terms. The objective of this thesis was to build a trophic model for each of the coastal lagoon systems of this protected area in order to test whether recently emerging estuarine systems can be stable or not in terms of their ecological attributes. In addition, the role of each functional group in the trophic network was determined and the effect of the connectivity of the system (a permanent mouth in Chantuto-Panzacola vs. temporary in Carretas-Pereyra) in said attributes was evaluated. According to the results, detritus was the most important group in both systems in terms of biomass and energy flows, and in second place were invertebrates, which acted as energy intermediaries between detritus and higher trophic levels. Regarding resilience and reserve energy (i.e. energy available to recover after a disturbance), the functional groups that participate the most in these properties were detritus, phytoplankton and zooplankton. The ecological attributes of both lagoon complexes revealed that they are ecosystems that have developed by 30% and that presented characteristics of this level of development, such as dominance of juvenile organisms, preponderance

of omnivory in the trophic network, abundance of parallel energy pathways, high primary production with respect to system respiration, and little recycling of nutrients. However, certain attributes related to stages with a higher degree of development were also detected, such as a high richness of species and a network-like trophic web based on detritus. In spite of their geological youth and their degree of development, the two lagoon systems have a series of mechanisms that allow them to remain stable, despite drastic environmental changes and temporary connectivity. Paradoxically, the little development present in these lagoons is an important element in the stability of the ecosystem. The osmoregulatory capacity of the species, as well as the replacement of these, together with the weak interactions in the trophic network, the omnivory and the accumulation of reserve energy, provide stability to the system. The effects of the temporary closure of Carreras-Pereyra were reflected in an increase in the biomass of several functional groups, such as detritus, some invertebrates and several groups of fish with secondary estuarine and freshwater affinities. This would indicate that Carretas-Pereyra remained closed for a long time and that the openings of its mouth lasted little. The main difference between Chantuto-Panzacola and Carretas-Pereyra, derived from connectivity and considering the sum of the energy flows, was found in the growth of the system. In contrast to the difference in surface area of each system (37 km^2 in Carretas-Pereyra vs. 180 km^2 in Chantuto-Panzacola), Charretas-Pererya had a higher growth than its neighboring system. The findings in this study agreed with what has been reported for other estuarine lagoon systems. In conclusion both systems have elements that provide stability despite their geological and ecological youth. These mechanisms prevent the functioning of the system from collapsing and allow it to recover despite drastic environmental changes, including the temporary closure of the system.

INTRODUCCIÓN GENERAL

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Las lagunas costeras son ecosistemas que se definen como cuerpos acuáticos continentales someros, ubicados en depresiones por debajo del promedio máximo de las mareas más altas; por lo general están orientadas en su eje mayor a lo largo de la línea de costa, separadas del océano por una barrera y mantienen una comunicación con éste de manera permanente o temporal a través de una o más bocas (Lankford, 1977; Kjerfve, 1994). Esto último puede resultar determinante en el funcionamiento de estos ecosistemas, ya que la interrupción en la conectividad puede modificar en gran medida sus características físico-químicas, hidrológicas, morfológicas y biológicas (Parkinson y Stretch, 2007; Santangelo et al., 2007; Pires et al., 2011).

Estas lagunas pueden ser desde dulces hasta hipersalinas, dependiendo de factores tales como escurrimientos de la cuenca, precipitación local, evaporación e intrusión marina (Smith, 1994). Otros factores, como el oxígeno disuelto, temperatura y transparencia, también pueden fluctuar drásticamente de manera espacial y temporal a lo largo de un ciclo completo, lo que en conjunto convierte a las lagunas costeras en ambientes altamente estresantes (McLusky y Elliott, 2004; Elliott y Quintino, 2007). Esto otorga a las lagunas costeras una peculiar heterogeneidad ambiental, lo que origina una gran variedad de microhábitats y gradientes ecológicos, esenciales para el mantenimiento de su diversidad biológica (Esteves et al., 2007).

Ecológicamente, destacan por ser sitios de anidación y crianza para muchas especies de peces e invertebrados (Contreras, 2010), y por encontrarse entre los ecosistemas más productivos del mundo (Kennish y Paerl, 2010; Chapman, 2012). Lo anterior les confiere la capacidad de sostener, a nivel mundial, importantes pesquerías artesanales de peces, crustáceos y moluscos, así como actividades asociadas a la acuicultura intensiva y extensiva de dichos organismos (Pérez-Ruzafa y Marcos, 2012).

Además de los beneficios alimentarios y económicos derivados de las pesquerías, las lagunas costeras juegan un papel importante en el control de inundaciones, procesamiento de nutrientes, almacenamiento y provisión de agua, prevención de erosión y en la absorción de impactos originados por fenómenos meteorológicos. Su diversidad biológica y paisajística, además de otorgarles un elevado valor estético, permite llevar a cabo actividades relacionadas con la recreación, educación e investigación (Chapman, 2012; Pérez-Ruzafa y Marcos, 2012).

En nuestro país, los bienes y servicios ecosistémicos mencionados son proporcionados por aproximadamente 130 sistemas lagunares, conformados por más de 600 lagunas costeras (Contreras, 2010), las cuales ocupan un área de 15,000 km^2 (Lara-Domínguez et al., 2011). De acuerdo con Lankford (1977), estas lagunas surgieron aproximadamente hace 5,000 años, por lo que se consideran ambientes de reciente creación, geológicamente muy jóvenes.

A pesar de los beneficios otorgados por las lagunas costeras, en México son varios los factores que ponen en riesgo la integridad de estos ecosistemas, por ejemplo los asociados con el desarrollo urbano y turismo (tala inmoderada de manglares, mal manejo de aguas residuales, construcción de caminos y complejos hoteleros), la explotación petrolera y la alteración de los elementos hídricos de la cuenca (modificación de los cauces de los ríos, obras de dragado y canalizaciones mal planificadas) (Ruiz-Luna y Berlanga- Robles 2003; Murray 2007; Contreras, 2010).

Ante tales amenazas es fundamental conocer y comprender el funcionamiento de un ecosistema que nos ofrece una serie de invaluables bienes y servicios, ya que esto nos ayudaría a establecer o mejorar estrategias de manejo que se adecuen a las particularidades de las lagunas costeras. Entender cómo estos ambientes funcionan también nos permitiría predecir su comportamiento ante cambios ambientales (naturales o antrópicos) de diferente magnitud. Dado que resulta complicado estudiar el comportamiento de los ecosistemas a través de observaciones directas, se han desarrollado estrategias y métodos conocidos como análisis de tramas ecológicas (ENA, por sus siglas en inglés) para analizar e

identificar las propiedades holísticas de los ecosistemas a través de las interacciones que ocurren dentro de éste (Fath et al., 2007).

Actualmente existen distintos programas y modelos computacionales para estudiar el funcionamiento de los ecosistemas mediante la estrategia planteada por el ENA. Entre las opciones para modelar ecosistemas acuáticos se encuentran Ecopath con Ecosim (Polovina, 1984; Christensen y Pauly, 1992), STELLA (Richmond y Peterson, 1997; Spieles y Mitsch, 2003), Atlantis (Fulton et al., 2004; 2011) EcoNet (Kazanci, 2007), EcoTroph (Gascuel y Pauly, 2009), StrathE2E (Heath et al., 2014), y una gran variedad de rutinas para el paquete estadístico R conocidas como enaR (Lau et al., 2017). Todas estas opciones trabajan con base en una serie de ecuaciones y la mayoría contempla flujos de biomasas a través de interacciones tróficas, mientras que otras agregan además algunas variables ambientales y sociales.

Hoy en día una de las herramientas con mayor solidez, respaldo académico e informativo, y ampliamente conocida y utilizada a nivel mundial es Ecopath con Ecosim (EwE, por sus siglas en inglés), ya que desde su creación se han construido más de 400 modelos tróficos de ecosistemas acuáticos (Colléter et al., 2015). Además, existen más de 600 publicaciones que lo avalan (Villasante et al., 2016), en temas como modelos tróficos, manuales, críticas, revisiones, entre otros. Por su parte, la plataforma en línea EcoBase pone a disposición un repositorio de acceso abierto conformado por 192 modelos descargables y 458 modelos con metadatos (EcoBase, 2019). La popularidad de este programa crea un lenguaje común que permite comparar modelos tróficos de todo el mundo, lo que facilita el entendimiento de las generalidades y del funcionamiento de los ecosistemas acuáticos (Castellanos-Galindo et al., 2017).

El funcionamiento de EwE se basa en un conjunto de ecuaciones lineales, una para cada especie o grupo funcional, que representan un balance de flujos de biomasa en el ecosistema que se supone se encuentra en equilibrio; es decir, todas las entradas de materia al sistema deberían ser iguales a las de salida para cada grupo funcional (Polovina, 1984). EwE permite crear modelos estáticos o dinámicos para

evaluar la transferencia de energía entre los componentes bióticos del sistema, y a la vez conocer a las especies o grupos funcionales clave de este proceso. También es posible estudiar, y predecir, los impactos de ciertos cambios ambientales, de la sobrepesca o de la introducción de especies exóticas en la trama trófica. Además puede estimar el grado de desarrollo de un ecosistema, así como el estado de salud de éste a través de ciertos parámetros otorgados por el mismo programa (Christensen et al., 2008).

En México se han construido alrededor de 30 modelos tróficos para distintos tipos de ecosistemas acuáticos (EcoBase, 2019); en el caso particular de las lagunas costeras, tan solo una pequeña fracción de ellas cuenta con un modelo trófico construido con EwE. En la vertiente del Atlántico se han elaborado modelos de las lagunas Tamiahua (Abarca-Arenas y Valero-Pacheco, 1993), Mandinga (de la Cruz-Agüero, 1993), Celestún (Chávez et al., 1993; Vega-Cendejas y Arreguín-Sánchez, 2001), Tampamachoco (Rosado-Solórzano y Guzmán del Próo, 1998), Términos (Manickhand-Heileman et al., 1998; Abascal-Monroy et al., 2016), Alvarado (Cruz-Escalona et al., 2007) y la bahía de Chetumal (Castelblanco-Martínez et al., 2012). En la vertiente del Pacífico, el número de modelos existentes es mucho menor, ya que tan solo se han explorado por esta vía las lagunas de Huizache-Caimanero (Zetina-Rejón et al., 2003) y la Bahía Magdalena (Cruz-Escalona et al., 2013), ambas en la porción septentrional de esta vertiente.

Al sur del Pacífico mexicano, en el estado de Chiapas, se encuentra la Reserva de la Biosfera La Encrucijada (REBIEN), reconocida nacional e internacionalmente en distintas categorías. Es considerada por la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad como una región terrestre y marina prioritaria (Arriaga et al. 1998; 2000), así como un Área de Importancia para la Conservación de las Aves (AICAS) (Benítez et al., 1999). Ostenta la categoría de sitio Ramsar por ser un humedal valioso para el funcionamiento del sistema costero; mantiene la diversidad biológica, genética y ecológica de la región gracias a la calidad de su biota; provee sustento a más de 200 especies de aves residentes y a más de 90 migratorias. Además, esta reserva posee la vegetación de manglar más alta del Pacífico

Americano, así como el único bosque de zapotonal inundable existente en Mesoamérica (CONANP, 2019).

La REBIEN está integrada por los sistemas lagunares costeros Chantuto-Panzacola y Carretas-Pereyra, que en conjunto abarcan un área de 217 km^2 y son considerados como humedales de gran importancia biológica y socioeconómica debido a la biodiversidad que albergan y a su elevada producción pesquera (Carabias-Lillo et al., 1999). Ambos sistemas se caracterizan por ser depresiones inundadas protegidas del mar por barreras arenosas originadas por corrientes y olas, que surgieron dentro de los últimos 5,000 años (Lankford, 1977). Mientras que Chantuto-Panzacola posee una conexión permanente con el mar, Carretas-Pereyra ha experimentado una conectividad intermitente en los últimos años (Rivera-Velázquez, 2008; Gómez-González et al., 2012).

Ambos sistemas lagunares han sido ampliamente estudiados en los últimos 20 años desde el punto de vista biótico, abiótico y socioeconómico. En Chantuto-Panzacola, los trabajos ictiofaunísticos (principalmente ecología de comunidades) se han realizado por parte de Díaz-Ruiz et al. (2004), Ovilla-Hernández (2009), Gómez-González (2011) y Gómez-González et al. (2012). En el área del plancton, Gutiérrez-Mendieta et al. (2006) y Varona-Cordero et al. (2010) analizaron la variación espacio-temporal de la comunidad fitoplanctónica, mientras que Álvarez-Silva et al. (2006) hizo lo mismo con la comunidad zooplanctónica. Los macrocrustáceos han sido abordados por Díaz-Medina (2011), Barba-Macías et al. (2012) y Rivera-Velázquez et al. (2016). Los cocodrilos del sistema están sujetos a un monitoreo por parte de la Comisión Nacional de Áreas Naturales Protegidas (REBIEN, 2010) y sobre las aves existe un trabajo de Acuna et al. (1994) y una lista publicada en el programa de manejo de la reserva (Carabias-Lillo et al., 1999). García-Morales (2007) caracterizó las distintas pesquerías de escama que existen en este sistema lagunar y dio a conocer las principales especies que mantienen esta actividad. En cuanto a las variables ambientales, Gómez-Ortega (2013) realizó durante un ciclo anual una caracterización espacio-temporal de los parámetros físico-químicos de las lagunas que integran al sistema.

En el caso de las comunidades bióticas de Carretas-Pereyra, la ictiofauna fue examinada por Velázquez-Velázquez et al. (2008) y Gómez-González et al. (2012). Villatoro-Álvarez (2006) realizó estudios puntuales sobre la biología trófica de cinco especies de peces estuarinos. Los macrocrustáceos fueron estudiados por Rivera-Velázquez et al. (2008; 2016), Díaz-Medina (2011) y Barba-Macías et al. (2012), el fitoplancton por Varona-Cordero et al. (2010), la estructura del manglar por Romero-Berny y Tovilla-Hernández (2009) y las aves por Acuna et al. (1994). Los estudios pesqueros están representados por los trabajos de Rivera-Velázquez et al. (2009), quienes trabajaron con la pesquería artesanal de camarón. Los aspectos relacionados con la morfometría y tipos de fondo de las lagunas de Carretas-Pereyra fueron analizados por Cruz-Angeles (2000), Márquez-García et al. (2006) y Calva-Benítez et al. (2009).

Si bien los ecosistemas lagunares costeros de la REBIEN han sido ampliamente analizados, los numerosos trabajos realizados sobre los componentes bióticos de éstos se limitan, en muchos casos, a describir el comportamiento espacio-temporal de las comunidades. Aunque estos estudios asocian el comportamiento de éstas últimas con las variables físico-químicas, la relación entre todos los componentes bióticos queda relegada a un segundo plano, impidiendo así tener una aproximación holística al ecosistema lagunar costero, el cual se encuentra en un estado de constante perturbación (Odum, 1969). Las lagunas costeras de la REBIEN poseen hasta ahora los elementos necesarios para ser estudiados a través del ENA, lo que permitirá conocer por primera vez cómo trabajan éstas a nivel ecosistema.

OBJETIVOS

Considerando lo anterior, el presente trabajo tiene como objetivo general construir un modelo trófico, con el enfoque EwE, para cada uno de los sistemas lagunares estuarinos de la REBIEN con el fin de comprender el funcionamiento y dinámica de cada sistema.

Como objetivos específicos se plantearon los siguientes:

- Definir a los grupos funcionales y determinar el papel de éstos en el flujo de energía de cada sistema lagunar.
- Identificar y describir las características ecológicas, estrategias y mecanismos que presentan las lagunas costeras para hacer frente a las perturbaciones.
- Determinar el grado de desarrollo de cada uno de los sistemas lagunares.
- Evaluar el funcionamiento de una laguna costera que mantiene una conexión temporal con el mar.

Los objetivos anteriormente señalados se abordaron a través de dos capítulos, uno para cada sistema lagunar de la REBIEN: I) Young does not mean unstable: a trophic model for an estuarine lagoon system in the Southern Mexican Pacific, para Chantuto-Panzacola, y II) A trophic model for a periodically closed coastal lagoon system in the Southern Mexican Pacific, correspondiente a Carretas-Pereyra. En ambos capítulos se atienden los primeros tres objetivos específicos, sin embargo, cada capítulo trata las peculiaridades de cada complejo lagunar.

En el Capítulo I se utiliza a Chantuto-Panzacola como ejemplo de cómo funciona, desde el punto de vista trófico, un sistema lagunar costero tropical de reciente creación geológica. Se describe el papel de cada grupo funcional en el flujo de materia dentro del ecosistema, así como las interacciones tróficas que ocurren entre éstos y los impactos, directos e indirectos, derivados de dichas interacciones. La suma de tales flujos converge en una serie de parámetros que permiten evaluar no solo el grado de desarrollo del ecosistema, sino que también su estabilidad y estado

de salud. A pesar de ser un ecosistema joven, Chantuto-Panzacola posee los elementos necesarios para mantenerse estable y saludable.

El Capítulo II versa sobre los distintos mecanismos que entran en acción en Carretas-Pereyra tras experimentar una conexión temporal con el mar. Este tipo de conectividad ha sido expuesta como un fenómeno que altera en gran medida las características biológicas y ambientales de una laguna costera. Por lo tanto, aquí se detallan las características ecosistémicas, y estrategias de cada grupo funcional, que ayudan a encarar y atenuar los efectos de tal perturbación. Los hallazgos de este estudio indican que Carretas-Pereyra posee una gran resiliencia y que la conectividad temporal no impacta negativamente en su funcionamiento.

CAPÍTULO I

Juventud no significa inestabilidad: un modelo trófico para un sistema lagunar estuarino en el sur del Pacífico mexicano

(Artículo publicado en Hydrobiologia, 2019)

CrossMark

PRIMARY RESEARCH PAPER

Young does not mean unstable: a trophic model for an estuarine lagoon system in the Southern Mexican Pacific

Jesús M. López-Vila · **Juan J. Schmitter-Soto** · **Ernesto Velázquez-Velázquez** ·
Everardo Barba-Macías · **Isaías H. Salgado-Ugarte**

Abstract A trophic model is presented for the coastal lagoon system Chantuto-Panzacola, Southern Pacific Mexico, with the aim of estimating its degree of development and functionality. Thirty-four functional groups (one for birds, one crocodilians, 20 fishes, nine zoobenthos, two plankton, one detritus) were analyzed using Ecopath's approach, with species biomass, diet composition, and data of species' production and consumption. Diet was examined from stomach contents for the 39 most abundant fish species, the rest being determined from literature. Detritus was the most important component of the ecosystem in terms of biomass and flows, whereas diverse groups of zoobenthos linked detritus to upper functional groups. Consumers' trophic level fluctuated between 2.00 and 4.08, with crocodilians as top predators. The size of the system, in terms of matter flows, was 7,133 g m^{-2} year^{-1}; this value was greater than those recorded in other estuarine systems. Chantuto-Panzacola has a short geological age and is in an intermediate development stage; however, its youth and immaturity are accompanied by attributes which confer stability and environmental health, such as high productivity, high omnivory, and a great reserve potential that the system uses to face

J. M. López-Vila (✉)
Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Tercer Circuito s/n, Ciudad Universitaria, Coyoacán. A.P. 70-153, C.P. 04510 Mexico City, Mexico
e-mail: jesus.lopez@unicach.mx

J. M. López-Vila
Centro de Investigaciones Costeras, Instituto de Ciencias Biológicas, Universidad de Ciencias y Artes de Chiapas, Calle Juan José Calzada y Prolongación Calzada de Guadalupe, C.P. 30500 Tonalá, Chiapas, Mexico

J. J. Schmitter-Soto
El Colegio de la Frontera Sur, Unidad Chetumal, Av. Centenario km 5.5, C.P. 77014 Chetumal, Quintana Roo, Mexico

E. Velázquez-Velázquez
Museo de Zoología, Instituto de Ciencias Biológicas, Universidad de Ciencias y Artes de Chiapas, Libramiento Norte Poniente No. 1150, C.P. 29039 Tuxtla Gutiérrez, Chiapas, Mexico

E. Barba-Macías
El Colegio de la Frontera Sur, Unidad Villahermosa, Carr. Villahermosa-Reforma km 15.5,
C.P. 86280 Villahermosa, Tabasco, Mexico

I. H. Salgado-Ugarte
Laboratorio de Biometría y Biología Pesquera. Facultad de Estudios Superiores Zaragoza Campus II, Universidad Nacional Autónoma de México, Batalla 5 de Mayo s/n esquina Fuerte de Loreto, Iztapalapa,
C.P. 09239 Mexico City, Mexico

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disturbances (overhead). The quality of the model was relatively high with respect to others.

Introduction

Coastal lagoons are subsidized environments (Day & Yáñez-Arancibia, 1985; Contreras, 1988), catalogued among the most productive ecosystems in the world (Yáñez-Arancibia, 1985; Kennish & Paerl, 2010; Chapman, 2012). These systems have a complex ecological structure, with a variety of habitats and biodiversity (Day & Yáñez-Arancibia, 1985). They are also crucial sites for nesting, nursing, and shelter for many fishes and invertebrates (Verdiell-Cubedo et al., 2013; Fonseca et al., 2015; Tournois et al., 2017), as well as for fisheries (Pérez-Ruzafa & Marcos, 2012; Marcos et al., 2015).

These ecosystems also provide us with some goods and services that include nutrient processing, water regulation, food provision (through fisheries and aquaculture), recreation, and aesthetic value (Chapman, 2012; Basset et al., 2013). Notwithstanding their relevance, coastal lagoons and their biodiversity are nowadays highly threatened by anthropogenic activities, such as pollution by sewer effluents, eutrophication, draining of wetlands, overfishing, urban development, oil and gas exploration, and modifications to the natural flow of rivers. All these factors are able to modify, directly or indirectly, the biodiversity, ecology, function, and structure of these ecosystems (Day et al., 2013; Camacho-Ibar & Rivera-Monroy, 2014).

In ecosystems, species participate in complex networks of ecological interactions (Sint & Traugott, 2016) where a flow or energy exists among the different elements or compartments of the network, which can be depicted as food webs (Pasquaud et al., 2007). These food webs, and the description of their flows, have been proposed as a good strategy to represent the structure and functioning of the ecosystems (Bendoricchio & Palmeri, 2005; Pasquaud et al., 2007). A powerful and widely used tool to evaluate the structure and functioning of aquatic ecosystems are

food web models (Belgrano et al., 2005), one of which, Ecopath with Ecosim (EwE), has been designed to evaluate energy flow through trophic linkages under mass balance (Christensen & Pauly, 1992). EwE also supplies information that allow for calculating the development of the system (ascendency), its development potential (development capacity), and its reserve energy (overhead).

Up to date, more than 400 mass-balanced models of aquatic ecosystems (freshwater and marine) have been constructed in the world using EwE (Colléter et al., 2015), and information about the use of this tool is available in more than 600 publications (Villasante et al., 2016). Such models and information provide a common framework to compare global food webs and understand the generalities and functioning of aquatic ecosystems (Castellanos-Galindo et al., 2017).

In Mexico, there are about 640 coastal lagoons, which can be grouped in more than 120 lagoon systems; only a very small fraction of these has been explored from an energy flow perspective to understand their functioning and health status. Trophic models exist for seven systems in the Gulf of Mexico and Caribbean Sea, e.g., for the coastal lagoons of Tamiahua (Abarca-Arenas & Valero-Pacheco, 1993), Mandinga (de la Cruz-Agüero, 1993), Celestún (Chávez et al., 1993; Vega-Cendejas & Arreguín-Sánchez, 2001), Tampamachoco (Rosado-Solórzano & Guzmán del Próo, 1998), Términos (Manickchand-Heileman et al., 1998; Abascal-Monroy, 2014), Alvarado (Cruz-Escalona et al., 2007), and the Bay of Chetumal (Castelblanco-Martínez et al., 2012). In the Pacific coast, there are only two published trophic models, for the lagoon system Huizache-Caimanero (Zetina-Rejón et al., 2003) and Magdalena Bay (Cruz-Escalona et al., 2013).

Chantuto-Panzacola is an important coastal lagoon system of recent geological formation (Contreras, 2010) in the southern Pacific coast of Mexico; it is part of a RAMSAR site (CONANP, 2017) and is considered an Important Bird Area (IBA) (Vidal et al., 2009). This system is protected as part of the La Encrucijada Biosphere Reserve (LEBR) and several studies describe its biodiversity (e.g., Álvarez Silva et al., 2006; Gutiérrez Mendieta et al., 2006; Gómez-González, 2011; Peña-Martínez, 2011; Barba-Macías et al., 2012) without analyzing the relationship among all the components of its diversity. This means that

there is as yet no attempt to model its ecosystem functioning. Therefore, our objective is to build a trophic model of a recently emerged tropical coastal lagoon complex that is inside of a protected area to test whether a young system such as this is stable or unstable in terms of its ecological attributes.

Materials and methods

Study site

The estuarine lagoon system Chantuto-Panzacola is on the coast of the State of Chiapas, Mexico (15°09′N, 92°55 W), within LEBR (Fig. 1). Its extension is 180 km^2 and it comprises five lagoons: Chantuto, Campón, Teculapa, Cerritos, and Panzacola. The system is connected to the Pacific Ocean via the mouth of San Juan. Several rivers drain into the lagoons, among which are San Nicolás, Cintalapa, and Huixtla. Climate is warm humid, with an annual precipitation of 1,300–3,000 mm and a natural vegetation of mangrove forests and other emergent and submerged plants (Álvarez Silva et al., 2006). Annual mean water temperature, salinity, dissolved oxygen, pH, and depth are 29.6°C, 14.3 ppm, 2.7 mg l^{-1}, 7.55, and 0.98 m, respectively (Gómez-Ortega, 2013).

Fieldwork

In order to complement the information from the literature on the study area (composition, community structure and biomass of fishes, macroinvertebrates and plankton), two expeditions were carried out: one
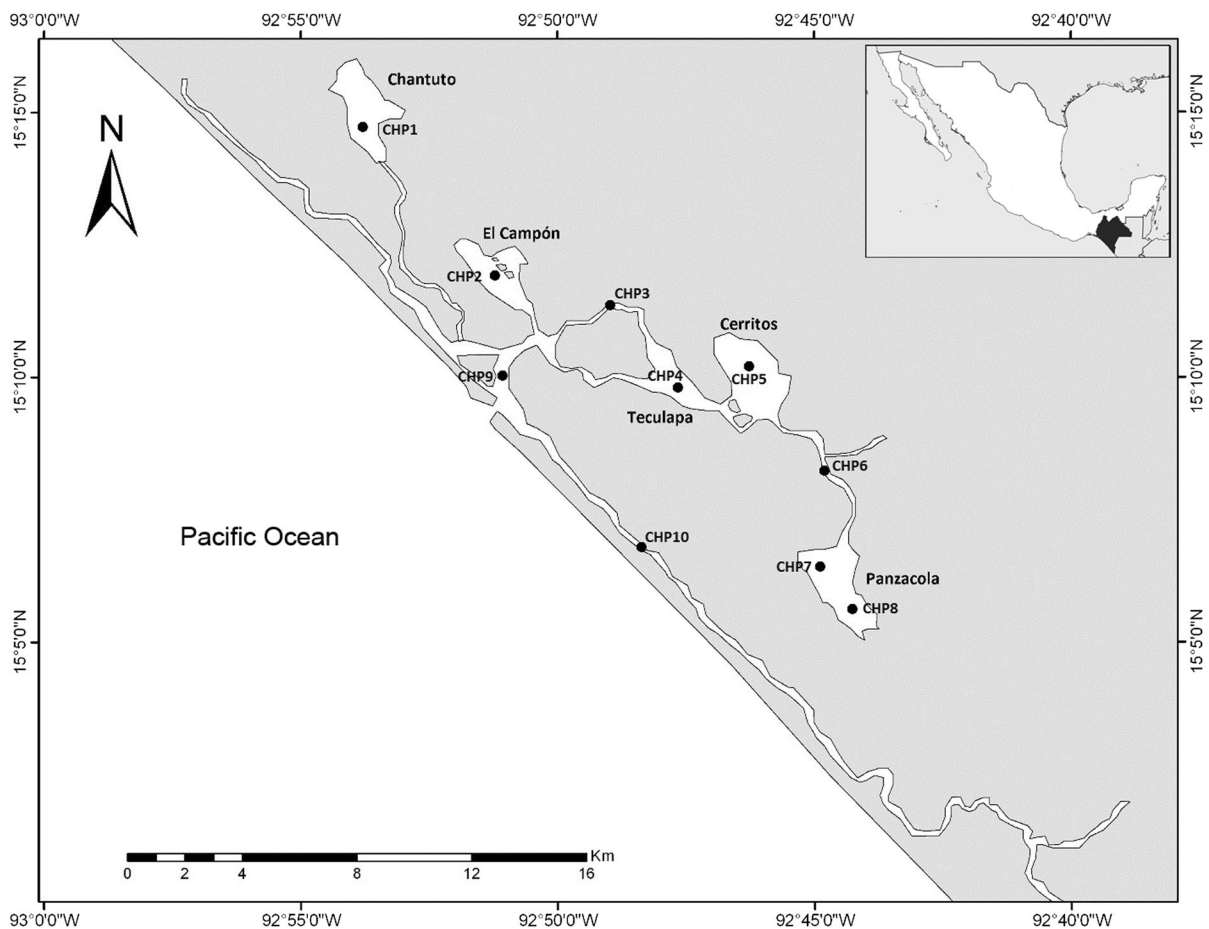

Fig. 1 Study site, the coastal lagoon system Chantuto-Panzacola, Pacific coast of Mexico, with sampling stations (filled circle)

in March (dry season), and the other in September (wet season), 2015. In every visit, 10 stations distributed over the whole system (Fig. 1) were sampled for zoobenthos (mainly crustaceans, polychaetes, mollusks) and detritus.

Sampling was conducted with a Van Veen dredge (opening 295 × 190 mm), used twice at every station. We homogenized the sediment in a bucket and then emptied it into a container, where it was standardized to 1681 cm^3 per sample. In order to assess the small-sized infaunal organisms from the sediment, we sifted the latter through sieves of diverse mesh size (0.482, 0.990, 1.981, and 3.352 mm), then we fixed the infauna in 70% ethanol, for later identification and weighing with an analytical scale in the laboratory. A subsample of 1 g (wet weight) was kept in plastic bags for drying and later processed in the laboratory for determination of organic matter by loss on ignition (Dean, 1974).

The Ecopath model

The trophic model was built using the program Ecopath with Ecosim (EwE) version 6.4.3. This software allows an estimation of the main production sources in the system, energy transfers among the diverse biotic components, impacts on the system through biomass and consumption of the different species groups, and the variation of all parameters by season. It is a mass balance model, that is, all inputs of matter and energy into the system should be equal to the outputs by species group, which is verified by simultaneous linear equations (Polovina, 1984; Christensen & Pauly, 1992; Christensen et al., 2008).

To build the trophic model, it is necessary to define the functional groups, and then the relevant parameters for each one, i.e., biomass (*B*), production/biomass (*P/B*) and consumption/biomass (*Q/B*) ratios, and ecotrophic efficiency (*EE*). These data are complemented with a predator–prey matrix that indicates what fraction of each functional group is part of the diet of every other such group. EwE is based on a set of linear equations, one for every functional group as prey (*i*) and as predator (*j*), representing biomass flows in the ecosystem, which is assumed to be in balance.

The master equation of EwE is

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + B_i \cdot (P/B)_i \cdot (1 - EE_i) + \sum_{j-1}^{n} B_{j\cdot}(Q/B)_j \cdot DC_{ji}$$

with all parameters defined above, except DC_{ji}, the fraction of prey *i* in the diet of predator *j*, and *Yi,* the total fishery catch rate of *i*. The term preceded by the summation represents the total consumption of prey *i* over all predators *j*. In general, the equation represents the balance between production (growth) and loss (mortality) for every group *i*.

Functional groups

Functional groups are species or sets of species that play a definable role in the flow of matter and energy in the ecosystem (Blondel, 2003); they can be recognized as trophic guilds or as taxa, and can be further subdivided according to size or age (Christensen & Pauly, 1992; Christensen et al., 2008), or grouped according to abundance or commercial importance in fisheries (Zetina-Rejón et al., 2003). In tropical ecosystems, species have to be grouped, because they are too numerous for a species-based model to be manageable (Christensen & Pauly, 1992; Christensen et al., 2008).

The following criteria were used to delimit functional groups: ecological or taxonomic relationship among species; similar diets and numerical abundance (in the case of *Dormitator latifrons*, which was placed in its own functional group because of its seasonal migration, a phenomenon not seen in other eleotrids). *Atractosteus tropicus*, an overexploited species, was placed in its own functional group to facilitate future viability analyses for it. García-Morales (2007) characterized the fishing activities in the study area; we took into account this work and selected certain species as functional groups because of their regional economic value, in order to inform future models that evaluate the effect of the fishing over these species in different scales of time. In total, 34 groups were defined; most of them comprised several species (Table 1). There is no seagrass in our study area unlike in other systems (e.g., Manickchand-Heileman et al., 1998; Cruz-Escalona et al., 2007; Castelblanco-Martínez et al., 2012).

Table 1 Functional groups of the lagoon system Chantuto-Panzacola and their constituent species

Functional group	Constituent species
Water birds	Podicipediformes, Pelecaniformes, Ciconiiformes, Anseriformes, Falconiformes, Gruiformes, Charadriiformes
Crocodilians	*Caiman crocodilus, Crocodylus acutus*
D. latifrons	*Dormitator latifrons*
Eleotrids	*Eleotris picta, Gobiomorus maculatus*
S. guatemalensis	*Sciades guatemalensis*
Ariid catfishes	*Cathorops liropus, C. steindachneri, Notarius kessleri*
Jacks	*Caranx caninus, C. sexfasciatus, Hemicaranx zelotes, Oligoplites altus, O. saurus, Selene brevoorti*
Snooks	*Centropomus medius, C. nigrescens, C robalito, C. viridis*
Anchovies	*Anchoa lucida, A. mundeola, A. starksi, A. ischana, Anchovia macrolepidota*
Sciaenids	*Cynoscion albus, Bairdiella armata, Micropogonias altipinnis, Stellifer* cf. *walkeri*
Gobiids	*Aboma etheostoma, Ctenogobius sagittula, Gobionellus microdon*
Mugilids	*Mugil curema, M. cephalus, M. hospes*
Gerreids	*Diapterus brevirostris, Eucinostomus currani, E. dowii, Gerres simillimus*
Pleuronectiforms	*Achirus mazatlanus, Citharichthys gilberti, Trinectes fonsecensis*
Poeciliids	*Poecilia nelsoni, P. sphenops, Poeciliopsis turrubarensis*
S. annulatus	*Sphoeroides annulatus*
Cichlids	*Amphilophus trimaculatus, Astatheros macracanthus, Oreochromis niloticus*
Snappers	*Lutjanus argentiventris, Lutjanus colorado*
A. tropicus	*Atractosteus tropicus*
Planktivore fishes	*Atherinella guatemalensis, Lile gracilis, L. nigrofasciata, Membras gilberti, Hippocampus ingens, Hyporhamphus snyderi*
Carnivore fishes	*Elops affinis, Roeboides bouchellei, Synodus scituliceps*
Omnivore fishes	*Anableps dowei, Astyanax aeneus, Kyphosus elegans, Polydactylus approximans, Rhamdia guatemalensis*
Litopenaeus	*Litopenaeus stylirostris, L. vannamei, L. occidentalis*
Macrobrachium	*Macrobrachium americanum, M. tenellum, Palaemonetes ritteri*
Other shrimps	*Alpheus* sp., *Farfantepenaeus brevirostris, Hyppolyte williamsi, Sergestes pestafer, Sicyonia aliaffinis*
Callinectes	*Callinectes arcuatus, C. toxotes*
Grapsids	*Clibanarius panamensis, Sesarma rhizophorae, Uca* sp.
Insects	Formicidae, Odonata, unidentified larvae
Polychaetes	Polychaeta, Sipunculids
Infauna	Tanaidacea, Isopoda, Ostracoda, Cumacea, Amphipoda
Bivalves	Bivalvia
Zooplankton	Cnidarians, gastropods and polychaetes larvae, cladocerans, copepods, cirripedia larvae, decapod larvae, fish eggs
Phytoplankton	Diatoms, dinoflagellates, euglenophytes, cyanophytes, chlorophytes, silicoflagellates
Detritus	Organic matter

Entry data

To build the trophic model, it is required to enter the values of B (as mean biomass per unit area, in g m^{-2}), P/B, Q/B, and EE into the master equation. The biomass per area of several functional groups was estimated from previous work in the study site. For fish groups, we relied on Gómez-González (2011) and Gómez-González et al. (2012), who determined, from March 2006 to February 2007, the fish fauna structure in the study area using a 6-m-diameter cast net with a 1.27-cm mesh. For macrocrustaceans, we relied on Barba-Macías et al. (2012); in this study, the authors surveyed an area of 50 m^2 of coastal lagoon soft

bottoms by trawling a renfro net in each sampling. Gutiérrez Mendieta et al. (2006) reported phytoplankton biomass in the area as mg l^{-1}, which were transformed to g m^{-3} and then divided by mean depth, as a weighing procedure to obtain g m^{-2}. The same transformation was needed for zooplankton, with data from Álvarez Silva et al. (2006).

Peña-Martínez (2011) determined the relative abundance of *Crocodylus acutus* and *Caiman crocodilus* in our study site. To derive biomass, we used weight data from Charruau et al. (2010) for *C. acutus* and from Ojasti (1993) for *C. crocodilus*. To express biomass per unit area, the area of the study site was estimated using Google Earth ®. Biomass of bivalves, polychaetes, meiobenthic crustaceans, and detritus was estimated from our own field data. In the case of detritus, we extrapolated the content of organic matter of a 1-g subsample to the content of the container that we used to standardize our sediment sample. To express the biomass per unit of area (g m^{-2}), the biomass (expressed in volume) was divided by the depth of the standardized container. For birds and insects, biomass was estimated by EwE. All the biomasses used in this model were expressed in wet weight.

The parameters *P/B* and *Q/B* for each functional group were obtained from diverse sources. For fishes, we used the "life history" tool provided in the website FishBase (Froese & Pauly, 2016). This tool uses information from the population traits published in FishBase itself, in addition to average water temperature in the study site information from Gómez-González (2011) and Gómez-Ortega (2013). For other groups, these parameters were adapted from other published models developed for similar, and if possible near, coastal lagoons (Table 2). When functional groups included two or more species, the values were averaged.

The *EE* represents the part of the production of every functional group that is utilized within the ecosystem. It ranges from 0 to 1, where values close to 1 mean that the group is under considerable pressure from predation or fishing and is calculated as 1 minus other mortality. Mortality consists of organisms dying due to diseases, starvation, etc., and organisms concerned end up as part of the detritus. In the case of a detritus group, *EE* is defined as the ratio between the flow out of a detritus box, and the flow into the same box. Ecotrophic Efficiency is the hardest parameter to

quantify, but it can be calculated by EwE, when the other three required parameters (*B, P/B, Q/B*) are known (Christensen et al., 2008). In this study, *EE* was estimated by EwE for all functional groups, except for birds and insects, whose values were taken from Arreguín-Sánchez et al. (2007) and Vega-Cendejas & Arreguín-Sánchez (2001), respectively.

In addition to the parameters discussed above, the predator–prey matrix is essential. It needs to be built based on the feeding habits of the species that compose each functional group. Out of the 34 groups used in our model, 20 consisted of fishes, the most conspicuous and important components of nekton and the local fisheries. Therefore, fish diets were determined from specimens at the ichthyological collection at UNICACH (30 individuals per species), the result of collections reported by Gómez-González (2011) and Gómez-González et al. (2012). When material was scarce or not available, diet was ascertained from the literature, same as for birds, crocodilians, and invertebrates (Table 2).

Balancing the model

Before entering data to EwE, we followed the PREBAL (pre-balance) method proposed by Link (2010), to examine the slopes of biomass, production, and consumption ratios based on trophic levels, these relations should follow certain pattern. Then, we checked that our data accomplished the assumptions of the PREBAL method, and we introduced the input data to EwE in order to make a first run.

After the first run, we inspected our output data in order to check that the values of *EE* for each functional group were less than or equal to 1. Values of *EE* larger than 1 indicate that, according to the model, more is being demanded of a functional group than is being produced (Christensen et al., 2008), this also means that our model is unbalanced. So as to avoid the latter, we followed the general rules suggested by Christensen et al. (2008) to get $EE \leq 1$, i.e., to start balancing the group with the highest *EE* above 1, and then searching in the mortality-by-predation matrix those predators that exerted the highest pressure on the group being balanced, and modifying slightly the diet of these predators if needed, taking care not to change the ratios in it. The process was applied to all groups; if some of them still had an $EE > 1$, their biomass was checked, and in necessary case increased, especially

Table 2 Sources of input data for the trophic model of Chantuto-Panzacola ([a]*P/B*, [b]*Q/B*, [c]Diet)

References	Functional group
Abarca-Arenas and Valero-Pacheco (1993)	Other shrimps[c]
Albertoni et al. (2003)	*Macrobrachium*[c]
Arreguín-Sánchez et al. (2007)	Water birds[a,b,c]
Carr and Adams (1973)	Pleuronectiforms[c]
Cruz-Escalona et al. (2009)	Infauna[a,b], Omnivore fishes[c]
de la Cruz-Agüero, (1993)	Gobiids[a,b]
Díaz-González and Soto (1988)	Omnivore fishes[c]
Franco Moreno (2011)	Carnivore fishes[c]
Froese and Pauly (2016)	Anchovies[a], *D. latifrons*[a,b], Carnivore fishes[a,b], Cichlids[a,b], Eleotrids[a,b], Jacks[c], Omnivore fishes[a,b], Planktivore fishes[c], Pleuronectiforms[a,b], Sciaenids[a,b], Snappers[a,b], Snooks[a,b], *S. annulatus*[a,b]
García Santos (2007)	*A. tropicus*[c]
Geers (2012)	*A. tropicus*[a,b]
Macal López and Velázquez-Velázquez (2013)	Snooks[c]
Manickchand-Heileman et al. (1998)	Grapsids[a,b], Phytoplankton[a,b,c]
Palomares et al. (1993)	Insects[a]
Paul (1981)	*Callinectes*[c]
Poon et al. (2010)	Grapsids[c]
Robles (2007)	Sciaenids[c]
Sánchez Rueda (2002)	Mugilids[c]
Santos et al. (1996)	Crocodilians[c]
This study	Anchovies[c], Ariid catfishes[c], Carnivore fishes[c], Cichlids[c], Eleotrids[c], Gobiids[c], Jacks[c], Omnivore fishes[c], Planktivore fishes[c], Pleuronectiforms[c], Poeciliids[c], *S. guatemalensis*[c], Sciaenids[c], Snappers[c], *S. annulatus*[c]
Vega-Cendejas and Arreguín-Sánchez (2001)	Insects[b,c], Other shrimps[a,b]
Villanueva et al. (2006a)	Crocodilians[a,b]
Villatoro Álvarez (2006)	*D. latifrons*[c], Eleotrids[c], Gobiids[c]
Villegas & Schmitter-Soto (2008)	Crocodilians[c]
Zetina-Rejón et al. (2003)	Anchovies[b], Ariid catfishes[a,b], Bivalves[a,b,c], *Callinectes*[c], Infauna[c], *Litopenaeus*[c], *Macrobrachium*[a,b], Mugilids[a,b], Poeciliids[a,b], Polychaetes[c], *S. guatemalensis*[a,b], Zooplankton[a,b,c]

for those groups where we suspected an underestimation of biomass due to the sampling method. In parallel, the values of *P/B* and *Q/B* for groups with *EE* > 1 were modified, usually by increasing *P/B* and decreasing *Q/B*. The process continued iteratively until *EE* ≤ 1 was achieved for all groups. Attention was paid to the brute efficiency value (*P/Q*), which should be between 0.1 and 0.3 for most groups, and the respiration/biomass ratio (*R/B*), which should be between 1 and 10 for fishes and between 50 and 100 for microorganisms (Christensen et al., 2008).

Trophic level, mixed trophic impact, and pedigree index

The trophic level (*TL*) of each group was determined as the weighted average *TL* of the prey of each functional group, plus 1 (Christensen & Pauly, 1992). EwE assigns *TL* = 1 to primary producers (phytoplankton) and detritus. Ecopath also incorporates a routine based on the method proposed by Ulanowicz & Puccia (1990), which indicates the possible effect, direct or indirect, of changes in biomass in the interaction among functional groups in a steady-state system. This routine, known as Mixed Trophic Impact, is depicted by a graphic that shows the direct and

indirect impact that the change of the biomass of groups mentioned to the left of the histograms (rows) have on the biomass of the other groups mentioned above the histograms (columns). The bars pointing upwards indicate positive impacts, while the bars pointing downwards show negative impacts (as seen in Fig. 3). The bars should not be interpreted in an absolute sense: the impacts are relative, but comparable between groups (Christensen et al., 2008).

Finally, the quality of the model was checked by applying the pedigree index, an average of estimated uncertainties for every parameter at every functional group (Christensen et al., 2008). For each input data, this index was recorded for the calculation of an overall index of model quality, based on the origin and quality of input data. Scores for each input data were assigned, from 0 for inputs that did not originate from local data, to 1 for inputs that were obtained in local data. Scores were averaged over all parameters and functional groups of a model to provide an overall pedigree index of quality (Zetina-Rejón et al., 2003). This index can take values from 0 to 1, hence higher values of this index indicate higher quality of the model.

Ecosystem's traits

EwE is able to calculate some statistics and indices that provide us a better understanding about the activity and organization of the ecosystem, such as ascendency (A), that refers to the size and organization of total flows and to the information content of a system, and is calculated using base 2 logarithms; A is used as a measure of system growth and development. Other useful output parameters are the development capacity (C), the upper limit of A, which shows the development potential of the system, and the overhead (O), i.e., the difference between A and C, interpreted as the reserve potential of the system facing a disturbance. EwE also estimates two dimensionless indices known as relative ascendency (A/C) and relative overhead (O/C); the first one refers to the organization of the food web, and the second one to the ecosystem's strength in reserve (Ulanowicz, 1986).

Total System Throughput (TST) is an indicator that quantifies the size of the entire system in terms of flows (Ulanowicz, 1986) and in this work is expressed in g m^{-2} year^{-1}; the Finn's cycling index (FCI) is the fraction of an ecosystem's throughput that is recycled

(Finn, 1976) and is expressed as a percentage. The omnivory index (OI), calculated as the variance of the TL of the prey of a predator indicates that the consumer is a specialist when $OI = 0$, i.e., its prey belong in a single TL, whereas a higher value means that the consumer's prey come from several different TLs (Christensen & Pauly, 1992). Connectance index (CI) is the ratio of the number of actual links to the number of possible links in a food web (Christensen & Walters, 2004), and total primary production/total respiration ratio (TPP/TR) is an indicator of the degree of development of an ecosystem, where values close to 1 imply maturity, contrary to any significant departure from a ratio of 1 (Odum, 1969).

Results

Output data and trophic structure

During model balancing, part of the original information used to feed the model, concerning both the input data and the predator–prey matrix, was modified in order to attain $EE \leq 1$ in all the functional groups. The final output data and the predator–prey matrix used to build the model are shown in Tables 3 and 4, respectively.

Most of the biomass per unit area in the studied system was found at the base of the trophic web: 96.5% of the biomass consisted of detritus (94.6%) and phytoplankton (1.9%). Overall, 2.5% of the total biomass were benthic and planktonic invertebrates (infauna, polycheates, zooplankton, *Litopenaeus*, and bivalves). The remaining 1% of the biomass was divided among the other 27 functional groups. The highest values for P/B occurred in the lower trophic levels, especially in phytoplankton, zooplankton, insects, and infauna, in contrast to the upper levels, snappers and crocodrilians. As for the ratio Q/B, invertebrate groups (zooplankton, insects, infauna, and polychaetes) displayed the highest values, whereas top predators (crocodilians) had the lowest values.

In view of their high EE, the groups that experienced the greatest predation pressure were zooplankton, polychaetes, ariid catfishes, infauna, gobiids, eleotrids, poeciliids, and cichlids. The EE of detritus was only 0.299 (see Table 3 for all the parameters by group). The TL of consumers varied from 2.004 to

Table 3 Input data for the trophic model of system Chantuto-Panzacola

Code	Functional group	B (g m^{-2})	P/B (year^{-1})	Q/B (year^{-1})	EE
1	Water birds	(0.042)	0.930	5.500	0.250
2	Crocodilians	0.266	0.250	0.800	(0.017)
3	*D. latifrons*	1.022	1.120	14.00	(0.087)
4	Eleotrids	0.473	0.715	7.500	(0.962)
5	*S. guatemalensis*	1.006	0.785	2.436	(0.418)
6	Ariid catfishes	0.550	0.607	2.500	(0.990)
7	Jacks	0.504	0.733	7.483	(0.712)
8	Snooks	0.572	0.883	7.000	(0.041)
9	Anchovies	2.700	1.200	9.257	(0.840)
10	Sciaenids	0.024	0.978	10.27	(0.095)
11	Gobiids	0.740	2.000	8.367	(0.979)
12	Mugilids	2.710	1.090	4.273	(0.752)
13	Gerreids	0.560	1.270	11.60	(0.637)
14	Pleuronectiforms	0.800	1.380	12.20	(0.491)
15	Poeciliids	0.400	4.100	12.50	(0.956)
16	*S. annulatus*	0.034	0.840	7.400	(0.313)
17	Cichlids	0.481	1.700	20.00	(0.910)
18	Snappers	0.418	0.370	5.350	(0.059)
19	*A. tropicus*	0.025	0.562	3.471	(0.079)
20	Planktivore fishes	0.427	2.648	24.25	(0.533)
21	Carnivore fishes	0.080	1.100	11.40	(0.667)
22	Omnivore fishes	0.198	1.270	18.00	(0.815)
23	*Litopenaeus*	14.36	3.163	10.20	(0.169)
24	*Macrobrachium*	1.115	1.228	4.172	(0.820)
25	Other shrimps	2.121	4.010	14.86	(0.677)
26	*Callinectes*	2.450	2.228	6.285	(0.827)
27	Grapsids	0.029	3.801	14.16	(0.815)
28	Insects	(0.583)	15.54	39.00	0.820
29	Polychaetes	9.500	7.160	23.41	(0.991)
30	Infauna	5.818	10.44	23.80	(0.988)
31	Bivalves	16.83	2.241	9.680	(0.243)
32	Zooplankton	13.50	21.90	84.96	(0.993)
33	Phytoplankton	44.97	60.80	–	(0.304)
34	Detritus	2211	–	–	(0.299)

Figures in parentheses were calculated by EwE

B biomass (expressed as wet weight), *P/B* ratio production/biomass, *Q/B* ratio consumption/biomass, *EE* ecotrophic efficiency)

4.08. Top predators were the crocodilians (4.128), whereas primary consumers were mugilids, poeciliids, and polychaetes (*TL* from 2.004 to 2.070). Within the fish group, snappers, snooks, and *Atractosteus tropicus* were the main predators, and the latter showed a close relationship with *Dormitator latifrons* (see Table 5 for the *TL* of every group).

Groups that contributed the most biomass to the flow to detritus were those consisting of invertebrates, whose *TL* places them at the mid-lower part of the trophic web (zooplankton, *Litopenaeus*, bivalves, and polychaetes). Most of these same groups attained high respiration values and assimilated most biomass in this estuarine food web (zooplankton, polychaetes, bivalves, *Litopenaeus*, and infauna). According to the *OI*, most specialized groups included mugilids (*OI* = 0.005) and poeciliids (*OI* = 0.008). The groups that preyed on a greater diversity of *TL* were omnivore fishes, *Callinectes*, and gerreids, with an *OI* of 0.610, 0.513, and 0.495, respectively.

Table 4 Predator–prey matrix of the trophic model of the system Chantuto-Panzacola

	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1	Water birds		0.045														
2	Crocodilians	0.006	0.001														
3	*D. latifrons*	0.154															
4	Eleotrids		0.042			0.031	0.030							0.030			
5	*S. guatemalensis*		0.121														
6	Ariid catfishes								0.025								
7	Jacks	0.099							0.061								
8	Snooks	0.117															
9	Anchovies					0.200	0.193	0.100	0.276		0.245						
10	Sciaenids	0.010															
11	Gobiids				0.100	0.018	0.110	0.003			0.071			0.060	0.049		
12	Mugilids	0.024						0.344	0.081								
13	Gerreids		0.164						0.048								
14	Pleuronectiforms							0.001						0.080			
15	Poeciliids		0.108		0.048												
16	*S. annulatus*																
17	Cichlids		0.020			0.150	0.229	0.015									
18	Snappers	0.099															
19	*A. tropicus*	0.008															
20	Planktivore fishes	0.296	0.128		0.076				0.011								
21	Carnivore fishes	0.041	0.074		0.007												
22	Omnivore fishes		0.197														
23	*Litopenaeus*				0.233	0.136	0.190	0.096	0.470	0.064	0.179				0.031		
24	*Macrobrachium*		0.003		0.004	0.018	0.013				0.013						
25	Other shrimps		0.050			0.174		0.113			0.196				0.412		
26	*Callinectes*		0.007		0.025	0.067	0.077	0.026	0.028	0.011					0.015		0.413
27	Grapsids																0.104
28	Insects		0.036	0.068	0.158	0.156	0.124										
29	Polychaetes	0.082			0.015	0.033	0.017	0.027		0.032	0.027	0.218	0.004	0.300	0.320	0.007	
30	Infauna			0.001				0.032		0.035	0.258	0.157		0.057	0.090		0.282
31	Bivalves	0.060	0.004	0.004	0.092			0.010			0.047			0.238			0.201
32	Zooplankton			0.542	0.240	0.015	0.014	0.231		0.820	0.010	0.133					

Table 4 continued

	Functional group	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
33	Phytoplankton									0.036							
34	Detritus			0.385								0.445	0.996	0.234	0.081	0.993	

	Functional group	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
1	Water birds																
2	Crocodile																
3	*D. latifrons*			0.631													
4	Eleotrids			0.040													
5	*S. guatemalensis*		0.136														
6	Ariid catfishes		0.103														
7	Jacks																
8	Snooks																
9	Anchovies					0.461											
10	Sciaenids																
11	Gobiids																
12	Mugilids		0.264														
13	Gerreids						0.063										
14	Pleuronectiforms						0.005										
15	Poeciliids	0.120		0.105			0.059										
16	*S. annulatus*		0.004														
17	Cichlids																
18	Snappers																
19	*A. tropicus*																
20	Planktivore fishes					0.010	0.050										
21	Carnivore fishes			0.098													
22	Omnivore fishes			0.030		0.176											
23	*Litopenaeus*		0.113	0.061	0.060							0.074	0.020				
24	*Macrobrachium*			0.033		0.127	0.043		0.030		0.040						
25	Other shrimps		0.238			0.152			0.030								
26	*Callinectes*		0.112			0.009	0.007				0.203						
27	Grapsids		0.029														

Table 4 continued

	Functional group	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32
28	Insects	0.273			0.052	0.064	0.349		0.144				0.009				
29	Polychaetes	0.236						0.279	0.098		0.011			0.010	0.100		
30	Infauna				0.029		0.001	0.112	0.058	0.500	0.041	0.130		0.044	0.097		
31	Bivalves										0.438	0.200					
32	Zooplankton				0.770			0.091	0.013	0.100		0.050	0.280		0.100	0.212	0.160
33	Phytoplankton				0.088					0.300			0.115		0.074	0.591	0.620
34	Detritus	0.371					0.422	0.518	0.622	0.100	0.192	0.600	0.596	0.946	0.629	0.197	0.220

The flow diagram (Fig. 2) displays all trophic interactions among functional groups, as well as their placement by *TL* and the degree of energy flow. The most important flow occurred at the base of the trophic web, mainly between detritus and mugilids, poeciliids, and polychaetes. The interactions between phytoplankton, and bivalves and zooplankton were important as well, and also from the latter group to anchovies and planktivore fishes. The graph of mixed trophic impacts is shown in Fig. 3; detritus was the group that benefitted directly or indirectly the greatest amount of other groups. Our model obtained a pedigree index of 0.63, a relatively high value.

Ecosystem's traits

The traits of the ecosystem, relevant to estimate its degree of development, are shown in Table 6. Total throughput was 7,133 g m^{-2} year^{-1}, out of which 28.2% was consumed, 24.5% exported, 14.9% used in respiration, and 33.4% returned to detritus. The ratio total primary production/total respiration was 2.576; the connectance index represented 19% of the possible connections among the functional groups in the trophic web. Finn's cycling index showed that only 6.8% of the production in the system is recycled. The *OI* for Chantuto-Panzacola was 0.258.

The *C* of the system was 26,705 flowbits (t km^{-2} year bits), out of which 29.5% corresponds to *A* and 70.5% to *O*. The functional groups that contributed the most to *O* (70.2%) were zooplankton, phytoplankton, and detritus. Finally, the mean transfer of the system was 10.91%.

Discussion

Our modeling exercise represents the first effort to understand the structure and functioning of a coastal lagoon system of the Mexican South Pacific through the analysis of the interaction among functional groups and the quantification of its flows. Our data allowed us to estimate the degree of development for Chantuto-Panzacola. The results obtained were within what was reported in other tropical coastal lagoons from Mexico and other estuarine ecosystems of America.

The quality of a model depends on the quality of the input data. Therefore, we used as much information

Table 5 Biological parameters calculated by EwE for the diverse functional groups of the lagoon system Chantuto-Panzacola. Biomass is expressed as wet weight

Functional group	Trophic level	Flow to detritus (g m^{-2} year^{-1})	Respiration (g m^{-2} year^{-1})	Assimilation (g m^{-2} year^{-1})	Omnivory index
Water birds	3.989	0.075	0.145	0.184	0.329
Crocodilians	4.080	0.108	0.104	0.170	0.318
D. latifrons	2.744	3.905	10.30	11.44	0.347
Eleotrids	3.455	0.722	2.499	2.837	0.106
S. guatemalensis	3.773	0.950	1.171	1.960	0.122
Ariid catfishes	3.773	0.278	0.766	1.100	0.112
Jacks	3.371	0.861	2.648	3.017	0.170
Snooks	3.816	1.286	2.700	3.205	0.173
Anchovies	3.185	5.517	16.76	20.00	0.074
Sciaenids	3.697	0.072	0.179	0.203	0.107
Gobiids	2.664	1.269	3.473	4.953	0.361
Mugilids	2.004	3.049	6.310	9.264	0.005
Gerreids	3.061	1.557	4.486	5.197	0.495
Pleuronectiforms	3.371	2.514	6.704	7.808	0.275
Poeciliids	2.007	1.073	2.360	4.000	0.008
S. annulatus	3.716	0.069	0.173	0.201	0.204
Cichlids	2.741	1.998	6.878	7.696	0.337
Snappers	3.839	0.593	1.635	1.789	0.428
A. tropicus	3.796	0.031	0.057	0.071	0.218
Planktivore fishes	3.121	2.600	7.156	8.288	0.131
Carnivore fishes	3.928	0.212	0.642	0.730	0.080
Omnivore fishes	2.860	0.760	2.601	2.853	0.610
Litopenaeus	2.559	67.06	71.77	117.2	0.343
Macrobrachium	2.500	1.176	2.352	3.721	0.426
Other shrimps	2.798	9.052	16.71	25.21	0.427
Callinectes	3.25	4.025	6.860	12.32	0.513
Grapsids	2.458	0.106	0.225	0.339	0.392
Insects	2.345	6.183	9.137	18.20	0.294
Polychaetes	2.070	45.06	109.9	177.9	0.088
Infauna	2.358	28.40	50.03	110.8	0.307
Bivalves	2.253	61.13	92.62	130.3	0.237
Zooplankton	2.190	231.4	622.0	917.6	0.190
Phytoplankton	1.000	1903	–	–	–
Detritus	1.000	–	–	–	0.297

from the Chantuto-Panzacola lagoon system itself as possible. Except for the biomass of birds and insects, estimated by EwE, all biomass data were obtained by ourselves or from previous work carried on at our study site. More than half of the diets of the fish

functional groups were determined from local material, especially for dominant species. The nature of the information used to build our model favored the pedigree index score, relatively high compared to other models in Mexican tropical coastal lagoons, such
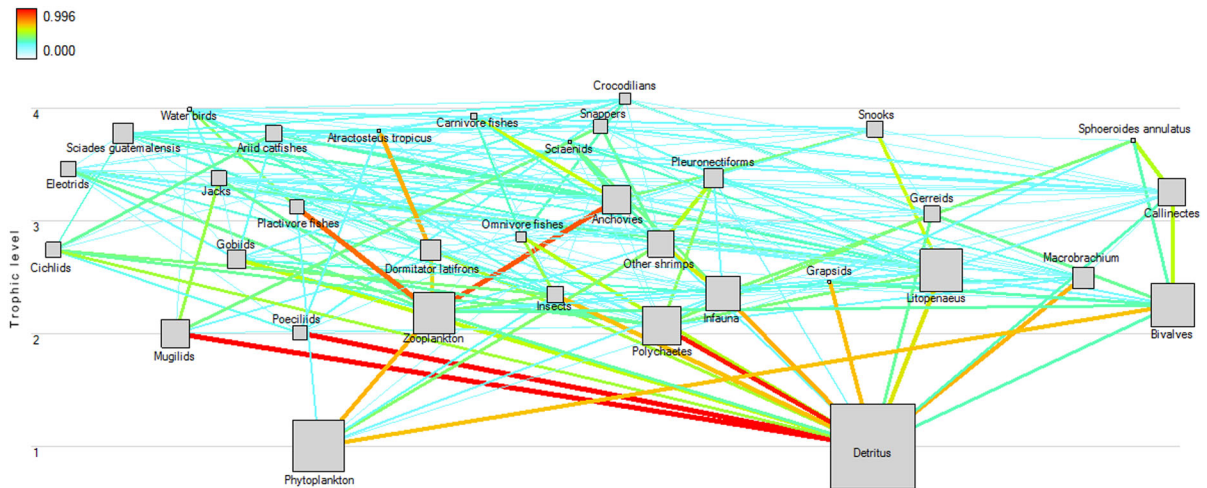
Fig. 2 Trophic web and energy flow in the Chantuto-Panzacola system. The area of the squares is proportional to the biomass of each functional group. Breadth of the lines are proportional to energy flow (in g m^{-2} year^{-1}). Biomass is expressed as wet weight

as Alvarado (0.50: Cruz-Escalona et al., 2007), Chetumal Bay (0.49: Castelblanco-Martínez et al., 2012), or Términos Lagoon (from 0.47 to 0.58: Manickchand-Heileman et al., 1998; Abascal-Monroy, 2014).

The highest biomass, *P/B*, and *Q/B* occurred in functional groups at lower *TL*, such as zooplankton, polychaetes, bivalves, infauna, and insects. Invertebrates are clearly important in these ecosystems, as energy conveyors between the detritus and

phytoplankton and upper *TL* groups (fishes, birds). This pattern has also been reported in other coastal lagoons (e.g., Manickchand-Heileman et al., 1998; Vega-Cendejas & Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003; Villanueva et al., 2006b).

Some of the groups that link energy between producers and higher consumers, for instance zooplankton, infauna, and polychaetes, showed high *EE* values, meaning they are both very abundant and highly consumed. This was also observed in
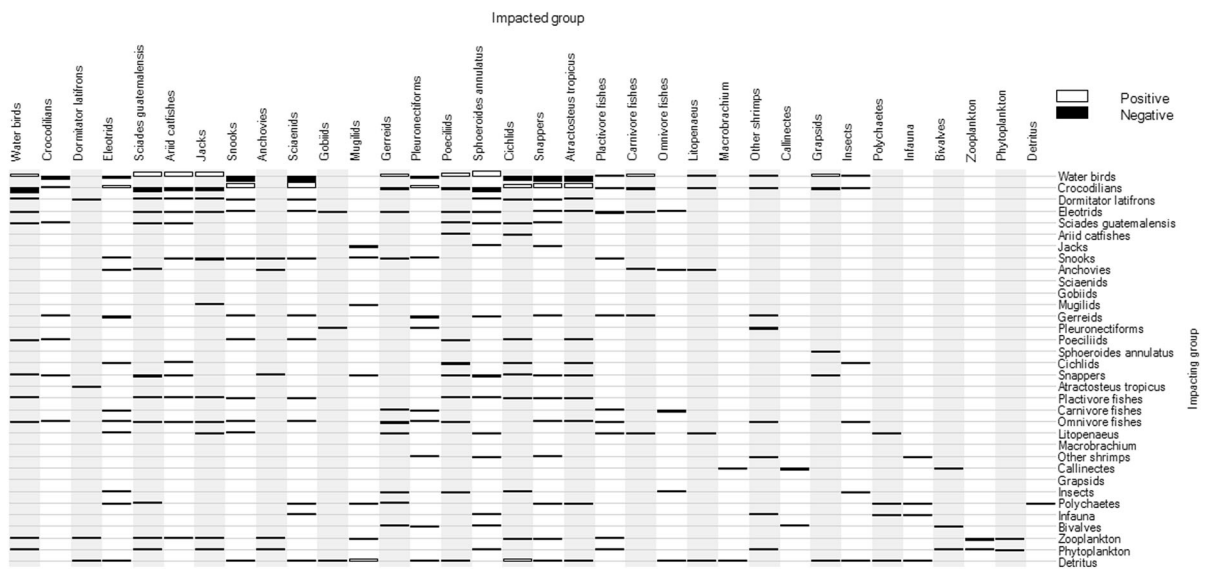

Fig. 3 Graph of mixed trophic impacts. Horizontally, impacted groups; vertically, those that exert the impact. White rectangles over the horizontal axis are positive impacts; black rectangles under the axis, negative

Table 6 General synecological traits of the system Chantuto-Panzacola. Biomass is expressed as wet weight

Parameter	Value	Units
Sum of all consumption	2013	g m^{-2} year^{-1}
Sum of all exports	1673	g m^{-2} year^{-1}
Sum of all respiratory flows	1061	g m^{-2} year^{-1}
Sum of all flows into detritus	2386	g m^{-2} year^{-1}
Total system throughput	7133	g m^{-2} year^{-1}
Sum of all production	3283	g m^{-2} year^{-1}
Calculated total net primary production	2734	g m^{-2} year^{-1}
Total primary production/total respiration	2.576	
Net system production	1673	g m^{-2} year^{-1}
Total primary production/total biomass	21.81	
Total biomass/total throughput	0.018	year^{-1}
Total biomass total (excluding detritus)	125.31	g m^{-2}
Connectance index	0.19	
System omnivory index	0.25	
Pedigree index	0.63	
Ascendency	7883	Flowbits
Overhead	18,822	Flowbits
Development capacity	26,705	Flowbits
Finn's cycling index	6.83	%

Huizache-Caimanero (Zetina-Rejón et al., 2003), Alvarado (Cruz-Escalona et al., 2007), and Chetumal Bay (Castelblanco-Martínez et al., 2012). Some fish groups also displayed a high *EE*, among them eleotrids, ariid catfishes, gobiids, poeciliids, cichlids, carnivores, and omnivores. This occurred because they had a low biomass, but a high predation pressure. In the case of ariid catfishes, García-Morales (2007) reported that there is fishing pressure over this functional group in our study area.

Fishes are the most conspicuous component of nekton. They have a great dispersal potential and life cycles which often include migration from the sea to the coastal lagoon and vice versa (e.g., snooks, jacks, mugilids), or from the rivers to the lagoons (e.g., *Dormitator latifrons*), according to ontogeny and reproduction. Thus, fishes are vehicles for energy exchange among different aquatic environments, transforming and exporting energy from primary producers. They are reservoirs and regulators of energy in the trophic web (Yáñez-Arancibia, 1985).

The *EE* was low for detritus in Chantuto-Panzacola, same as in the other tropical systems mentioned above for comparison, with the exception of Celestún (Vega-Cendejas & Arreguín-Sánchez, 2001), where *EE* of detritus was high (0.640). In spite of sustaining 29

functional groups in our model, the consumption of detritus is lower than its accumulation in these ecosystems, which causes biomass and energy to increase in the lagoons or to be exported in greater amounts (Zetina-Rejón et al., 2003) to the adjacent marine ecosystem.

In addition to its very large biomass, detritus was also relevant because of its role in energy flow, since its contribution to the system's overhead was 25%, and its links to other groups were very important. Therefore, it can be stated that this system is controlled by bottom-up dynamics. Detritus is a significant component in costal lagoon ecosystems (Zetina-Rejón et al., 2003; Villanueva et al., 2006b).

Total System Throughput was greater than in the other coastal lagoons mentioned above, except for Chetumal Bay (Castelblanco-Martínez et al., 2012) and Río de la Plata estuary (Lercari et al., 2014), much more productive and bigger in size (considering the sum of the flows) than the other compared systems (Table 7). The degree of development (*A*) and the reserve potential (*O*) of Chantuto-Panzacola were similar to the reference coastal lagoons mentioned above.

The values of ascendency and relative ascendency for Chantuto-Panzacola indicate that this coastal

lagoon system has barely reached one-third of its total development, very similar to other coastal lagoon complex of Mexico: Celestún, Alvarado, and Huizache-Caimanero, systems with the same geological age that Chantuto-Panzacola (Lankford, 1977). In the absence of major disturbances (those that drastically change the energy flow or the trophic structure, e.g., hurricanes, massive mangrove deforestation), the ecosystem is expected to continue developing, and as a consequence, the ascendency would increase too (Ulanowicz, 2004; Scharler, 2009). Ascendency can be used to evaluate quantitatively whether a system has grown or shrunk, developed or regressed (Ulanowicz, 2000; Patrício et al., 2003). If we wanted to evaluate this in Chantuto-Panzacola, we would have to develop temporal models (whether they are monthly or yearly) with the help of the Ecopath's tool Ecosim, because the present model is a static one.

As for Finn's cycling index, Chantuto-Panzacola was above the estimates for Alvarado (Cruz-Escalona et al., 2007), Río de la Plata estuary (Lercari et al., 2014), and Bahía Málaga (Castellanos-Galindo et al., 2017), but below Términos (Manickchand-Heileman et al., 1998), Huizache-Caimanero (Zetina-Rejón et al., 2003), and Celestún (Vega-Cendejas & Arreguín-Sánchez, 2001). Taking into account the possible number of connections in the trophic web, in Chantuto-Panzacola only 19% actually occurred, below the usual situation in other systems (Table 7).

The TPP/TR ratio for Chantuto-Panzacola was 2.57, which means that only a rather small fraction of the production is being consumed. This signals an undeveloped state, especially when coupled with the observation that most fishes and macroinvertebrates in the system occur in juvenile stages. According to the TPP/TR ratio, Chantuto-Panzacola would be closer from a maturity stage than Celestún, Huizache-Caimanero, Chetumal, Bahía de Málaga, and Río de la Plata estuary. On the other hand, the system also displays some traits that Odum (1969) considered symptomatic of a mature development state, among them the preponderance of detritus in nutrient cycling, as well as its relatively high species diversity. Vega-Cendejas & Arreguín-Sánchez (2001) claim that mangrove-associated ecosystems in general tend to be transitional between immaturity and maturity.

For greater clarity, we can resort to a historical perspective: according to Lankford (1977), the estuarine coastal lagoon system Chantuto-Panzacola started forming 5,000 years ago. By then mangrove was already present, although present-day vegetation conditions were reached only 3,500 years ago (Joo-Chang et al., 2015). Thus, our study area can be regarded as geologically young, which might help explain its low maturity degree. Somewhat paradoxically, immaturity can confer stability due to the lower complexity of the system (Pérez-España & Arreguín-Sánchez, 2001), which allows greater speed and flexibility of reaction towards environmental change (Colombo, 1977). We think it is important to associate the attributes of our ecosystem with their age to argue that some young ecosystems may have some degree of development relatively away from a purely immature state, and still be able to deal with certain stressors. Although Christensen (1995) classified coastal lagoons with lower maturity than other aquatic ecosystems, several works have reported coastal lagoons as stable ecosystems despite its development degree (e.g., Vega-Cendejas & Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003; Villanueva et al., 2006b; Abascal-Monroy et al., 2016).

Odum (1969) thought that coastal lagoons will always be in an intermediate state of maturity, because they are perpetually undergoing disturbance by the freshwater input from rivers and the tidal action, with its marine influence. This implies a much slower development, compared to systems free from such periodic environmental fluctuations. Given that these disturbances do not affect negatively ecosystem structure, nor components and flows in the trophic web, a system collapse is unlikely. On the contrary, facing periodic minor disturbances (or even long-term, but low in intensity), ecosystems can develop slowly, continuously adapting to the disturbance and hence absorbing its impact (Bendoricchio & Palmeri, 2005), adjusting the distribution of its energy flows. This ecosystem trait can be attributed in part to the overhead, the potential energy reserve of the system, used when this suffers disturbance, since an ecosystem with insufficient overhead is not capable to create an effective response to environmental challenges (Ulanowicz, 2004). Overhead was high in Chantuto-Panzacola (70.5%) compared with Río de la Plata estuary (Lercari et al., 2014) and Bahía Málaga (Castellanos-Galindo et al., 2017), and similar to the other lagoon ecosystems (Table 7).

Estuarine ecosystems are known to be highly stressful habitats due to the rapid and intense spatial

Table 7 Comparison of traits in Chantuto-Panzacola and other estuarine systems in tropical America; all models used wet weight as unit, except Términos

Trait	Términos[a]	Celestún[b]	Alvarado[c]	Huizache-Caimanero[d]	Chetumal[e]	Chantuto-Panzacola	Bahía Málaga[f]	Río de la Plata estuary[g]
PI	0.47–0.58	–	0.50	0.73	0.49	0.63	0.60	0.61
TST	3710	4581	2683	6669	22,2304	7133	6469	45,683
TPP/TR	–	15.90	1.30	3.35	7.05	2.57	5.40	10.46
A/C (%)	–	23.56	28.72	29.42	–	29.50	44.03	53
O/C (%)	–	76.44	71.28	70.76	–	70.50	55.97	47
FCI (%)	7	13.40	0.07	9.90	–	6.83	2.180	0.82
CI (%)	41	30	30	30	37	19	19	24

PI pedigree index, *TST* total system throughput, *TPP/TR* total primary production/total respiration, *A/C* relative ascendency, *O/C* relative overhead, *FCI* Finn's cycling index, *CI* onnectance Index

[a]Manickchand-Heileman et al. (1998)

[b]Vega-Cendejas & Arreguín-Sánchez (2001)

[c]Cruz-Escalona et al. (2007)

[d]Zetina-Rejón et al. (2003)

[e]Castelblanco-Martínez et al. (2012)

[f]Castellanos-Galindo et al. (2017)

[g]Lercari et al. (2014)

and temporal variation of its physicochemical variables (e.g., salinity, dissolved oxygen, temperature, among others) (McLusky, 1981; McLusky & Elliot 2004; Elliott & Quintino, 2007; Villanueva, 2015). Gómez-González (2011) recorded contrasting seasonal and spatial environmental data in Chantuto-Panzacola where temperature went from 24.6°C to 34.9°C, dissolved oxygen from 0.02 mg/l to 8.41 mg/l, total dissolved solids changed from 0.05 mg/l to 36.7 mg/l, pH from 6.6 to 8.9, transparency from 0.05 m to 1.33 m, and salinity from freshwater (0.1 ppm) to euhaline conditions (38 ppm). Salinity was an abiotic factor that evidently influenced the fish fauna of Chantuto-Panzacola (Gómez-González, 2011) and has been pointed as a driver of the composition and structure of aquatic organisms' communities in estuarine environments (Barletta et al., 2005; Whitfield et al., 2006; Sosa-López et al., 2007; Sánchez-Botero et al., 2009).

A strategy to deal with a stressful changing environment resides in the physiological and behavioral adaptations of the species that dwell in these ecosystems. In Chantuto-Panzacola, 52 out of the 63 fish species used to construct our model were tolerant to changes in salinity (eight were secondary freshwater, seven estuarine resident and 32 marine

euryhaline). In addition, the benthic infaunal community is highly tolerant of changing and adverse environmental conditions such as low oxygen and low and variable salinity (Elliot & Quintino, 2007). Euryecy, diadromy, and other mechanisms allow species to face environmental variability and to turn stress into usable resources (Villanueva et al., 2006b; Elliott & Quintino, 2007; Villanueva, 2015) in coastal lagoons; these mechanisms contribute to ecosystem stability (Day & Yáñez-Arancibia, 1985).

Stability can be considered as the ability of an ecosystem to maintain its state over time, against external and internal forces that drive it away from that state (Saint-Béat et al., 2015), or as the capacity of the community to respond in a certain way to perturbation from an equilibrium state (Mikkelson, 1997). Grimm et al. (1992) proposed that, in order to have a complete stability judgement of an ecological system, it is necessary to analyze of several stability properties such as constancy (staying essentially unchanged), resistance (staying essentially unchanged despite the presence of potentially disturbing external influences), resilience (returning to the referential state after a temporal external influence has been applied), and persistence (persistence through time of populations).

In terms of stability, we took some results of Ecopath to explain or demonstrate that despite its development phase, Chantuto-Panzacola can be considered as a stable system. In the case of Connectance Index for our system, this was smaller (19%) than that recorded in the other estuarine systems. It might indicate weak interactions in the food web, but this kind of interaction can be beneficial for the system since weak interactions act as a stabilizing force in trophic networks owing to their capacity to change within ecosystems (Saint-Béat et al., 2015). In a food web, omnivory can confer stability to the ecosystem (Vandermeer, 2006) because omnivory increases the resistance of the latter due to its capacity to buffer oscillations and perturbation in ecosystems (Saint-Béat et al., 2015). Omnivory also can generate parallel pathways in the food web, these pathways ensure to have more than one route of transference if that other routes are disturbed (Scharler, 2009). The Omnivory Index of Chantuto-Panzacola indicates that most species in the food web are generalists, therefore our system would be experiencing the aforementioned condition. The Overhead of our system was quite high, which means that Chantuto-Panzacola possesses the capacity to cope with the effects of perturbations (Saint-Béat et al., 2015), in other words, this system has an elevated resilience (Lobry et al., 2008), which is a property of stability (Grimm et al., 1992).

Bendoricchio & Palmeri (2005) argued that ecosystem health resides in the capacity to maintain structure and function in time in the face of environmental disturbances. Although Chantuto-Panzacola is a young ecosystem, it is protected by its large overhead, the physiological and behavioral adaptations of its biota, its production excess (due to detritus and the TPP/TR ratio), an important degree of omnivory, and a complex trophic web. Other elements that favor ecosystem health are environmental heterogeneity (Day & Yáñez-Arancibia, 1985) and adequate input of freshwater and connection to the sea (Contreras, 1988). The seven affluent rivers into Chantuto-Panzacola and a permanent mouth to the Pacific Ocean ensure the hydrological health of the system.

Due to the complexity of ecosystems, the consideration of a single parameter (e.g., diversity, connectance, interaction strength) does not allow to establish a conclusion about the stability of ecosystems (Saint-Béat et al., 2015). So, we had to consider several ecosystem's traits, such as Overhead, Omnivory Index, stage of development, Connectance Index, Total Primary Production/Total Respiration ratio, detritus-based food web, and certain features of the biota (e.g., osmoregulatory ability) to conclude that Chantuto-Panzacola, although a young ecosystem with a development degree intermediate between immaturity and maturity, is protected by several mechanisms that confer health and stability. This is based on its capacity to cope with highly changing environmental conditions (Lobry et al., 2008), as seen in Chantuto-Panzacola and in other coastal lagoons of similar age.

The results of this model could help us not only to improve this static model by adding fishing information, a new box for mammals, and divide into several groups the water birds box, but we could also develop dynamic models in time and space with the Ecosim (Walters et al., 1997) and Ecospace (Walters et al., 1999) complements of Ecopath, respectively. With the help of these complements we could evaluate, in our study area, the effects of fishing and overfishing by experimental changes in the biomass of certain functional groups through time, which could be used to propose fisheries management plans. We could also model temporal variation and its influence in the ecosystem, climatic change (e.g., acidification and temperature rise of the oceans), and its effect in the trophic dynamic and ecosystem traits of this coastal lagoon. Habitat preferences could also be evaluated, as well as the fishing effect over the spatial distribution of the functional groups. To analyze stability as an ecosystem's ability to maintain its state over time, temporal models would need to be built in different scales for Chantuto-Panzacola to study how outputs and ecosystem traits behave (e.g., Abascal-Monroy et al., 2016).

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CAPÍTULO II

Un modelo trófico para un Sistema lagunar costero periódicamente cerrado en el sur del Pacífico mexicano

(Artículo enviado a International Review of Hydrobiology)

A TROPHIC MODEL FOR A PERIODICALLY CLOSED COASTAL LAGOON

SYSTEM IN THE SOUTHERN MEXICAN PACIFIC

Jesús M. López-Vila [a,b]*, Juan J. Schmitter-Soto [c], Ernesto Velázquez-Velázquez [d]

[a] Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México; Tercer Circuito s/n, Ciudad Universitaria, Coyoacán. A.P. 70-153, C.P. 04510, Mexico City, Mexico

[b] Centro de Investigaciones Costeras, Instituto de Ciencias Biológicas, Universidad de Ciencias y Artes de Chiapas. Calle Juan José Calzada s/n, Colonia Evolución, C.P. 30500. Tonalá, Chiapas, Mexico

[c] El Colegio de la Frontera Sur, Unidad Chetumal, Av. Centenario km 5.5, C.P. 77014 Chetumal, Quintana Roo, Mexico

[d] Museo de Zoología, Instituto de Ciencias Biológicas, Universidad de Ciencias y Artes de Chiapas. Libramiento Norte Poniente No. 1150, C.P. 29039. Tuxtla Gutiérrez, Chiapas, Mexico

* Corresponding author

E-mail address: jesus.lopez@unicach.mx

ABSTRACT

Carretas-Pereyra is an estuarine lagoon system located in the southern Mexican Pacific coast. Its connection to the sea is intermittent, because the mouth of the system closes seasonally under natural conditions, but it is often opened artificially for artisanal fishery purposes. In order to know the degree of development, structure, and functioning of this system, a trophic model was built using software Ecopath. The model was composed of 32 functional groups: one for birds, one for crocodylians, 18 for fishes, 9 invertebrates, 2 plankton, and detritus. The results are consistent with findings for lagoon systems with

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permanent connection to the sea. Some of the ecosystemic mechanisms probably used to face the abrupt changes induced by the opening of a sea inlet are: system omnivory, elevated overhead, efficient metabolism in phytoplankton, species replacement, and species adaptability to changing environmental conditions. These elements provide stability to the ecosystem and help in its recovery. Detritus, zooplankton, and phytoplankton were important components for the resiliency of the system. In spite of the biological and environmental changes induced by the intermittent opening of an inlet, Carretas-Pereyra has the necessary elements to absorb the impacts and function adequately.

1. INTRODUCTION

Understanding the functioning of a complex ecosystem, and the possible impact of different ecological changes on the system as a whole, calls for quantification of the trophic relationships between the different groups in the system (Mavuti et al., 1996). Measurements of biomass transfer between functional groups and trophic efficiency provide information on ecosystem structure and function, which can be used to evaluate the impact of change on some groups and the way it is propagated through the whole ecosystem via the trophic web (Christensen and Pauly, 1992). One of the most widely used tools to evaluate this has been the trophic mass-balance model Ecopath (Colléter et al., 2015), useful to calculate ecosystem indicators, effects of environmental changes and fishing on the ecosystem, and to explore the policy implications of food web interactions (Christensen et al., 2008).

Estuaries and coastal lagoons are transitional zones between sea and freshwater sources, where populations of marine and freshwater species coexist. Fishes and invertebrates inhabit these biotopes permanently, cyclically, or occasionally, making use of the changing

environmental conditions. Accordingly, many of these species possess particular physiological adaptations, allowing them to tolerate extreme environmental changes occurring in those ecosystems (Day Jr. and Yáñez-Arancibia, 1985).

Coastal lagoons may have a permanent or temporal connection to the sea through natural or artificial openings. When such mouths are natural, changes in connectivity are due to sedimentation, rain regime, flooding, tide action, and influence of rivers (Baldock et al., 2008). Artificial inlets are intended to renew and enrich water quality, prevent flooding, or generally manage the ecosystem, particularly to improve fisheries (Lanés et al., 2015). In any case, the effects of such an action can greatly modify the biological and environmental conditions of coastal lagoons (Suzuki et al., 1998).

Carretas-Pereyra is a lagoon system located in the Biosphere Reserve "La Encrucijada" (BRLE), southern Pacific slope of Mexico. It is included among the terrestrial and marine regions for conservation priority (Arriaga Cabrera et al., 1998; 2000). It is also a Ramsar site (No. 815), attested by the Convention on Wetlands of International Relevance, due to its high diversity, and for holding the most conserved coastal wetland in Mexico. It is also a high valued ecosystem because it provides important biological resources for small-scale fisheries. Historically, Carretas-Pereyra has experienced several temporary openings to the sea (SEMARNAP, 2001; Rivera-Velázquez, 2008; Gómez-González, 2007; Gómez-González et al., 2012).

We used the Ecopath approach to model the structure of the food web in the Carretas-Pereyra system, with the objective to evaluate the status and ecological properties of the ecosystem under intermittent connectivity conditions. The model has the potential to be used to better understand the ecological characteristics of similar semi-closed ecosystems and aid in their management.

2. MATERIALS AND METHODS

2.1. Study area

The Carretas-Pereyra system is located in the central coast of the Mexican state of Chiapas, between 15°23' and 15°32' N, and 93°06' and 93°15' W. It has an area of 37 km^2 and includes four lagoons: Pereyra, Carretas, Bobo, and Buenavista. The system is connected to the sea through an ephemeral inlet in Laguna Pereyra (Contreras-Espinosa, 2010), and the rivers Coapa, Pijijiapan, Bobo, Progreso, and Margaritas flow into the lagoons. This complex, together with the neighboring system Chantuto-Panzacola, integrate the core zone of BRLE (Carabias et al., 1999). There is a distance of 28 km between the closest lagoons in both systems, and 56 km between their mouths.

The climate in the region is tropical with summer rains, and a yearly precipitation of ca. 3000 mm (Contreras-Espinosa, 2010). Vegetation is mainly mangrove forests (*Rhizophora mangle*, *Laguncularia racemosa*), floating and submerged plants, and remnants of low and medium-height forest (Carabias et al., 1999). The system is shallow, and seasonally changes from freshwater to brackish (Velázquez-Velázquez et al., 2008). The main productive activity in the area is the artisanal fishery of shrimp and fish.

2.1.1. Connectivity of the system

For Carreras-Pereyra there is no detailed record on the periodicity and duration of the open and closed phases, nor studies that specifically assess the temporality of the system connection. Some works have indicated at different times the state in which the inlet of the system was located. According to this information, Carretas-Pereyra was connected to the sea in an ephemeral way, but due to the runoffs discharged into the system in 1998 by the tropical storm Javier, the inlet stayed open (SEMARNAP, 2001), and remained so from that year through dredging (Rivera-Velázquez, 2008). From April 1999 to May 2003 the

bathymetry of the mouth was analyzed, although the closure of the inlet was not reported, in 2001 a critical value was recorded in its depth: 0.43 m (Calva-Benítez et al., 2009). Between May 2004 and April 2005 Gómez-González (2007) and Gómez-González et al. (2012) reported that the system maintained an intermittent connection for much of this period. In 2015 we found the system in an open phase.

2.2. Field work

The fishes of this system have been studied by Velázquez-Velázquez et al. (2008) and Gómez-González et al. (2012), who mentioned that during their sampling period the system had an intermittent connection to the sea. For crocodylians, there is an ongoing monitoring program (Reserva de la Biosfera la Encrucijada, 2010). As for invertebrates, Barba-Macías et al. (2012) analyzed the community of benthic macrocrustaceans, and the planktonic assemblage was studied by Varona-Cordero et al. (2010). In none of these works was mentioned the state of the inlet.

Few or no data were available on the infauna (microcrustaceans, polychaetes, mollusks) or the amount of organic matter in the detritus. In order to obtain this yet undocumented information, the system was sampled in March (dry season) and September (rains) in 2015, at 10 sites throughout the lagoon complex (Fig 1); in this year the inlet was open. At every site a Van Veen dredge (mouth 295×190 mm) was used twice; the sediment was homogenized and a volume de 1681 cm^3 was kept, to be sifted for infauna at 0.482, 0.990, 1.981, and 3.352 mm mesh size. The organisms were fixed in 70% ethanol and taken to the laboratory to be identified and weighed to the nearest 0.01 g. To determine the amount of organic matter, the method of weight loss on ignition was used (Dean Jr, 1974) on a subsample of 1 g of sediment from each site.
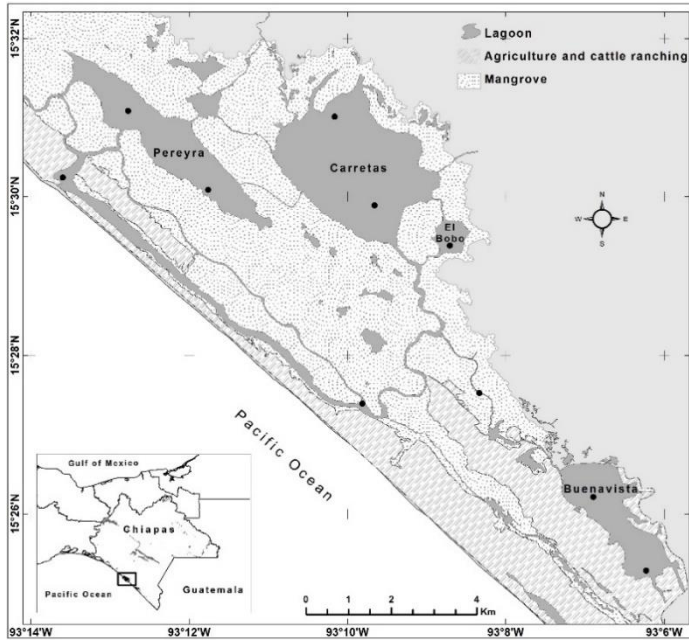
Fig 1. Study area and sampling sites (black circles) in the Carretas-Pereyra lagoon system, Pacific Mexico.

2.3. The Ecopath model

The trophic model was built using the program Ecopath with Ecosim (EwE) version 6.4.3., which is based in a set of linear equations, one for every functional group as prey (*i*) and as predator (*j*), representing biomass flows in the ecosystem, which is assumed to be in balance. The master equation of EwE is:

$$B_i \cdot (P/B)_i \cdot EE_i = Y_i + B_i \cdot (P/B)_i \cdot (1-EE_i) + \sum_{j-1}^{n} B_j \cdot (Q/B)_j \cdot DC_{ji}$$

where *B* is the biomass, *P/B* and *Q/B* are the production/biomass and consumption/biomass ratios respectively, *EE* is the ecotrophic efficiency, *DCji* is the fraction of prey *i* in the diet of predator *j*, and *Yi*, the total fishery catch rate of *i*. For a description of what the software requires, more details of its master equation and algorithms, and what it can provide, see Christensen et al. (2008).

2.4. Functional groups

The numerous species in an ecosystem can be grouped and organized as trophic guilds or as taxa, and can be further subdivided according to size or age (Christensen et al., 2008), or sorted according to abundance or commercial importance in fisheries (Zetina-Rejón et al., 2003). In order to delimit functional groups, we took into account ecological or taxonomic relationship among species, diet similarity, and numerical abundance. *Dormitator latifrons* was placed in its own functional group because of its seasonal migration, a phenomenon not seen in other eleotrids. Some species were selected as functional groups because of their regional economic value; to do so we took as reference the work of García-Morales (2007), who characterized the fishing activities in the neighboring lagoon system, Chantuto-Panzacola. In total, 32 functional groups were defined (Table 1). The information of each functional group is not differentiated by periods of open or closed inlet, instead of that the data used was pooled.

Table 1 Functional groups of the lagoon system Carretas-Pereyra and their constituent taxa

Functional group	Constituent taxa
Water birds	Podicipediformes, Pelecaniformes, Ciconiiformes, Anseriformes, Falconiformes, Gruiformes, Charadriiformes
Crocodylians	*Caiman crocodilus, Crocodylus acutus*
Ariid catfishes	*Cathorops liropus*
A. guatemalensis	*Ariopsis guatemalensis*
Jacks	*Caranx caninus, Oligoplites altus, O. saurus*
Snooks	*Centropomus medius, C. nigrescens, C robalito*
Snappers	*Lutjanus argentiventris*
Cichlids	*Amphilophus trimaculatus, Astatheros macracanthus, Oreochromis niloticus*
S. annulatus	*Sphoeroides annulatus*
Pleuronectiforms	*Achirus mazatlanus, Citharichthys gilberti*
Gerreids	*Diapterus brevirostris, Eucinostomus currani, Gerres simillimus*
D. latifrons	*Dormitator latifrons*
Anchovies	*Anchoa lucida, A. curta, Anchovia macrolepidota*
Mugilids	*Mugil curema, M. cephalus, M. hospes*
Poeciliids	*Poecilia nelsoni, P. sphenops, Poeciliopsis fasciata, P. turrubarensis*
Eleotrids	*Gobiomorus maculatus*

Gobiids	*Awaous transandeanus, Gobionellus microdon*
Omnivore fishes	*Astyanax aeneus*
Planktivore fishes	*Atherinella guatemalensis, Lile gracilis, L. nigrofasciata*
Carnivore fishes	*Elops affinis, Roeboides bouchellei*
Litopenaeus	*Litopenaeus stylirostris, L. vannamei*
Other shrimps	*Farfantepenaeus brevirostris*
Macrobrachium	*Macrobrachium tenellum*
Callinectes	*Callinectes arcuatus, C. toxotes*
Grapsids	*Goniopsis pulchra, Grapsus* sp.
Insects	Formicidae, Odonata, unidentified larvae
Bivalves	Bivalvia
Infauna	Tanaidacea, Isopoda, Ostracoda, Cumacea, Amphipoda
Worms	Polychaeta, Enteropneusta
Zooplankton	Cnidarians, gastropods and polychaetes larvae, cladocerans, copepods, cirripedia larvae, decapod larvae, fish eggs
Phytoplankton	Diatoms, dinoflagellates, euglenophytes, cyanophytes, chlorophytes, silicoflagellates
Detritus	Organic matter

2.5. Input data

Biomass (as mean biomass per unit area, in $g \cdot m^{-2}$) for fish groups was taken from Gómez-González (2007) and Velázquez-Velázquez et al. (2008); for macrocrustaceans, from Barba-Macías et al. (2012); for phytoplankton, from Gutiérrez Mendieta et al. (2006). The biomass of bivalves, worms, meiobenthic crustaceans, and detritus was estimated from our own field data. In the case of birds and crocodylians, the reference of biomass was taken from a model for Chantuto-Panzacola (López-Vila et al., 2019). For grapsids, insects, and zooplankton, biomass was estimated by EwE. The parameters P/B (production/biomass) and Q/B (consumption/biomass) were obtained for fishes from FishBase (Froese and Pauly, 2018), using its tool "life history". For all other groups, these data were modified from other published models built up for similar, and if possible near, coastal lagoons (Supplementary material, Table 1). In case functional groups were made up of two or more species, the respective values were averaged.

The fourth parameter in the mass-balance model, EE (ecotrophic efficiency), i.e. the part of the production of every functional group that is utilized within the ecosystem, can be calculated by EwE, when the other three required parameters are known (Christensen et al., 2008). In this study, EE was estimated by EwE for all functional groups, except for insects (from Vega-Cendejas and Arreguín-Sánchez, 2001), grapsids and zooplankton (from López-Vila et al., 2019).

To build the predator-prey matrix (Supplementary material, Table 2), the feeding habits information of the species that constitute each functional group was used. Out of the 32 groups used in our model, 18 consisted of fishes, the main component of nekton and the local fisheries; fish diets were ascertained from specimens at the ichthyological collection at UNICACH (30 individuals per species). When material was scarce or not available, data from the literature were used, same as for birds, crocodylians, and invertebrates (Supplementary material, Table 1).

2.6. Balancing the model

In order to identify issues of model structure and data quality before balancing the model, we followed the PREBAL method (Link, 2010). Thereafter, we checked that the values of EE were less than or equal to 1, and followed the general rules (Christensen et al., 2008) to balance the model. The process went on for all groups; if some of them still had an EE > 1, their biomass was checked, and in necessary case increased, especially for those groups where biomass was suspected to be underestimated due to the sampling method. In parallel, the values of *P/B* and *Q/B* for groups with *EE* > 1 were modified, usually by increasing P/B and decreasing *Q/B*. The process continued iteratively until *EE* ≤ 1 was achieved for all groups.

2.7. Relevant output of the model

The software EwE can calculate some of the parameters associated with the food habits of

the functional groups or metabolic aspects of them, such as trophic level (*TL*), omnivory

index (*OI*), flow to detritus, and respiration; EwE can also depict all flows, biomasses and

trophic interactions in a single chart, the flow diagram (Christensen et al., 2008).

Several other distinctive attributes of an ecosystem are calculated by EwE. Ascendency (*A*)

combines system size and flow organization, i.e. it is a natural descriptor of the growth and

development of the system; development capacity (*C*) is an upper limit of *A*, whereas

overhead (*O*) is the difference between *A* and *C* and is interpreted as the reserve potential of

the system facing a perturbation; finally, total system throughput (*TST*), or production, the

sum of all the energy flows (Ulanowicz, 2004).

3. RESULTS

The results here presented are a depiction of annual average biomasses and trophic flows of

Carretas-Pereyra from 2004 to 2015; therefore, the effects (direct and indirect) of the

intermittent connection of the system to the sea over period are pooled over time in our

model.

The functional group with the largest biomass was detritus, with over 90% of the total

biomass. The 20 vertebrate groups accounted for less than 0.5%. The greatest production of

the system occurred at the base of the trophic web, i.e. phytoplankton and zooplankton, and

other invertebrates had the greatest consumption; *EE* of primary producers and detritus was

low (Table 2).

Table 2 Parameters of the balanced trophic model of Carretas-Pereyra. Numbers in parentheses were calculated by EwE. Highest values are represented in bold.

Code	Functional group	B (g·m^{-2})	P/B (yr^{-1})	Q/B (yr^{-1})	EE
1	Water birds	0.043	0.930	5.500	(0.151)
2	Crocodylians	0.163	0.250	0.800	(0.041)
3	Ariid catfishes	0.078	0.607	2.500	(0.951)
4	*A. guatemalensis*	0.080	0.785	2.436	(0.439)
5	Jacks	0.098	0.733	7.483	(0.886)
6	Snooks	0.353	0.883	7.000	(0.105)
7	Snappers	0.025	0.370	5.350	(0.612)
8	Cichlids	0.351	1.700	20.00	(0.127)
9	*S. annulatus*	0.006	0.840	7.400	(0.028)
10	Pleuronectiforms	0.968	1.380	12.20	(0.084)
11	Gerreids	0.309	1.270	11.60	(0.390)
12	*D. latifrons*	**5.085**	1.120	14.00	(0.039)
13	Anchovies	2.560	1.200	9.257	(0.237)
14	Mugilids	1.185	1.090	4.273	(0.343)
15	Poeciliids	1.382	4.100	12.50	(0.537)
16	Eleotrids	0.269	0.715	7.500	(0.520)
17	Gobiids	0.677	2.000	8.367	(0.336)
18	Omnivore fishes	0.150	1.270	18.00	(0.548)
19	Planktivore fishes	1.215	2.648	**24.25**	(0.036)
20	Carnivore fishes	0.030	1.100	11.40	(0.528)
21	*Litopenaeus*	17.86	3.163	10.00	(0.189)
22	Other shrimps	0.735	4.010	14.86	(0.756)
23	*Macrobrachium*	**27.89**	1.228	4.172	(0.279)
24	*Callinectes*	4.680	2.228	6.285	(0.612)
25	Grapsids	(0.040)	3.801	14.16	0.815
26	Insects	(2.715)	**15.540**	**39.00**	0.820
27	Bivalves	**20.68**	2.241	9.680	(0.320)
28	Infauna	5.361	**10.940**	23.80	(**0.966**)
29	Worms	8.972	7.860	**23.41**	(**0.990**)
30	Zooplankton	(22.25)	**21.90**	84.96	0.993
31	Phytoplankton	73.79	**60.80**	-	(0.317)
32	Detritus	**2384**	-	-	(0.246)

Consumers had a *TL* that varied between 2 (mugilids) and a little over 4 (crocodylians). As for the flow to detritus, the groups that provided most biomass to the particulate organic matter were phytoplankton and zooplankton. Concerning respiration and assimilation, invertebrates had the highest values, especially zooplankton, bivalves, and worms. As per

the *OI*, the most specialized groups were mugilids, planktivore fishes, and eleotrids, whereas cichlids and some invertebrates had the most general diets (Table 3).

Table 3 Biological parameters calculated by EwE for the functional groups of the coastal lagoon system Carretas-Pereyra. Highest values are represented in bold.

Functional group	Trophic level	Flow to detritus (g·m^{-2}·yr^{-1})	Respiration (g·m^{-2}·yr^{-1})	Assimilation (g·m^{-2}·yr^{-1})	Omnivory index
Water birds	3.980	0.081	0.149	0.189	0.318
Crocodylians	**4.057**	0.065	0.063	0.104	0.281
Ariid catfishes	3.529	0.041	0.109	0.156	0.129
A. guatemalensis	3.449	0.074	0.093	0.157	0.104
Jacks	3.361	0.155	0.517	0.589	0.120
Snooks	3.696	0.773	1.665	1.976	0.173
Snappers	3.632	0.031	0.100	0.110	0.258
Cichlids	2.622	1.925	5.019	5.616	**0.384**
S. annulatus	3.781	0.013	0.030	0.035	0.200
Pleuronectiforms	3.269	3.586	8.112	9.448	0.156
Gerreids	2.932	0.970	2.475	2.868	0.356
D. latifrons	2.721	19.71	51.25	56.95	0.354
Anchovies	3.226	7.083	15.89	18.96	0.050
Mugilids	2.003	1.861	2.759	4.051	0.003
Poeciliids	2.073	6.075	8.153	13.82	0.091
Eleotrids	3.161	0.496	1.423	1.615	0.009
Gobiids	2.413	2.032	3.178	4.532	0.306
Omnivore fishes	3.222	0.628	1.976	2.167	0.068
Planktivore fishes	3.244	9.038	20.31	23.57	0.007
Carnivore fishes	3.856	0.084	0.241	0.274	0.082
Litopenaeus	2.480	81.53	86.39	142.9	0.338
Other shrimps	2.798	2.905	5.790	8.738	**0.427**
Macrobrachium	2.466	47.95	58.83	93.08	**0.399**
Callinectes	3.240	9.932	13.10	23.53	**0.506**
Grapsids	2.457	0.142	0.302	0.455	**0.389**
Insects	2.345	28.77	42.52	84.71	0.294
Bivalves	2.252	71.53	113.8	**160.1**	0.237
Infauna	2.358	27.52	43.42	102.1	0.307
Worms	2.070	42.72	97.51	**168.0**	0.087
Zooplankton	2.190	**381.6**	**1025**	**1513**	0.190
Phytoplankton	1	**3065**	-	-	-
Detritus	1	-	-	-	0.285

Figure 2 depicts the trophic interactions among the functional groups of the Carretas-Pereyra system, as well as the flows of biomass and their *TL*. The most important flows originate from phytoplankton to *Litopenaeus*, bivalves, and zooplankton, and from detritus mainly to mugilids, poeciliids, and worms. Among consumers, the most relevant flow occurs from zooplankton to anchovies and other planktivore fishes. As *TL* increases, the biomass of each group and flow decreases.
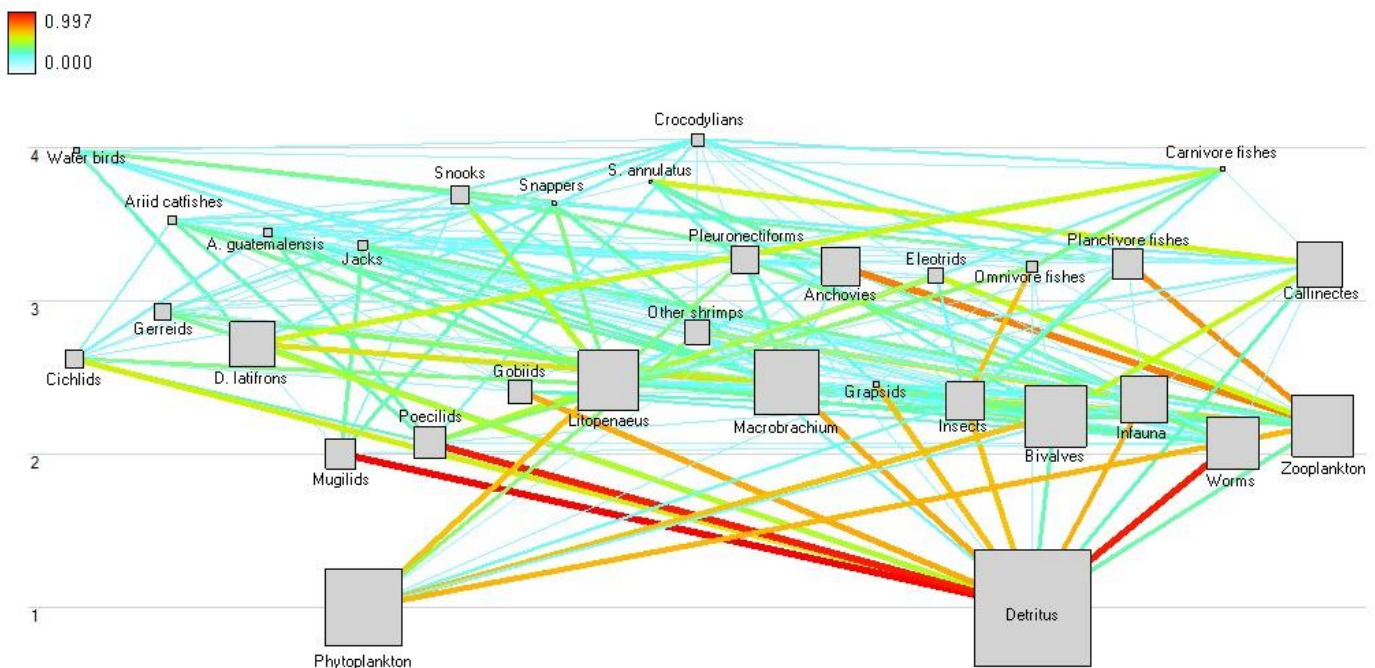

Figure 2 Flow diagram (g·m⁻²·yr⁻¹) of the Carretas-Pereyra system. The area of the squares is proportional to the biomass of each functional group. Breadth of the lines is proportional to energy flow. The ordinate axis shows the trophic level.

Table 4 shows the ecosystem parameters. Ca. 26.9% of the *TST* was consumed, 25.3% exported from the system, 14.2% was part of the respiration, and 33.6% returned to detritus. Only 19.9% of all possible connections in the system actually occurred. Out of the total development capacity, 30.1% corresponded to *A* and 69.9% to *O*. Finally, the quality

of the model, considering the nature of the data used to build it, was assessed as good, given the pedigree index.

Table 4 General ecosystem traits of the Carretas-Pereyra system.

Parameter	Value	Units
Sum of all consumption	3,054	$g \cdot m^{-2} \cdot yr^{-1}$
Sum of all exports	2,876	$g \cdot m^{-2} \cdot yr^{-1}$
Sum of all respiratory flows	1,610	$g \cdot m^{-2} \cdot yr^{-1}$
Sum of all flows into detritus	3,814	$g \cdot m^{-2} \cdot yr^{-1}$
Total system throughput	11,355	$g \cdot m^{-2} \cdot yr^{-1}$
Sum of all production	5,320	$g \cdot m^{-2} \cdot yr^{-1}$
Calculated total net primary production	4,487	$g \cdot m^{-2} \cdot yr^{-1}$
Total primary production/total respiration	2.786	
Net system production	2,876	$g \cdot m^{-2} \cdot yr^{-1}$
Total primary production/total biomass	22.43	
Total biomass/total throughput	0.018	yr^{-1}
Total biomass total (excluding detritus)	200	$g \cdot m^{-2}$
Connectance index	0.199	
System omnivory index	0.232	
Pedigree index	0.623	
Ascendency	12,396	Flowbits
Overhead	28,726	Flowbits
Development capacity	41,122	Flowbits
Finn's cycling index	6.2	%
Mean transfer of the system	7.75	%

4. DISCUSSION

Several trophic models of estuarine lagoon systems that have a permanent connection to the sea are available (e.g. Cruz-Escalona et al., 2013; Abascal-Monroy et al., 2016; Bueno-Pardo et al., 2018). However, the functioning of ecosystems with a temporary connection to the sea has been studied less often (e.g. Milessi et al., 2010; Scharler, 2012). Carretas-Pereyra used to have a temporary connection to the sea; after 1998 the mouth of the system was kept open artificially by dredging, and connectivity became intermittent again in 2003-2005 (Gómez-González et al., 2012).

The temporary closing of mouths that connect coastal lagoons to the sea can modify physicochemical, hydrological, geomorphological, and biological traits of these systems (Suzuki et al., 1998; Parkinson and Stretch, 2007; Santangelo et al., 2007; Pires et al., 2011). These effects have been reported for Carretas-Pereyra by Gómez-González et al. (2012), who recorded fewer species in this system (67) than in Chantuto-Panzacola (143). The authors argued that the difference between these systems, especially in terms of marine species, could be due to the interruption of the sea connection.

In coastal lagoon systems with such an intermittent connection to the sea, the most representative fishes in terms of abundance are freshwater and estuarine species, tolerant to salinity fluctuations (Sánchez-Botero et al., 2009; Lanés et al., 2015). In Carretas-Pereyra, dominant freshwater fishes are *Poecilia sphenops*, *P. nelsoni*, and *Astatheros macracanthus*, as well as the estuarine species *Dormitator latifrons* and *Lile gracilis* (Gómez-González, 2007). *Astatheros macracanthus*, *L. gracilis, P. sphenops*, and *P. nelsoni* predominated in the dry season, whereas during the rainy season the dominant species was *D. latifrons*. Our model reflects as well the importance of *D. latifrons*, whose biomass was far over any other vertebrate and even some invertebrates. Poeciliids and planktivore fishes (which include *L. gracilis*) had greater biomass than other functional groups consisting of fishes.

Varona-Cordero et al. (2010) analyzed the phytoplankton community and the effect of environmental variables on it in Carretas-Pereyra. They found that composition and structure of this community varied seasonally, with freshwater and brackish species being dominant in the rainy season and marine species in the dry season, and greater biomass in the latter season. These authors explain that during the drought tidal influence causes the

water column to be better mixed, resuspending sediment and providing more nutrients. However, the effect of the inlet opening or closing was not explicitly discussed.

The effect of temporary connectivity on phytoplankton and zooplankton has not been examined directly in Carretas-Pereyra. In Brazilian coastal lagoons, there was a substantial loss of phytoplanktonic biomass immediately after an opening to the sea (Suzuki et al., 1998, and a gradual increase after its closure (Santangelo et al., 2007). This process can take from some days up to two years.

When the connection to the sea is closed, phytoplankton assimilates nutrients efficiently and rapidly, thus increasing its biomass. Sometimes, this recovery can occur sooner during the rains, because of the increase in availability of alochthonous material from rivers that flow into the lagoons. This increased biomass might restore the base of the trophic web in these environments (Suzuki et al., 1998; 2002).

Zooplankton composition, structure, and biomass are also influenced by the environmental conditions, mainly salinity, that depend on whether the connection to the sea is open or closed (Santangelo et al., 2007; Setubal et al., 2013). When the mouth to the sea opens, zooplankton loses biomass, which is eventually recovered after the connection closes, depending on the recovery of phytoplankton (Perissinotto et al., 2010) and former environmental conditions (Duggan and White, 2010). The frequency and intensity of inlet openings and closures, as well as the species present in each phase, influence as well the recovery of the zooplankton community (Santangelo et al., 2007).

In estuarine ecosystems that are seasonally connected to the sea, the highest values of biomass and abundance of zooplankton occur during the closed phase (Carrasco et al., 2010). Although the Carretas-Pereyra is much smaller in area than Chantuto-Panzacola, the biomass of phytoplankton and zooplankton in the former, which is only temporarily

connected to the sea, was greater than in the latter, which has a permanent connection (López-Vila et al., 2019).

Such a loss of biomass has also been recorded in benthic invertebrates after opening a connection between the lagoon system and the sea (Netto et al., 2012). The meiofauna seems to be an exception, because closing and opening of inlets do not seem to have an effect on these organisms (Kandratavicius et al., 2015).

The biomass of detritus was greater in Carretas-Pereyra than in Chantuto-Panzacola, in spite of the enormous difference in area between both systems. This suggests that the magnitude and duration of the opening at Carretas-Pereyra was not strong or long enough to let an important amount of biomass escape. Longer periods of isolation allow detritus to accumulate, especially from the mangrove, which is able to contribute up to 90% of its fallen leaves to coastal lagoon waters (Flores-Verdugo et al., 1987). As for the magnitude, the artificial inlet was narrow. Although other coastal lagoons have displayed a significant reduction of organic matter and detritus after the opening of an inlet (Flores-Verdugo et al., 1987; Netto et al., 2012), this was not the case in Carretas-Pereyra, perhaps because of factors related to mangrove productivity, duration and magnitude of the opening to the sea, geomorphology, bathymetry, and hydrodynamics of the system, as well as the transport of marine sediment by wave action into the lagoons.

As for the ecological attributes of the ecosystem, those related to the organization of the trophic web (relative ascendency) and energy reserve (relative overhead), Carretas-Pereyra displayed values similar to other coastal lagoon systems (Table 5). These values are within the intervals reported for temperate coastal lagoons, e.g. the Ria de Aveiro, Portugal (Bueno-Pardo et al., 2018), or lagoons with an ephemeral inlet to the sea, e.g. La Rocha, Uruguay (Milessi et al., 2010). The relative ascendency of Carretas-Pereyra indicates that

the ecosystem has had a development of ca. 30% with respect to its total potential. The other 70% (relative overhead) would be utilized as an energy reserve to recover from any disturbance; the functional groups that contribute the highest amount of energy for this process are detritus, phytoplankton, and zooplankton. Concerning the size of the system, as estimated via the *TST*, although Carretas-Pereyra is much smaller than other lagoons in the Pacific (e.g. Bahía Magdalena, Chantuto-Panzacola, Huizache-Caimanero) and Atlantic coasts of Mexico (Celestún, Alvarado), the sum of all flows was much greater in our study area.

The ratio *TPP*/*TR* has been proposed by Odum (1969) as one of the elements useful to evaluate the degree of development of the ecosystem. Values close to 1 indicate maturity, and values above or below unity reflect lower stages of development. Thus, the coastal lagoon here studied is still in development, but closer to maturity compared to other systems, where this ratio is greater than in Carretas-Pereyra (e.g. Celestún, Ria de Aveiro). The ratio *TPP*/*TR* in our study area is similar to neighboring Chantuto-Panzacola. The proportion of *TST* that is recycled in Carretas-Pereyra (as per the *FCI*) was below the value reported for other coastal lagoons; the same is true for connectance. These indicators are also similar to those obtained in Chantuto-Panzacola. Using data from the field, either collected directly or from published works on the same study area, increases greatly the quality of the model. In the present case, the pedigree index is quite high, very close to the IP of 0.78 at Huizache-Caimanero (Zetina-Rejón et al., 2003).

Table 5 Comparison of ecological attributes among selected coastal lagoon systems. Abbreviations: *PI*, Pedigree index; *TST*, Total System Throughput; *TPP/TR*, Total Primary Production/Total Respiration; *A/C*, Relative Ascendency; *O/C*, Relative Overhead; *FCI*, Finn's cycling index; *CI*, Connectance Index.

Trait	Bahía Magdalena[a]	Celestún[b]	Alvarado[c]	Huizache-Caimanero[d]	Chantuto-Panzacola[e]	Ria de Aveiro[f]	La Rocha[g]	Carretas-Pereyra[h]
PI	-	-	0.5	0.73	0.63	0.66	0.68	0.62
TST	3,361	4,581	2,683	6,669	7,133	24,544	451	11,355
TPP/TR	1.14	15.9	1.3	3.35	2.57	5.49	2.29	2.78
A/C (%)	21.9	23.56	28.72	29.42	29.5	40.72	27.4	30.14
O/C (%)	78.1	76.44	71.28	70.76	70.5	59.28	72.6	69.86
FCI (%)	8.6	13.4	0.07	9.9	6.83	5.31	-	6.2
CI (%)	19.5	30	30	30	19	23	23	19.9

[a] Cruz-Escalona et al. (2013), [b] Vega-Cendejas and Arreguín-Sánchez (2001), [c] Cruz-Escalona et al. (2007), [d] Zetina-Rejón et al. (2003), [e] López-Vila et al. (2019), [f] Bueno-Pardo et al. (2018), [g] Milessi et al. (2010), [h] this work.

Some authors consider the closing and opening of inlets as a disturbance, because this process drastically alters water physico-chemistry and therefore structure of biotic communities (Sánchez-Botero et al., 2009; Santangelo et al., 2007), especially salinity (Lanés et al., 2015). Nevertheless, ephemeral inlets favor species of fishes and invertebrates whose life cycles depend on estuarine conditions, mitigates eutrophication (Santangelo et al., 2007), and ameliorates ecosystem health (Contreras-Espinosa, 1988). In addition, a temporary connection also influences in readjustment of sediments, geomorphology, and hydrodynamics of the coastal lagoon (Pires et al., 2011).

In spite of the abiotic impacts due to the ephemeral character of the inlet, the adaptations and mechanisms of the populations of the functional groups allow the estuarine ecosystem to recover after the changes in connectivity to the sea. Under an intermittent connection, fishes are capable tolerate temporary physicochemical changes, especially in salinity (Griffiths, 2010), thanks to the osmoregulatory capacity of estuarine and secondary freshwater fishes, which are an important component in such systems as Carretas-Pereyra.

Phytoplankton displayed species replacement in response to environmental changes in our study area. This community is therefore highly adapted to its environment, because it can rapidly recover its biomass after the inlet opens (Suzuki et al., 1998). Similarly, zooplankton also adapts easily to changes in water quality (Santangelo et al., 2007) and other impacts due to inlet openings (Setubal et al., 2013). Infauna is able to tolerate drastic changes in dissolved oxygen concentration and salinity without much species turnover (Elliott and Quintino, 2007).

Detritus biomass in Carretas-Pereyra favored, either directly or indrectly, most other functional groups. It proved to be an important component in the reservoir of matter and energy that the ecosystem could resort to, to recover from a disturbance. Organic matter in detritus is also fundamental, because the trophic web is supported mainly by this functional group. The strategies of every functional group contribute to the stability of the ecosystem (Day Jr. and Yáñez-Arancibia, 1985).

At the ecosystem level, our model shows attributes that also help in recovery after a transient connection to the sea. The omnivory index of Carretas-Pereyra proves that generalist species predominate, so, even given the species turnover associated to salinity changes, most species can feed from different trophic levels at every stage. This can generate alternate paths in the trophic web, which ensures that the transfer of energy and matter flows even if one path is affected (Scharler, 2009). Omnivory can also buffer disturbances and fluctuations, so it can strengthen ecosystem resistance (Saint-Béat et al., 2015). In estuarine ecosystems where open and closed phases alternate, Scharler (2012) indicates that omnivory is an important element for the ecosystem resilience, and as long as omnivory does not collapse, the system can be sustainable.

Weak interactions in the trophic web can be favorable for the ecosystem: they may act as a stabilizing factor (Saint-Béat et al., 2015). In our model, the connectance index showed that only 19% of the possible connections among functional groups actually existed. This weakness of the interactions is a further ecosystem trait that fosters stability of Carretas-Pereyra. The overhead of our trophic model was quite high, nearly 70%, so the system has a large amount of energy available to recover after a disturbance; this is a measure of resilience.

According to its ecosystem attributes (e.g. total primary production/total respiration ratio, Finn's cycling index, connectance index), as well as biological aspects (e.g. dominance of juvenile organisms), Carretas-Pereyra can be considered a developing ecosystem, with some degree of immaturity. This situation can confer stability, due to low complexity (Pérez-España and Arreguín-Sánchez, 2001), which allow ecosystems to respond rapidly and flexibly to environmental changes (Colombo, 1977). Coastal lagoons are usually immature relative to other aquatic ecosystems (Christensen, 1995); however, several studies consider them stable, in spite of their low development (e.g. Abascal-Monroy et al., 2016; Bueno-Pardo et al., 2018; López-Vila et al., 2019).

Stability implies that an ecosystem or community can maintain its characteristics in the face of disturbances (Margalef, 1969). The ecosystem attributes of Carretas-Pereyra are within the margins reported for other Mexican coastal lagoons, both with ephemeral inlets and with permanent mouths to the sea, which are considered stable, e.g. Celestún (Vega-Cendejas and Arreguín-Sánchez, 2001), Términos (Abascal-Monroy et al., 2016), or Chantuto-Panzacola (López-Vila et al., 2019). In conclusion, given the results of this model, which includes elements representing annual cycles, with both rainy and dry seasons, and consdering both the biological traits of the functional groups and the attributes

of the ecosystem, Carretas-Pereyra is a stable estuarine lagoon system, in spite of its ephemeral connection to the sea.

This work refers to a static trophic model that encompasses biomasses and trophic interactions that occurred in the period that includes the sampling of the functional groups, that is, "pooling" values for periods when the mouth was open and periods when it was closed, thus addressing the long-term the effects and consequences of ephemeral nature of the mouth. To have a more detailed approach to what happens in the functioning and structure of an ecosystem with temporal connection to the sea, a dynamic trophic model could be constructed using Ecosim, an Ecopath tool, or to elaborate static models exclusively for the events of before, during and after the opening of the mouth. The latter requires having more detailed information about each functional group (composition, structure, biomass, diets, interactions) in each stage of the event.

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Supplementary material

Table 1
Sources of input data and diets for the trophic model of Carretas-Pereyra (P/B, ratio production/biomass; Q/B, ratio consumption/biomass)

Functional group	*P/B*	*Q/B*	Diet
Water birds	Arreguín-Sánchez et al. (2007)		
Crocodylians	Villanueva et al. (2006b)		Santos et al. (1996); Villegas and Schmitter-Soto (2008)
Ariid catfishes	Zetina-Rejón et al. (2003)		This study
S. guatemalensis	Zetina-Rejón et al. (2003)		This study
Jacks	Froese and Pauly (2018)		This study; Froese and Pauly (2018)
Snooks	Froese and Pauly (2018)		Macal López and Velázquez-Velázquez (2013)
Snappers	Froese and Pauly (2018)		This study
Cichlids	Froese and Pauly (2018)		This study
S. annulatus	Froese and Pauly (2018)		This study
Pleuronectiforms	Froese and Pauly (2018)		This study
Gerreids	Froese and Pauly (2018)		This study
D. latifrons	Froese and Pauly (2018)		Villatoro Álvarez (2006)
Anchovies	Froese and Pauly (2018)	Zetina-Rejón et al. (2003)	This study
Mugilids	Zetina-Rejón et al. (2003)		This study; Sánchez-Rueda (2002)
Poeciliids	Zetina-Rejón et al. (2003)		This study
Eleotrids	Froese and Pauly (2018)		This study; Villatoro Álvarez (2006)
Gobiids	de la Cruz-Agüero, (1993)		This study; Villatoro Álvarez (2006)
Omnivore fishes	Froese and Pauly (2018)		This study; Cruz-Escalona et al. (2009); Díaz-González and Soto (1988)
Planktivore fishes	Froese and Pauly (2018)		This study
Carnivore fishes	Froese and Pauly (2018)		This study; Franco Moreno (2011); Yáñez-Arancibia (1978)
Litopenaeus	Zetina-Rejón et al. (2003)		
Other shrimps	Vega-Cendejas and Arreguín-Sánchez (2001)		Abarca-Arenas and Valero-Pacheco (1993)
Macrobrachium	Zetina-Rejón et al. (2003)		Albertoni et al. (2003)
Callinectes	Zetina-Rejón et al. (2003)		Paul (1981)
Grapsids	Manickchand-Heileman et al. (1998)		Poon et al. (2010)
Insects	Palomares et al. (1993)	Vega-Cendejas and Arreguín-Sánchez (2001)	
Bivalves	Zetina-Rejón et al. (2003)		

Infauna	Cruz-Escalona et al. (2007)	Zetina-Rejón et al. (2003)
Worms		Zetina-Rejón et al. (2003)
Zooplankton		Zetina-Rejón et al. (2003)
Phytoplankton		Manickchand-Heileman et al. (1998)

Table 2

Prey-predator matrix for the Carretas-Pereyra trophic model.

Prey \ predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1 Water birds		0.046	0.004												
2 Crododylians	0.007	0.001													
4 Ariid catfishes							0.014	0.081							
5 *A. guatemalensis*		0.120	0.185					0.088							
6 Jacks	0.107						0.016								
7 Snooks	0.138														
8 Snappers	0.024														
9 Cichlids		0.020	0.040	0.103	0.100	0.016									
10 *S. annulatus*								0.001							
11 Pleuronectiforms						0.002						0.030			
12 Gerreids		0.134	0.080				0.049								
13 *D. latifrons*	0.204	0.103	0.100												
14 Anchovies				0.123	0.090	0.087	0.252								
15 Mugílids	0.024					0.227	0.098	0.203							
16 Poecíliids		0.115	0.085	0.203	0.201				0.187						
17 Eleotrids		0.043	0.085	0.003	0.003							0.018			
18 Gobiids			0.000	0.011	0.008	0.002					0.032	0.021			
19 Omnivore fishes		0.126	0.132												
20 Planctivore fishes	0.260	0.116	0.128				0.017								
21 Carnivore fishes	0.021	0.095	0.090												
22 *Litopenaeus*				0.248	0.200	0.154	0.422	0.280			0.289			0.100	
23 Other shrimps		0.036						0.001							
24 *Macrobrachium*		0.007		0.217	0.183	0.189	0.115	0.209			0.194			0.116	
25 *Callinectes*				0.043	0.013	0.013	0.017	0.106		0.483	0.026				
26 Grapsids								0.031		0.141					
27 Insects		0.039	0.070	0.005	0.105				0.284			0.005	0.071		
28 Bivalves	0.116	0.001	0.001			0.012				0.164		0.371	0.004		
29 Infauna				0.040	0.035	0.028				0.212	0.088	0.017		0.023	
30 Worms	0.098			0.001	0.029	0.021			0.038		0.280	0.278		0.002	0.003
31 Zooplankton				0.002	0.033	0.249					0.031	0.003	0.521	0.735	
32 Phytoplankton														0.024	
33 Detritus									0.492		0.062	0.257	0.404		0.997

Table 2 (continued)

Prey \ predator	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
1 Water birds																
2 Crocodylians																
4 Ariid catfishes																
5 *A. guatemalensis*																
6 Jacks																
7 Snooks																
8 Snappers																
9 Cichlids						0.063										
10 *S. annulatus*																
11 Pleuronectiforms				0.001												
12 Gerreids																
13 *D. latifrons*						0.477										
14 Anchovies																
15 Mugílids																
16 Poecíliids		0.406		0.303												
17 Eleotrids						0.088										
18 Gobiids																
19 Omnivore fishes						0.258										
20 Planctivore fishes																
21 Carnivore fishes																
22 *Litopenaeus*		0.016			0.047					0.074	0.020					
23 Other shrimps									0.019							
24 *Macrobrachium*									0.024	0.040						
25 *Callinectes*						0.019				0.203						
26 Grapsids				0.042												
27 Insects	0.050	0.105		0.600	0.235	0.096			0.145			0.009				
28 Bivalves			0.028	0.014						0.437	0.200					
29 Infauna			0.005		0.018		0.108	0.500	0.058	0.042	0.130			0.097	0.044	
30 Worms	0.005	0.021	0.140				0.210		0.099	0.012				0.100	0.010	
31 Zooplankton		0.452	0.186	0.008	0.699		0.091	0.100	0.013			0.280	0.212	0.100		0.160
32 Phytoplankton							0.591	0.300			0.050	0.115	0.591	0.074		0.620
33 Detritus	0.945		0.641	0.033			0.000	0.100	0.641	0.192	0.600	0.596	0.197	0.629	0.946	0.220

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DISCUSIÓN GENERAL Y CONCLUSIONES

DISCUSIÓN GENERAL Y CONCLUSIONES

La Encrucijada fue decretada como Reserva de la Biosfera en el año de 1995 (Carabias-Lillo et al., 1999) y durante 24 años se han realizado en ella investigaciones en diferentes áreas del conocimiento (e.g. Velázquez-Velázquez et al., 2016); sin embargo, previo a este trabajo, los estudios se habían desarrollado sin explorar las interacciones (directas e indirectas) entre todos los componentes bióticos del ecosistema. Es por esto que los modelos tróficos aquí presentados son la primera propuesta de un estudio holístico, a nivel ecosistema, para las lagunas costeras de la región sur del Pacífico mexicano y del estado de Chiapas.

La calidad de los modelos generados estuvo en función de la información suministrada para su creación. Para evaluar esto, Ecopath utilizó un análisis de sensibilidad llamado Índice de Pedigree (IP) (Funtowicz y Ravetz, 1990), el cual valora la información de entrada de acuerdo a su origen (área de estudio vs. ecosistemas similares cercanos, datos provenientes de campo vs. datos obtenidos bibliográficamente). Tomando esto en cuenta, ambos modelos obtuvieron un IP relativamente alto (Chantuto-Panzacola= 0.63, Carretas-Pereyra= 0.62) respecto a lo reportando en otros sistemas lagunares estuarinos tropicales, más aun si consideramos que uno de los IP más altos obtenido para este tipo de ecosistemas ha sido de 0.75 (Zetina-Rejón et al., 2003).

El uso de publicaciones realizadas en el área de estudio, el empleo de material biológico procedente de ésta y la obtención de datos en campo, para determinar dietas y biomasas de la mayoría de los grupos funcionales, favoreció la obtención de un elevado IP. Fueron pocos los casos en los que se recurrió a literatura de otros sistemas estuarinos tropicales cercanos al nuestro para completar dietas y biomasas. En contados grupos funcionales (aves, insectos, zooplancton y grapsidos) la biomasa fue estimada por Ecopath.

Aunque el número y tipos de grupos funcionales fue muy similar en ambos sistemas lagunares (*Atractosteus tropicus* y los esciénidos no estuvieron en Carretas-Pereyra), la composición y biomasa de éstos variaron entre sistemas,

principalmente por efecto de las variables físicoquímicas y de la conectividad temporal de uno de los sistemas. El ejemplo más evidente se observó en la comunidad íctica, ya que en Chantuto-Panzacola se han registrado 143 especies mientras que en Carretas-Pereyra 67. Gómez-González et al. (2012) argumentaron que esta diferencia se debió principalmente a que la boca de Carretas-Pereyra se mantuvo cerrada por varios meses, lo cual evitó la entrada de especies marinas al sistema. Además de esto, el uso de artes de pesca fijas conocidas como "tapos" interrumpen el desplazamiento de los peces, ya que estas artes son colocadas en los principales canales del sistema (Gómez-González, 2007).

En Carretas-Pereyra, los poecílidos, peces planctívoros (incluido *Lile gracilis*) y *Dormitator latifrons* registraron una biomasa elevada respecto a los otros grupos funcionales ícticos, particularmente *D. latifrons*, cuya biomasa por unidad de área sobrepasó notablemente a la de cualquier otro grupo funcional. Los tres grupos antes mencionados pertenecen al componente dulceacuícola y estuarino, los cuales suelen ser dominantes en sistemas estuarinos con conexión temporal con el mar, ya que sus características fisiológicas les permiten tolerar los cambios en la salinidad (Sánchez-Botero et al., 2009; Lanés et al., 2015) originados por dicha conexión. En contraste, en un sistema siempre conectado al mar, como Chantuto-Panzacola, los grupos funcionales ícticos con mayor biomasa fueron las anchoas y las lisas, ambos grupos constituidos por especies marinas eurihalinas.

Los grupos conformados por los productores primarios (detritus y fitoplancton, en nuestros modelos) y por invertebrados, también tuvieron una mayor biomasa en Carretas-Pereyra, a pesar de que este sistema es mucho más pequeño que Chantuto-Panzacola. En otros sistemas con conexión temporal se ha detectado una pérdida notable en la biomasa de la comunidad planctónica, así como en el detritus, inmediatamente después de la apertura de la boca (Suzuki et al., 1998; (Perissinotto et al., 2010; Netto et al., 2012); sin embargo, este efecto no fue perceptible en Carretas-Pereyra. Además de que la boca de este sistema estuvo cerrada la mayor parte del año, la concentración de biomasa de los grupos antes mencionados podría indicar que la magnitud y duración de la apertura de su boca fue débil y corta

respectivamente. Aunado a esto, la comunidad fitoplanctónica tiene la capacidad de recuperar su biomasa rápidamente después de la apertura (Suzuki et al., 1998; Suzuki et al., 2002), y en consecuencia se recupera también la biomasa del zooplancton (Perissinotto et al., 2010).

Pese a las diferencias en la composición y biomasa de cada grupo funcional, los niveles tróficos (NT) fueron similares entre ambos sistemas lagunares de la Encrucijada. La mayor cantidad de biomasa, así como del flujos energéticos, se encontró en la base de ambos modelos, sobre todo en el NT 1 (detritus y fitoplancton); de acuerdo con la matriz de impactos tróficos, este nivel influyó de manera positiva en casi todos los grupos funcionales, por lo que se puede decir que ambos sistemas lagunares costeros tienen un sistema de control *bottom-up* (Villanueva et al., 2006). Este tipo de control se ha observado en otras lagunas costeras tropicales (e.g. Vega-Cendejas y Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003; Castelblanco-Martínez et al., 2012), templadas (e.g. Bueno-Pardo et al., 2018) e incluso en lagunas con bocas temporales (e.g. Milessi et al., 2010).

En segundo orden de importancia se encontraron los NT 2 al 2.7, conformados principalmente por invertebrados, en los cuales se apreció una biomasa no tan considerable como la de los productores, pero sí mayor a la de los vertebrados. Los grupos funcionales ubicados en estos niveles actúan como intermediarios energéticos entre los productores primarios y los niveles tróficos superiores (Villanueva, 2004), en este caso peces, reptiles y aves. Estas últimas tres comunidades estuvieron entre los NT 3 y 4, y aunque la biomasa en estos niveles representó menos del 1% de la biomasa total en cada uno de los sistemas lagunares, los organismos comprendidos en estos NT tienen la capacidad de desplazarse fácilmente a otros ambientes. Esta propiedad les permite exportar energía producida en las lagunas costeras a otros ecosistemas adyacentes.

Villanueva et al. (2006) argumentaron que una alta biodiversidad incrementa el número de especies redundantes por grupo funcional, lo cual resulta benéfico para el funcionamiento del ecosistema, ya que estas especies pueden compensar la ausencia temporal de otras dentro de su mismo NT, o compensar la falta de un NT

similar. Este proceso fue evidente en nuestro estudio, ya que pese a que hubo una menor riqueza de especies en Carretas-Pereyra por el cierre temporal de su boca, el número y la funcionalidad de los NT fue muy semejante a la de Chantuto-Panzacola.

A nivel ecosistémico, se encontraron ciertas particulares en cada sistema, algunas de ellas consecuencia de la conexión intermitente, y también caracterísitcas en común entre ambos complejos lagunares. Una de las propiedades a destacar, debido a la diferencia en superficie entre complejos lagunares, fue la Producción Total del Sistema (PTS). A pesar de que Carretas-Pereyra tan solo ocupa un 20% de lo que abarca el área de Chantuto-Panzacola, la PTS fue mayor en el primer sistema mencionado (11,355 $gm^{-2}yr^{-1}$ vs. 7,133 $gm^{-2}yr^{-1}$). Dado que la PTS es un indicador que cuantifica el tamaño de todo el sistema (Ulanowicz, 2004), Carretas-Pereyra es más grande que Chantuto-Panzacola en términos de flujos energéticos.

La Ascendencia relativa (A/C), utilizada para medir el nivel de organización de la trama trófica y el grado de desarrollo del ecosistema (Ulanowicz, 1986), fue prácticamente igual en ambos sistemas: 30.1% en Carretas-Pereyra vs. 29.5% en Chantuto-Panzacola. Estos porcentajes señalan que ambos sistemas lagunares han alcanzado casi un tercio de su desarrollo total; la diferencia respecto al 100% es la energía de reserva que el sistema puede utilizar para recuperarse después de afrontar una perturbación. En los ambientes estuarinos se han registrado desarrollos que van desde el 21.9% (e.g. Bahía Magdalena, Cruz-Escalona et al., 2013), hasta el 40.72% (e.g. Ria de Aveiro, Bueno-Pardo et al., 2018), por lo que los valores aquí obtenidos se encuentran dentro de lo esperado para este tipo de ecosistemas.

La biomasa de ciertos grupos funcionales suele ser mayor durante la fase cerrada de un sistema lagunar estuarino, por lo que se espera un valor elevado en la PTS en esta etapa. Por su parte, la A/C se incrementará en el sistema siempre y cuando la fase cerrada haya durado lo suficiente como para permitir este aumento (Scharler, 2012). Considerando la diferencia de área entre los sistemas de este estudio y una mayor biomasa por unidad de área en varios grupos funcionales de Carretas-

Pereyra, se podría decir que la magnitud de la apertura artificial de la boca, aunado al prolongado tiempo que este sistema se mantuvo cerrado (Gómez-González et al., 2012), permitió el aumento de la PTS y A/C en Carretas-Pereyra. Por otra parte, Chantuto-Panzcola mantuvo siempre una conexión permanente con el mar, lo cual evitó la acumulación de biomasa dentro de este sistema.

La proporción Producción Total del Sistema/Respiración Total (PTS/RT) fue de 2.78 en Carretas-Pereyra y de 2.57 en Chantuto-Panzacola; parece haber existido un mayor aprovechamiento energético en éste último. Odum, (1969) sugirió esta proporción como un indicador de la madurez de un ecosistema cuando los valores son cercanos a 1. Esta caracterísitca se ha encontrado más cercano a etapas maduras en otros sistemas lagunares estuarinos tropicales, como por ejemplo laguna de Alvarado con 1.3 (Cruz-Escalona et al., 2007) y Bahía Magdalena con 1.14 (Cruz-Escalona et al., 2013). No obstante, también se han encontrado valores por encima de los nuestros, como los de Celestún con 15.9 (Vega-Cendejas y Arreguín-Sánchéz, 2001), el del complejo Huizache-Caimanero con 3.35 (Zetina-Rejón et al., 2003) o el de la bahía de Chetumal con 7.05 (Castelblanco-Martínez et al., 2012). Por lo tanto, los sistemas lagunares del presente estudio se encuentran, de manera relativa, cercanos a la madurez, con base en la proporción PTS/RT.

El Índice de Conectancia (IC) fue de 19.0% y 19.9% en Chantuto-Panzacola y Carretas-Pereyra, respectivamente. Estos valores están dentro de los más bajos en comparación con otras lagunas costeras tropicales: Celestún (Vega-Cendejas y Arreguín-Sanchéz, 2001), Huizache-Caimanero (Zetina-Rejón et al., 2003) y Alvarado (Cruz-Escalona et al., 2007), todas ellas con un IC de 30%. De acuerdo con Odum (1971), la trama trófica experimenta un cambio de linear a forma de red en la medida que el ecosistema va madurando, por consiguiente este índice puede asociarse con el grado de desarrollo del ecosistema (Christensen et al., 2000). Los valores de IC de los sistemas lagunares de la REBIEN estarían indicando un ecosistema estuarino en una fase poco madura.

El Índice de Ciclaje de Finn (ICF) demostró que se recicló un porcentaje muy pequeño de toda la producción de las lagunas de este estudio (Chantuto-Panzacola:

6.83%, Carretas-Pereyra: 6.2%). El bajo porcentaje, junto con la proporción PTS/RT y el IC, expone que una pequeña parte de la producción energética de las lagunas de la Encrucijada se está aprovechando. Esto se corrobora por la baja Eficiencia Ecotrófica observada en el NT 1 de ambos sistemas lagunares (entre 0.246 y 0.317).

En términos generales, y con base en los parámetros ecosistémicos discutidos anteriormente, los resultados obtenidos en ambos modelos tróficos estuvieron dentro de lo esperado para esto tipo de ecosistemas (e.g. Manickchand-Heileman et al., 1998; Villanueva et al., 2006; Cruz-Escalona et al., 2007; Milessi et al., 2010; Abascal-Monroy et al., 2016), los cuales han sido clasificados como los menos maduros en comparación con otros ecosistemas acuáticos (e.g. plataformas continentales, mares, arrecifes de coral) (Christensen, 1995). Esto se debe principalmente a que las lagunas costeras están en un estado de disturbio constante ocasionado por la mezcla de dos masas de agua con características físico-químicas propias (Odum, 1969), que entran en contacto a través de las bocas de los sistemas lagunares costeros.

Además de la proporción PTS/RT, existen otros indicadores propuestos también por Odum (1969) para distinguir entre etapas en desarrollo y etapas de madurez de un ecosistema. En los modelos de los dos sistemas lagunares costeros aquí tratados, la relación PTS/RS, la dominancia de organismos de tallas pequeñas (la gran mayoría en estadios juveniles) y la Ascendencia relativa los ubican como ecosistemas en desarrollo. Por otro lado, la participación del detritus en la regeneración de nutrientes y como base de una trama trófica en forma de red, así como la alta diversidad de especies le otorgan propiedades de un ecosistema cercano a una fase madura. De acuerdo con Vega-Cendejas y Arreguín-Sánchez (2001), las características energéticas de ecosistemas asociados al manglar ubican a éstos en una transición entre sistemas maduros e inmaduros caracterizados por una alta productividad, biomasa y riqueza de especies.

Según Lankford (1977), Chantuto-Panzacola y Carretas-Pereyra surgieron aproximadamente hace 5,000 años, de manera que son ecosistemas muy jóvenes en términos geológicos. Por esta razón, y por sus etapas de desarrollo, así como

por la dinámica ambiental que experimentan, se esperaría que estas lagunas costeras fueran sistemas inestables. A pesar de lo anterior, distintos autores han catalogado a las lagunas costeras como ecosistemas estables (Vega-Cendejas y Arreguín-Sánchez, 2001; Zetina-Rejón et al., 2003; Villanueva et al., 2006; Abascal-Monroy et al., 2016), en donde, aunque parezca contradictorio, esta condición proviene en gran medida de la inmadurez. Este grado de desarrollo concede estabilidad debido a que la poca complejidad del sistema (Pérez-España y Arreguín-Sánchez, 2001) permite que éste reaccione con velocidad y flexibilidad ante una perturbación (Colombo, 1977).

Otros mecanismos que brindan estabilidad y que influyen en la salud de las lagunas de Chantuto-Panzacola y Carretas-Pereyra yacen en el metabolismo y en la capacidad osmorregulatoria de los organismos que las habitan. Esto les permite tolerar las fluctuaciones ambientales, espaciales o temporales, especialmente aquellas dictadas por la salinidad (Griffiths, 2010). Cuando las lagunas se cierran por períodos prolongados, los cambios en esta variable ambiental suelen marcarse en mayor medida, por lo que la tolerancia a estos cambios por parte de ciertas especies (e.g. peces estuarinos, dulceacuícolas secundarios) permite que el flujo energético del sistema siga funcionando sin afectar la estructura del mismo.

El fitoplancton y el zooplancton, además de estar bien adaptados a su ambiente y de responder rápidamente ante los cambios en las variables físico-químicas, también tienen la capacidad de recuperar rápidamente su biomasa tras perder grandes volúmenes de ésta después de la apertura de la boca de una laguna costera (Suzuki et al., 1998.; Santangelo et al., 2007; Setubal et al., 2013). La fauna que habita en los espacios intersticiales del sedimento de este tipo de ecosistemas también es capaz de tolerar cambios ambientales drásticos (Elliott y Quintino, 2007).

El Índice de Omnivoría (IO) en ambos sistemas demuestra que la gran mayoría de grupos funcionales están conformados por especies generalistas; esto es útil en el ecosistema, ya que permite la creación de vías energéticas paralelas que aseguran la transferencia de energía en caso de que una de estas vías se vea comprometida (Scharler, 2009). Este hecho toma mayor relevancia en Carretas-Pereyra, ya que el

cierre de la boca interviene directamente en el número de especies de cada grupo funcional. Saint-Béat et al. (2015) argumentaron que la omnivoría es capaz de fortalecer el ecosistema, debido a que puede amortiguar cambios producidos por disturbios y fluctuaciones ambientales, mientras que Scharler (2012) la ubica como un componente importante en la resiliencia del ecosistema. Bajo este escenario las conexiones tróficas pueden cambiar en la medida que el sistema también lo hace, así que participan en la estabilización de éste (Saint-Béat et al., 2015).

Es importante tener en cuenta que lo expresado en este trabajo está basado en un modelo, y como tal debe tomarse con ciertas reservas, ya que puede variar y diferir, en pequeña o gran medida, con lo que sucede en la realidad. Los modelos tróficos de ambos sistemas lagunares son la base para la construcción de otros modelos que permitirían contestar otras preguntas ligadas al funcionamiento del ecosistema, al manejo de los recursos, al efecto del cambio climático sobre los productores primarios y al resto de los grupos, evaluar la estabilidad temporal del sistema, e incluso explorar las consecuencias de la introducción de especies exóticas o de la desaparición de algún grupo funcional. Esto mismo también podría llevarse a cabo de manera dinámica mediante modelos temporales o espaciales con las herramientas Ecosim (Walters et al., 1997) y Ecospace (Walters et al., 1999), respectivamente.

Los modelos aquí presentados también son susceptibles de ser mejorados, siempre y cuando se cuente con información detallada para ello. Las dietas y biomasas de algunos grupos (principalmente invertebrados) podrían obtenerse de campo; grupos grandes (como el de las aves) podrían ser disgregados en grupos más específicos. Tener datos precisos sobre biomasas y grupos funcionales presentes en cada fase (cerrada o abierta) posibilitaría la elaboración de modelos estáticos, con los que se podría evaluar el comportamiento del ecosistema cuando las lagunas se mantienen aisladas y cuando tienen comunicación con el mar.

Finalmente, con base en los resultados obtenidos y en las discusión de éstos, es posible concluir que, aunque ambos sistemas lagunares surgieron recientemente en términos geológicos (ca. 5,000 años), y que se encuentran desarrollados a un

tercio de su capacidad total (con propiedades de fases inmaduras y algunas de maduras), poseen carcterísticas que les brindan estabilidad y salud, y por ello tanto pueden mantener su función y estructura ante los cambios ambientales. Entre estas características resaltan: la elevada energía de reserva, la proporción PTS/RT, una alta omnivoría, vías energéticas paralelas y las adaptaciones fisiológicas y de comportamiento de los componentes bióticos de estos ecosistemas. En el caso particular de Carretas-Pereyra, el cierre de su la boca no se prolongó lo necesario como para que el sistema reflejara una diferencia en su desarrollo respecto a lo reportado en laguas costeras, pero tampoco ocasionó una perturbación que modificara de manera negativa la estructura y el funcionamiento del sistema, este último no colapsó a pesar del cierre temporal.

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