El Colegio de la Frontera Sur

Conectividad entre el Mar Caribe y la Bahía de Corozal mediada por la migración del macabí, *Albula* spp.

Tesis

Presentada como requisito parcial para optar al grado de
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Con orientación en Conservación de la Biodiversidad

Por:

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Las personas bajo firmantes, miembros del jurado del jurado examinador de **Addiel U. Perez**. Hacemos constar que hemos revisado y aprobado la tesis titulada "**Conectividad entre el Mar Caribe y la Bahía de Corozal mediada por la migración del macabí, *Albula* spp.**" para obtener el grado de **Doctor en Ciencias en Ecología y Desarrollo Sustentable**.

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DEDICATORIA

Esta tesis es dedicada a mi familia:

Mi esposa Inair Perez quien me apoyó, aconsejó, motivó; y

A mis hijas Coralyse, Adelyn y Princelly Perez quienes fueron mi motivación y fuerza para este logro.

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TABLA DE CONTENIDOS

1.0 RESUMEN

Se utilizó un enfoque de métodos mixtos para determinar los movimientos estacionales y regionales del macabí (*A. vulpes*) en la Bahía de Corozal-Chetumal (CB) y la Costa del Caribe (CC). Se utilizaron entrevistas, cuestionarios, talleres, observación participante y notas de campo para recopilar el conocimiento local sobre tiempo y dirección del movimiento en relación a la estacionalidad, hábitat, alimentación y reproducción. Tambien se utilizaron experimentos de marcado-recaptura para: a) determinar la frecuencia de tallas, abundancia y distancias de migración; b) modelar movimiento y abundancia en asociación a variables bióticas y abióticas; c) modelar movimiento y supervivencia con modelos multi-estado en el programa MARK. Se encontraron tallas significativamente mayores en CC (35 $\pm$ 4.9 cm) que en CB (media = 28.6 $\pm$ 4.1 cm), debido a una posible mayor densidad y diversidad de presas en los fondos de pastos marinos de CC. Los movimientos a lo largo de la costa fueron: 1) locales de corta distancia, norte-sur y sur-norte, en ámbitos hogareños (distancias > 3.5 km), asociados con la alimentación y en secas y lluvias (febrero a octubre) durante altas temperaturas, y 2) migraciones de larga distancia (> 10 km) ida y vuela de este-oeste y oeste-este, entre CB y dos sitios de agregación de pre-desove (APD) en el norte de Belice y durante los nortes (noviembre a enero) cuando las temperaturas fueron más bajas. El movimiento resultó en: a) mayor abundancia de tallas pequeñas (<22 cm) en CB durante secas y lluvias y una mayor abundancia de tallas grandes ($\geq$ 22 cm) en CC durante nortes, y b) menor sobrevivencia en CB que en CC durante nortes debido a la migración. El macabí como una especie sombrilla tiene implicaciones y se recomienda que Belice y México desarrollen una estrategia binacional de conservación y manejo de los hábitats de forrajeo y APD para mantener poblaciones saludables.

Key Words: Albulidae, manejo pesquero, estuarino, conectividad de habitat, Mar Caribe.

2.0 CAPÍTULO I

2.1 Introducción general

El movimiento es una respuesta a variables bióticas (organismos vivos) y abióticas (elementos no vivos del medio ambiente) (Begon et al. 2006; Acolas y Lambert 2016) que implica el cambio de ubicación o posición (Thurow 2016). Se le conoce como una característica de comportamiento universal de los organismos (Dingle 2014) que resulta en la conectividad de hábitats y ecosistemas (Mumby 2006; Jones et al. 2009; Sheaves 2009). Debido a que el movimiento es una categoría amplia, en esta tesis se simplifica como movimientos locales y migratorios y se caracteriza por su comportamiento, objetivo, escala espacial y estacional.

El movimiento local es de corta distancia y se conoce principalmente como el forrajeo y la exploración. El forrajeo es un tipo de movimiento que ocurre en los ámbitos hogareños del pez. Tambien incluye comportamientos de "mantenimiento de estación", son repetitivos y en respuesta a los recursos locales (por ejemplo, la búsqueda de presas) u otros organismos (es decir, evitar a los depredadores) (Dingle y Drake 2007; Dingle 2014; Thurow 2016). La exploración es otro tipo de movimiento y también en respuesta a los recursos, pero de tipo exploratorio libre (Clapp et al. 1990). Aun caundo este tipo de migración se ha estudiado muy poco, generalmente se define como "un movimiento en el que el organismo va más allá del ámbito hogareño para establecerse permanentemente en uno nuevo y es un comportamiento que cesa hasta que se encuentra un ámbito hogareño o un recurso" (Dingle y Drake 2007, p.116).

Por otro lado, la migración suele ser un movimiento de larga distancia sincronizado y estacional de parte o de toda la población (Dingle y Drake 2007; Binder et al. 2011). Hay diferentes tipos: 1) la migración asociada con etapas específicas de la historia de vida en las larvas, juveniles, preadultos y adultos) y 2) la migración asociada con las transiciones entre ellos (por ejemplo, el comportamiento durante el transporte de larvas hacia los hábitats de reclutamiento de juveniles). El primero tiene como propósito la alimentación, la reproducción, el refugio (Thurow 2016), en el que el individuo se desplaza temporalmente de su ámbito hogareño a otro lugar. La alimentación implica una respuesta hacia los recursos, el refugio ante condiciones ambientales desfavorables y la reproducción al desarrollo hormonal relacionado con el

apareamiento. La migración reproductiva, conocida como la migración de desove, es un fenómeno que involucra el regreso a casa o el comportamiento hogareño (Binder et al. 2011; Thurow 2016) de vuelta a su sitio natal o no natal. Estos tipos de migraciones generalmente son detonados por variables abióticas o físicas como la temperatura, pero es difícil saber cuál es la más influyente, ya que están altamente correlacionadas (Binder et al. 2011). La migración asociada a las transiciones se conoce como migración ontogenética, y se considera una migración permanente. Por ejemplo, los peces arrecifales pasan de los hábitats de asentamiento a los hábitats de juveniles y luego a los hábitats de adultos (Mumby 2006).

Varias especies de peces tropicales, sobre todo de las familias de meros (Serranidae) y pargos (Lutjanidae), son conocidas por sus migraciones de desove. El macabí (*Albula* spp.) es otra especie también conocida por sus migraciones de desove en las Bahamas (Danylchuk et al. 2011). Habita en ambientes subtropicales y tropicales poco profundos y cerca de las costas en todo el mundo (Schultz 2000; Adams et al. 2008, 2013; Danylchuk et al. 2008). Tradicionalmente, se reconocían 23 especies de macabí, pero estudios recientes indican un total de 12 especies de *Albula* genéticamente distintas (ver Anexo 1 y Bowen et al. 2008; Wallace y Tringali 2010; Adams et al. 2013; Wallace 2014, 2015). En el Caribe se reportan cuatro especies: *A. nemoptera* (Smith et al. 2003), *A. vulpes*, *A. goreensis* (Colborn et al. 2001; Ault et al. 2008; Vásquez-Yeomans et al. 2009; Valdéz-Moreno et al. 2010; Adams et al. 2013; Wallace 2014), y una cuarta especie no descrita llamada *Albula.* sp. cf. *vulpes* (Wallace y Tringali 2010; Adams et al. 2013; Wallace 2014). Sin embargo, *A. vulpes* es la más importante, ya que es la más capturada en la pesca recreativa de captura y liberación de la región del Atlántico Occidental (Adams et al. 2008; Wallace 2014). En el Caribe se reportan los adultos de *A. vulpes* en los Pelican Cayes del sur de Belice (Smith et al. 2003), así como en Turneffe Atoll y Lighthouse Reef Atoll (Adams et al. 2008; Perez-Cobb 2012; Perez-Cobb et al. 2014) y en áreas compartidas entre Belice y México (Schmitter-Soto et al. 2009). También se reportan las larvas y juveniles de *A. goreensis* en playas arenosas del atolón Turneffe (Adams et al. 2008), y las larvas de *Albula* sp. F del sur de México y en el norte de Belice (Valdez-Moreno et al. 2010). Una cuarta especie, el adulto de *A. nemoptera*, ha sido reportada únicamente en los Pelican Cayes

en el sur de Belice, aunque el espécimen provino de la Bahía Amatique en Guatemala (Smith et al. 2003).

Generalmente el ámbito hogareño del macabí es relativamente pequeño, de aproximadamente menos de 5 km (Boucek et al. 2018). El macabi habita arroyos interiores de la costa (creeks) y a lo largo de la costa, y demuestra una gran fidelidad a ámbitos hogareños (Murchie et al. 2013), probablemente porque la alimentación es una necesidad básica para la supervivencia. Su dieta generalmente se compone de invertebrados y peces pequeños (Danylchuk et al. 2011; Murchie et al. 2011, 2013). Los juveniles (2.1-14.2 cm SL) se alimentan principalmente de invertebrados (poliquetos, anfípodos y copépodos) (Snodgrass et al. 2008), mientras que los pre-adultos (<44 cm FL) de camarones peneidos y los adultos (> 44 cm FL) de decápodos y teleósteos (Crabtree et al. 1998). Tambien se le cononce como un pez que, en secas y lluvias, cuando la temperatura del agua aumenta y los niveles de oxígeno bajan en los esteros costeros (Murchie et al. 2011), se mueve a hábitats cercanos a la costa (Murchie et al. 2013), probablemente en búsqueda de refugio. El macabí también realiza migraciones estacionales desde los esteros cercanos a la costa a sitios lejanos para reproducirse (Murchie et al. 2013; Danylchuk et al. 2011). Después del desove realiza otra migración de regreso a los ámbitos hogareños (Boucek et al. 2018). Por ello, el macabí presenta un patrón de movimiento local de corta distancia y asociado a la alimentación en ámbitos hogareños, migraciones de corta distancia como refugio a variables ambientales y migraciones de larga distancia para reproducirse (desove).

El macabí es un recurso pesquero que se captura y libera en un tipo de pesca recreativa conocida como pesca deportiva, que se carateriza por su práctica de captura y liberación (CR). Esta modalidad se realiza con artes de pesca, como la mosca ("fly") y cañas giratorias ("spinning") por pescadores en su mayoría no residentes (Perez-Cobb 2012; Perez-Cobb et al. 2014). La pesca de CR representa una fuente de ingreso a guías de pesca con mosca y spinning por proporcionar un sevicio (Herrera Pavón 2002) en países como México y Belice. En México, es capturado por los pescadores de pesca artesanales y subsistencia por comercio y como una fuente de alimento, respectivamente (Medina-Quej et al. 2009; Schmitter-Soto et al. 2009). Aunque no hay información sobre el impacto socio-económico de estas pesquerías en Mexico, la pesca

4

de CR en Belice del macabí, la palometa (*Trachinotus falcatus*) y el sábalo (*Megalops atlanticus*) generan cerca de US $ 35 millones al año, más de 2000 empleos a tiempo completo y emplea más de 100 pescadores como guías de pesca de CR (Fedler 2014).

A pesar de la importancia socio-económica del macabi, la mayoría de los estudios relacionados con esta especie en la región occidental del Caribe se han centrado en la identificación genética de las larvas (Vásquez-Yeomans et al. 2009; Valdez-Moreno et al. 2010), los juveniles (Adams et al. 2008) y presencia-ausencia de los pre-adultos y adultos (Schmitter-Soto et al. 2009). Por lo que existe una gran escasez de información sobre las pesquerías recreativas (Pérez-Cobb et al. 2014), en particular sobre los patrones de movimiento del macabí (*Albula vulpes*) en la región del Caribe. Esta falta de conocimiento dificulta la gestión de las actividades pesqueras, turísticas, y de desarrollo rural/urbano dentro y alrededor de áreas protegidas que afectan negativamente a esta especie y sus hábitats. Por lo tanto, para abordar la falta de conocimiento sobre la ecología de las poblaciones transfronterizas como el macabí, este estudio propuso determinar la conectividad mediada por la migración de este pez entre un estuario tropical y la costa adyacente del Mar Caribe compartida entre Belice y México.

2.2 Objetivos

General:

Determinar la conectividad regional y estacional mediada por la migración del macabí, *Albula vulpes*, dentro de la Bahía de Chetumal-Corozal (CB) y de esta con el Mar Caribe adyacente (CC).

Específicos:

1.) Determinar los movimientos del macabí relacionados con el uso de hábitat, la alimentación y la migracion de desove mediante el conocimiento local (de los pescadores).

2.) Determinar la distancia y la estacionalidad de la migración, así como una aproximación del origen y destino de dichos movimientos utilizando experimentos de marcado-recaptura.

3.) Caracterizar el uso de hábitat y estacionalidad de movimiento mediante el uso de datos ambientales (temperatura, salinidad, marea, viento, vegetación del fondo, abundancia y presencia-aucencia de depredadores) y datos de marca-recaptura en modelos.

4.) Inferir y clasificar los movimientos mediante la construcción de modelos conceptuales y matemáticos (por ejemplo, máxima probabilidad) utilizando datos de marca-recaptura.

2.3 Hipótesis

General:

El macabí pasará la mayor parte de su tiempo dentro de un ámbito hogareño relativamente pequeño, moviéndose distancias cortas para alimentarse, evitar a los depredadores o en respuesta a variables ambientales. Las migraciones estacionales serán a lo largo de la costa de larga distancia y asociadas con la reproducción y se espera que ocurran principalmente de norte-sur dentro de CB.

Específicas:

1) Habrá una migración de desove estacional desde CB al arrecife anterior y la laguna arrecifal de CC y que la migración para la alimentación se produce diariamente en ambas regiones.

2) Se encontará una migración a lo largo de la costa estacional para reproducirse en: a) distancias relativamente grandes (> 25 km) de norte-sur y de este-oeste dentro de CB en Mexico y Belice y b) distancias más cortas (<25 km) entre los bajos costeros (CB) y bajos arrecifales (CC) de este-oeste y de oeste-este) de ambos países.

3) Los movimientos serán: a) afectados principalmente por la salinidad en CB, b) por la temperatura del agua en CC, c) poco afectados por la presencia de depredadores y dirección del viento, y d) generalmente afectados por el tipo de fondo y nivel de las mareas.

4) Habrá un intercambio entre sitios cercanos que se correlacionarán con movimientos locales. Sin embargo, se espera que la tasa de intercambio sea mayor dentro de las regiones CB y CC, y menor entre dichas regiones.

3.0 CAPÍTULO II

Articulo aceptado.

Connectivity mediated by seasonal bonefish (*Albula vulpes*) migration between the Caribbean Sea and a tropical estuary of Belize and Mexico

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Abstract

Bonefish (*Albula vulpes*) are an important resource for catch-and-release fishing in the Caribbean Sea. Understanding movements within and between the Caribbean Coast (CC) and Chetumal-Corozal Bay (CB) in Mexico and Belize is crucial for identifying and protecting home ranges, migration routes, pre-spawning and spawning sites. We used a mixed-methods approach to document dynamics of bonefish movement. We collected fishers' local knowledge (LK) using qualitative methods including workshops, key informant interviews, participant observation and field notes about bonefish seasonal movements. We then we used mark-recapture (8816 tagged, 569 recaptured) method to understand bonefish movements by size, location and season. Bonefish were significantly larger in CC and CB. We documented several seasonal movement patterns. A southward movement within CB during the rainy season was likely driven by salinity changes. This was followed by an eastward long-distance migration during the norths or cold front season between the bay and the Caribbean Sea, likely for spawning, as we document likely spawning readiness, pre-spawning behavior and synchronized to the fore-reef at one of two pre-spawning aggregation sites in a World Heritage Site in the CC of Belize during November and December of 2018. There was then a northward movement during the dry season as a journey back to home ranges. The information presented herein can inform resource management and protected areas planning toward a bi-national conservation and management of bonefish and its habitats.

Keywords Mark-recapture, Local knowledge (LK), Sport fisheries, Albulidae, Pre-spawning, Fisheries Management

Introduction

Throughout their life history, fish often utilize multiple habitat types (Dingle and Drake 2007; Binder et al. 2011; Adams and Murchie 2015). Many species undergo a "seasonal synchronous and directed movement of part or all of a population between discrete habitats" known as migration (Binder et al. 2011). Migration can occur at all the life stages, primarily for the purposes of feeding, refuge and reproduction (Acolas and Lambert 2016; Closs and Warburton 2016; Couto et al. 2016; Miller 2016; Morais and Daverat 2016a,b; Thurow 2016). Migration can be triggered by exogenous cues, such as salinity, temperature, waves, tides and currents (Acolas and Lambert 2016; Begon et al. 2006; Binder et al. 2011; Yako et al. 2002), and by endogenous cues, such as hormone changes and body size (Couto et al. 2016), that affect behavior, including homing to breeding sites (Dingle and Drake 2007) and ontogeny (Mumby 2006), respectively. Regardless of the cues, fish migration results in habitat connectivity (Mumby 2006), also known as ecosystem connectivity (Steneck et al. 2009), or ecological links between habitats in time and space (Dingle and Drake 2007; Sheaves 2009).

Understanding fish migration is important for conservation and management of fishes and associated habitats. The ongoing and planned coastal development in the Caribbean Sea poses a serious threat to essential habitats, such as mangroves (Adams and Murchie 2015). The complex connections between habitats created by life-history migration (Sheaves 2009) of fish species can help managers mitigate impacts in various ways. The information can be used to create and advise management plans for marine protected areas, refuges and wildlife sanctuaries or to support local fisheries management planning and regulation (Bruckmeier and Neuman 2005). Such data can also provide insights to merge management into one approach of transboundary management practices, and initiatives to mitigate the effects of coastal development (Perez-Cobb et al. 2014).

Surprisingly, little information exists on habitat use pattern for many species of socio-economic importance, including bonefish (*Albula* spp.). Bonefish inhabit shallow and nearshore tropical and subtropical environments worldwide (Adams et al. 2008, 2013; Danylchuk et al. 2008). Recent studies identified 12 genetically distinct species of *Albula* (Bowen et al. 2008; Wallace 2014). Four species are present in the Caribbean: *A. nemoptera* (reported by Smith 2003), *A. vulpes, A. goreensis* (by Wallace 2014), and the undescribed but genetically distinct *A.* sp. cf. *vulpes* (Wallace and Tringali 2010). The species most important to the coastal recreational and subsistence fisheries in the Caribbean is *A. vulpes* (hereafter, bonefish), as it comprises almost 99% of the catch in the Caribbean and western Atlantic (Adams et al. 2008; Adams and Murchie 2015; Wallace and Tringali 2016).

9

In Florida and the Bahamas, bonefish long-distance migration has been associated with reproduction. Migration links multiple habitats within the coastal habitat mosaic via movements between inshore and nearshore home range habitats and offshore spawning habitats (Danylchuk et al. 2011; Adams and Murchie 2015; Murchie et al. 2015; Adams et al. this issue; Boucek et al. this issue). Bonefish make daily and short distance local movements from inshore habitats such as tidal creeks (Murchie et al. 2013, 2015) to nearshore habitats with substrates such as sand flats and algal plains (Danylchuk et al. 2011; Murchie et al. 2011). In contrast, bonefish undergo long distance and seasonal migrations for the purpose of reproduction. According to Danylchuk et al. (2011), bonefish migrate near full moon and new moon from foraging areas to pre-spawning aggregation sites, which tend to be shallow bays near deep water, where "porpoising" and ventral nudging are common behaviors made before and during spawning (Danylchuk et al. 2011), which occurs offshore, at night, in water exceeding 1000 m depth, though spawning appears to occur in the top 50 m of the water column.

In the Yucatan Peninsula, bonefish conservation and management regimes vary amongst countries and even within each country. In Mexico, the National Commission of Aquaculture and Fisheries declared in 2015 several bays in the Akumal area, Tulum, Quintana Roo, as a fisheries refuge zone, where bonefish and permit (*Trachinotus falcatus*) are managed as catch and release species (CONAPESCA 2018). However, outside of this area, bonefish is still allowed to be harvested by artisanal commercial and subsistence fishers (Medina-Quej et al. 2009). Yet, fly-fishing guides and artisanal fishers in some areas of the Yucatan Peninsula have informal agreements to practice catch-and-release of bonefish as a form of local management (Perez-Cobb et al. 2014). In Belize, recreational fishing is catch-and-consume (local recreational fishing, reef fishing and blue water fishing) and sport fishing is regulated as catch-and-release (Perez-Cobb et al. 2014). The latter is also called the flats fishery where fly fishing or spin-fishing equipment are used to land bonefish, permit and Atlantic tarpon (*Megalops atlanticus*). This fishery generates approximately US $17 million annually in direct expenditures, provides 2100 full-time jobs and employs more than 100 fly-fishing guides (Fedler 2014). Despite the efforts to make bonefish a catch and release species as a means of conservation in this region, this does not address the main threats to bonefish – coastal habitat loss and degradation, habitat fragmentation and water quality declines (Adams and Murchie 2015), by-catch in commercial fisheries (Herrera Pavón 2011) and lack of knowledge on locations of pre-spawning and spawning sites (Adams et al. this issue).

We employed a mixed-methods approach to determine the connectivity by bonefish migration between two regions – the Caribbean coast and a tropical estuary. We used local knowledge (LK) to estimate the seasonality of bonefish migration for reproduction. We then used mark-recapture methods to quantify the dynamics of bonefish migrations by size, region and season.

Materials and methods

Study area

This study was conducted from August 2015 to December 2017 along the Caribbean coast (CC) and in Chetumal-Corozal Bay (CB), spanning Mexico and Belize (Fig 1). CB is connected to the Caribbean Sea by its wide opening at the southern end, and by natural (Bacalar Chico at the-Mexico-Belize border and Boca del Rio in San Pedro,

Belize) and manmade (Canal de Zaragoza in Mexico) channels on its eastern side (Fig 1). The CB is an open-water, brackish bay comprised of flats with sandy and rocky bottom along the outer shoreline and with interior habitats of mangrove-lined creeks and wetlands and lagoons. Its depth varies from 0.5 m to 2.5 m deep (Hernández-Arana and Ameneyro-Angeles 2011). The CC is comprised of backreef lagoon system (Adams et al. 2006), a habitat mosaic of sand, seagrass, and patch reef in an area approximately 1 km wide between the shoreline and the barrier reef. Its depth is generally between 2 to 3 m and maximum 6 m (Grimshaw and Paz 2004).

The climatic annual average values in the study area are 26.5 ^{o}C in air temperature, 78% in relative humidity, 1244.7 mm in precipitation and 3.1 ms^{-1} in wind velocity (Carrillo et al. 2009). The marked weather patterns in the study area create seasons: cold front (locally called "nortes" but hereafter referred to as norths) - November to January; dry - February to May; and rainy - June to October. The bay and coast have similar mixed tides with semidiurnal predominance no higher than 0.3 m (Carrillo et al. 2009), and prevailing wind direction from the east and southeast throughout the year (except during weather associated cold fronts during the norths season when it is from the north or north-west). Finally, CC has normal marine salinity ranges, 34 to 36 psu and CB 18 to 40 psu year-round (pers. obs. at sampling sites), except close to the Hondo River and other affluents, where salinity drops to freshwater levels, especially during the rainy season (Carrillo et al. 2009).

Local knowledge

We used local knowledge (LK) (Berkes 2008) to estimate seasonality of bonefish movements for reproduction, We used a qualitative sampling design (de Vaus 2013) combined with a snowball technique (Arce-Ibarra and Charles 2008a, b; Perez-Cobb et al. 2014) whereby fishing guides an d local fishers acted as key informants and helped identify other experienced key informants. Once applied, the snowball sampling stopped when either i) interviewees provided no additional information, or ii) three days of field work elapsed at each one of the studied communities. Methods 1, 2 and 3 (below) were used from 10 February to 29 May 2016 and applied in four human communities: Xcalak in Mexico and Sarteneja, San Pedro and Caye Caulker in Belize. Method 4 was used from the start of study on 26th October 2015 to the end on 28th December 2017.

1) Rapid Rural Appraisal (Chambers 1981) was conducted in all communities to understand the dynamics of fishing activities so as to better implement workshops, interviews and mark-recapture methods.

2) A workshop was held in each community, during which three maps were presented for participants to identify with colored pins and labels: a) locations and names of fishing areas for bonefish, by season, b) type of fishing (commercial fishing and flats fishing) by season. This was important to assign spatiotemporal components of sampling.

3) Informal interviews were conducted, and based on the individual's interest of collaborating, knowledge and responses, it was then decided whether to continue with a formal face to face interview. The latter used structured and semi-structured questionnaires. Three main structured questions were asked, after giving a description of a spawning run: have you seen a bonefish "corrida" or migration (school larger in number than usual, moving fast and undistracted)? If so, in what direction? Have you seen pre-spawning schools

11

(schools in larger numbers than usual and displaying "porpoising" behavior)? Each of these questions, except for direction, was followed by a semi-structured question (with options and one open-ended option): during what time or month of the year was migration or the mentioned behavior observed?

4) Ethnographic field notes were collected through the study; a known participant observation method (Emerson et al. 2011), during which we recorded observations in field notes while observing fishing activities (fly fishing and heart-tail traps known as beach traps that encompasses over 50 m of meshed wire held by anchored poles and oriented perpendicular to the coast with a heart-shaped offshore end where fish are trapped), where mark-recapture (see below) was conducted.

Mark-recapture

We used a stratified sampling design with the study area divided into the previously defined regions (CC and CB) and seasons (norths, dry and rainy). Sampling for mark-recapture was conducted by a team of 3 to 4 persons and a local experienced bonefish fly-fishing guide on October 2015; January, June, November and December 2016; and January to December 2017. In each sample month, sampling occurred over a period of 4 days within each region for a total 8 days each sample month. Sample periods from September to February were on days spanning the full moon, so as to incorporate sampling during bonefish reproductive times (Danylchuk et al. 2011). Sites were selected based on knowledge gained from the LK process and known by guides to harbor bonefish. Sites were less than 1.2 m deep, with sturdy sand, rock, sandy-muddy and seagrass bottoms. The vessel (usually boats 8 m in length or smaller, with 15 to 60 HP motors) moved at 1-2 km/h approximately 500 m parallel to the coast. Bonefish were sighted and then encircled and captured using two light-colored seine nets, each 45 m long, 1.2 m high, and 2.5 cm mesh. The fish were removed from the seines with hand nets and kept in a nearly submerged floating cage (1 m x 0.5 m x 0.25 m), measured (fork length to the nearest 0.1cm) and marked with a dart tag (model PDS, Hallprint, Australia) in the left-side musculature between the first dorsal pterygiophores (Boucek and Adams 2011). Following the tag manufacturer's recommendation, only fish > 22 cm were marked, the rest counted. For each seine sample we recorded region, season, site name, date, time and site coordinates (latitude and longitude), and fish size and tag code for each marked and recaptured bonefish. We also evaluated from each seined sample the gonadal status of a sub-sample of at least 3 of the largest bonefish using cannulation for presence or absence of milt in males and eggs in females (see Adams et al. this issue for gonad sampling and behavioral observation procedures). Fish were handled for the shortest time possible, allowed to recover in another seine enclosure and then released *en masse* to reduce marking and predation mortality (Adams et al. 2009). Recaptured bonefish data were also reported by anglers and fly-fishing guides who fished throughout both regions and every day of the year and also by heart-tail traps set by fishers in CB of northern Belize, thereby sampling the regional bonefish population. Lastly, we observed for pre-spawning behavior especially late in the afternoon following Danylchuk et al. (2011) and Danylchuk et al. (this issue) in the Caribbean coast only.

Data analysis

Sampling periods for mark-recapture of bonefish were separated by season: norths (October 2015, January 2016), rainy (June 2016, November 2016), norths (December 2016 and January 2017), dry (February-May 2017), and rainy (June-September 2017). We then used a 2-way ANOVA to examine marked bonefish size by region (CC and CB) and season (dry, norths and rainy). To characterize bonefish movements, we performed two 2-way ANOVA tests to examine recaptured bonefish size and distance between mark and recapture locations, with region and season as factors. To estimate distance between tag and recapture sites, we measured the shortest distance along the shoreline over water, using GoogleEarth©. Data were log-transformed if necessary, and homoscedasticity was assessed with Bartlett's test. All analyses were conducted in RStudio version 1.0.153 (Venables and Smith 2003) and significance was assessed at $P < 0.05$.

Results

Local knowledge

Thirty interviews were conducted (17 in Belize and 13 in Mexico). Eight were with artisanal fishers (commercial and subsistence) and 22 with fly-fishing guides. Fifteen of them reported seeing bonefish moving "fast" during the so-called "runs". Twelve of 15 interviewees reported direction of bonefish movement and we noticed two general patterns. In CC, one interviewee reported northward and southward migrations, two reported northward migrations only, and four reported southward migrations only within CC, indicating a likely back and forth migration to a spawning location in CC. In CB, eight interviewees reported a southward migration, indicating a one-way migration, likely related by seasonality of weather patterns and migration for spawning. Two general timings were reported for the migration "run": from March to July of the rainy season and from September to January of the norths season. Only one guide from San Pedro (SP), Belize, indicated seeing bonefish displaying a "porpoising" behavior (i.e., breaking the surface of the water with their heads as if gulping air) in the fore-reef of Robles Point, north of SP during November of 2015. This indicated Robles Point was a possible pre-spawning aggregation site and further suggesting the reported migration was related to spawning that was also likely occurring during the norths season in Belize's Caribbean coast.

Mark-recapture

There were more sampling sites in CB than CC. Thus, from 8816 marked bonefish, we marked the most in CB (69.1%) than CC (30.9%). Weather conditions affected our mark effort throughout the seasons. The norths season was the shortest and the associated north and north-west wind direction largely affected the bay region and caused water to recede and produce lower water levels, as well as turbid waters. As a result, we marked the least during the norths season (22.6%) and also the rainy season (26.9%). The calm winds of the dry season allowed us to mark the most (50.5%) during our study (Table 1). When tagged bonefish were examined, bonefish were larger in CC (mean=35.0 cm, s.d. ± 4.9 cm) than in CB (28.6 cm, s.d. ± 4.1 cm; $F_{1,\,8810} = 4153.4$, $P < 0.05$). We found a general consistency in size differences amongst seasons ($F_{2,8810} = 63.94$, $P < 0.05$) and also amongst season within each region ($F_{2,\,8810} = 64.3$, $P < 0.05$) where bonefish were larger in CC than in CB in all seasons (Table 1).

13

A total of 569 bonefish (6.6 % of all marked fish) was recaptured, with 95.1% of recaptures taking place in CB and the remaining 4.9% in CC (Table 2). Also, 543 (95.4%) were recaptured through our seining effort, 25 (4.4%) by anglers and guides and one from a heart-tail trap (0.2%). Seasonally, regardless of region, 76.8% of recaptures were in the rainy season, 20.7% in the dry season and 2.5% in the norths season (Table 2). As with tagged fish, there was also a consistent difference in size between both regions ($F_{1, 563} = 122.40$, $P < 0.05$): bonefish were larger in CC (mean 38.6 cm, s.d. ± 5.2) than CB (mean 30.6 cm, s.d. ± 3.6). We also found significant differences amongst season ($F_{2, 563} = 3.46$, $P = 0.03$) but unlike tagged fish, these differences were marginal (Table 2). There were also size differences amongst seasons in each region ($F_{2, 563} = 5.38$, $P = 0.005$). However, recaptured bonefish were the largest in CC during the rainy season, and size differences were minimal across seasons in CB (Table 2).

Our recapture data showed bonefish moved between regions. Most recaptures (79.8%) were at the same location but others (20.2%) showed movement in different directions. Most bonefish moved south (9.8 %) in CB during the rainy season (e.g. one was marked in the rainy season and recaptured in the dry season, moved 77.1 km from Mexico's CB to Belize's CB) and north (6.3%) along the coastline of both regions (e.g., one was recaptured in a heart-tail trap and had moved 16.7 km northward in CB) after the north season and going into the dry season. The remaining (3.3%) showed a west movement from Robles Point of Belize's CC to different sites in CB and also a similar but reverse movement from CB to CC (0.7%) during the norths season. We only recaptured one marked bonefish that made a northward movement from Robles Point to Rio Huach (Mexico) and many making a southward movement long Belize's CC; both indicating a return journey to the site of origin, a coastal lagoon and CC respectively. We found no consistent difference of distance moved by bonefish between regions ($F_{1,563} = 0.41$, $P = 0.52$) as bonefish moved nearly similar distances in the Caribbean coast (CC mean = 2.4 km, s.d. ± 6.0 km) and the bay (CB mean = 1.6 km, s.d. ± 6.8 km). Nonetheless, there was significant difference in distance moved amongst seasons ($F_{2, 563} = 20.03$, $P < 0.05$) where bonefish covered the longest distances during the norths season (mean = 10.1 km, s.d. = 20.4 km: see Table 3), which corresponds with the bonefish spawning season. Although there was no consistent difference of distance amongst seasons of each region, bonefish seems to occupy different home ranges that vary seasonal. Bonefish moved the least in both regions (CC mean 0.3 km, s.d. 0.6 km and CB mean 0.9 km, s.d. = 5.0 km) during the rainy and covered the longest distances (> 1km) on the dry and north seasons in each region (Table 3).

Bonefish were cannulated in all seined samples but no eggs and milt were present, except Robles Point in Belize's CC during December and January of 2016, and November and December 2017. While sampling at this site and period we observed bonefish with protruded abdomens and cannulation was unnecessary as these fish spilled milt as they were handled, indicating they were reproductively active males. Other fish with less distended abdomens were also cannulated but had little milt and others (females with distended abdomens) had yellow coarse eggs or orange-sticky eggs (females with less distended abdomens). During our mark-recapture effort of October of 2017 we observed after 1600 h one school of bonefish moving "fast" in a northward direction at Robles Point. However, in November of the same year we received reports from fly-fishing guides of thousands of bonefish in two locations of Belize's CC: one approximately 1 km north of SP and the other at Robles Point (over 20 km north of SP). At these two sites for two consecutive days we observed bonefish breaking the surface of the water and

14

exposing their head and backs while swimming in a circular pattern. This behavior was initiated by one school that joined another until several schools had congregated in a single school of many thousands. We then followed a synchronized migration of the large school from the backreef lagoon, through a channel in the fringing coral reef, and toward the fore reef east of Robles Point.

Discussion

This study revealed three general patterns of bonefish movements that revealed both relatively small home ranges during the non-spawning season within our study regions (an estuarine system and the Caribbean coast), as well as seasonal longer-distance migrations that link these home ranges to a pre-spawning site, and we showed interactions of bonefish size with these patterns.

The larger average size of bonefish in the CC region was probably due to several reasons. The main one is greater prey availability in seagrass habitats that dominates this region. Recent studies have found that large bonefish likely consume a greater prey diversity in seagrass habitats (Murchie et al. this issue). In fact, adult bonefish that forage in seagrasses likely are more selective and benefit from higher energy densities than those that feed in sandy bottoms (Colton and Alevizon 1983). In this study, the CC region likely had a more diverse prey community because seagrass was a dominant habitat. In contrast, the CB region was dominated by open bottom. Similarly, the Florida Keys is largely dominated by seagrass habitats and the bonefish diet primarily consists of prey that live in seagrasses (Crabtree et al. 1998). In contrast, bonefish in the Caribbean have a slower growth rate than the Florida Keys (Adams et al. 2007), likely because most Caribbean bonefish habitats are mostly open bottom. An alternative explanation is ontogenetic shift, whereby juvenile and sub-adult bonefish inhabit CB, and move to CC once they reach maturity. However, based on mark-recapture we found a bidirectional movement, from CB to CC and from CC to CB, which were probably spawning migrations, thus indicating the presence of mature bonefish in both regions. In addition, other studies on bonefish movements and habitat use show no evidence of such ontogenetic shifts (Murchie et al. this issue).

Overall, most fish were recaptured near where they were tagged, which implies high site fidelity. This is similar to findings in the Bahamas (Murchie et al. 2013; Boucek et al. this issue). However, long-distance movement between mark and recapture locations revealed two larger-scale movement patterns that likely reflected abiotic seasonal changes and a spawning migration. First, both LK and tag-recapture results showed bonefish movement from north to south during the rainy season (June to October) and the norths season (November to January). Fishers, mainly from Belize, are familiar with the "corridas" because they associate this movement with the rainy season. In this study, we observed that fishers set their heart-tail traps at the beginning of the rainy season. These traps target fin fish, particularly Striped Mojarra (*Eugerres plumieri*), Grey Snapper (*Lutjanus griseus*) and Great Barracuda (*Sphyraena barracuda*) inside the bay (Medina-Quej et al. 2009). Presumably, these widespread southerly migrations are in response to decreasing salinity in the upper reaches of CB: for example, the Hondo River and fresh water springs in CB dilute the water to 2-8 ups (Carrillo et al. 2009). Thus, we hypothesize the first migration pattern was southward in reaction to the rainy season to find refuge in locations on the eastern side of CB where salinity was likely higher. Overall, our results are similar to others, who found that bonefish have high levels

of site fidelity (Murchie et al. 2013; Boucek et al. this issue), but differ in that we observed a seasonal movement likely associated with salinity changes – a scenario that no other studies have addressed.

Our study provides multiple pieces of evidence to support the conclusion that the migrations between CB and CC were for spawning. First, multiple bonefish tagged in CB migrated eastward, likely through the Canal de Zaragoza, Bacalar Chico and Boca del Rio, and were recaptured in CC, often at Robles Point, the likely pre-spawning aggregation site. Second, we observed full and protruded abdomens, males full of milt, and females with eggs at Robles Point. Third, we observed behaviors associated with pre-spawning (Danylchuk et al. 2011; Adams et al. this issue; Danylchuk et al. this issue), including "porpoising" and synchronized movement offshore at dusk. Thus, we also hypothesis this second migration pattern was for spawning and was triggered by low temperature changes of the norths season. We also posit that the seasonal movements of bonefish tagged in CC and recaptured in CB reflect a third pattern, a post-spawning return to foraging grounds. This is reflected by the tagging locations in CC and recaptures on flats of the bay where we registered bonefish making a northward ($\pm$ 3.4 km) movement pattern. A study of bonefish movement patterns in Grand Bahama had similar results: after spawning, bonefish showed moved through canals that connect pre-spawning sites to shallow flats habitats (Murchie et al. 2015). Boucek et al. (this issue) showed similar connection between foraging grounds – where bonefish showed high levels of site fidelity – and pre-spawning sites. Indeed, bonefish tagged at a pre-spawning site were later recaptured on the flats (Boucek et al. this issue), similar to this study.

This study characterized the spatio-temporal movements of bonefish in an estuarine bay and the Caribbean Sea that included movements across international boundaries, and connections between foraging grounds and a pre-spawning site. This work has important conservation implications. First, since they share the bonefish population that supports the economically important flats fishery for bonefish, it is imperative that Mexico and Belize formulate a comprehensive regional management strategy. This strategy should include not only protections against overharvest of bonefish, but should also address habitat protections that ensure the coastal habitat mosaic upon which bonefish depend remains intact and healthy. Third, since bonefish appear to return to the same pre-spawning sites (Danylchuk et al. 2011; Adams et al. this issue) annually, and as with many species these sites are traditionally used by adult fish throughout the region (Heyman et al. 2005; Heyman and Kjerfve 2008; Adams et al. this issue), specific protections must be given to Robles Point, part of the Belize Barrier Reef System and within Bacalar Chico region, a World Heritage Site (Grimshaw and Paz 2004). Indeed, data similar to that obtained in this study was used to delineate habitat protections for bonefish pre-spawning sites in the form of National Parks in the Bahamas (Adams et al. this issue; Boucek et al. this issue).

Bonefish rely on a habitat mosaic throughout their life history and are susceptible to habitat loss (Adams and Cooke 2015; Adams and Murchie; Murchie et al. this issue) further study efforts using acoustic tagging and telemetry and underwater video to characterize the timing, location and spawning dynamics of bonefish, as well as permit and tarpon, are necessary. Also, because, migration is an undistracted movement without cessation for resources along the way (Dingle and Drake 2007), further studies are necessary to define seasonal migration and foraging movements at a larger seascape and what cues are triggering such movements. Finally, a diversity of habitats support bonefish ontogeny (Murchie et al. this issue) and age, growth and maturity data are important to

compare bonefish populations of both regions. Such information is essential to inform recreational-sport fisheries management and direct decision-making for a socio-economically important fishery.

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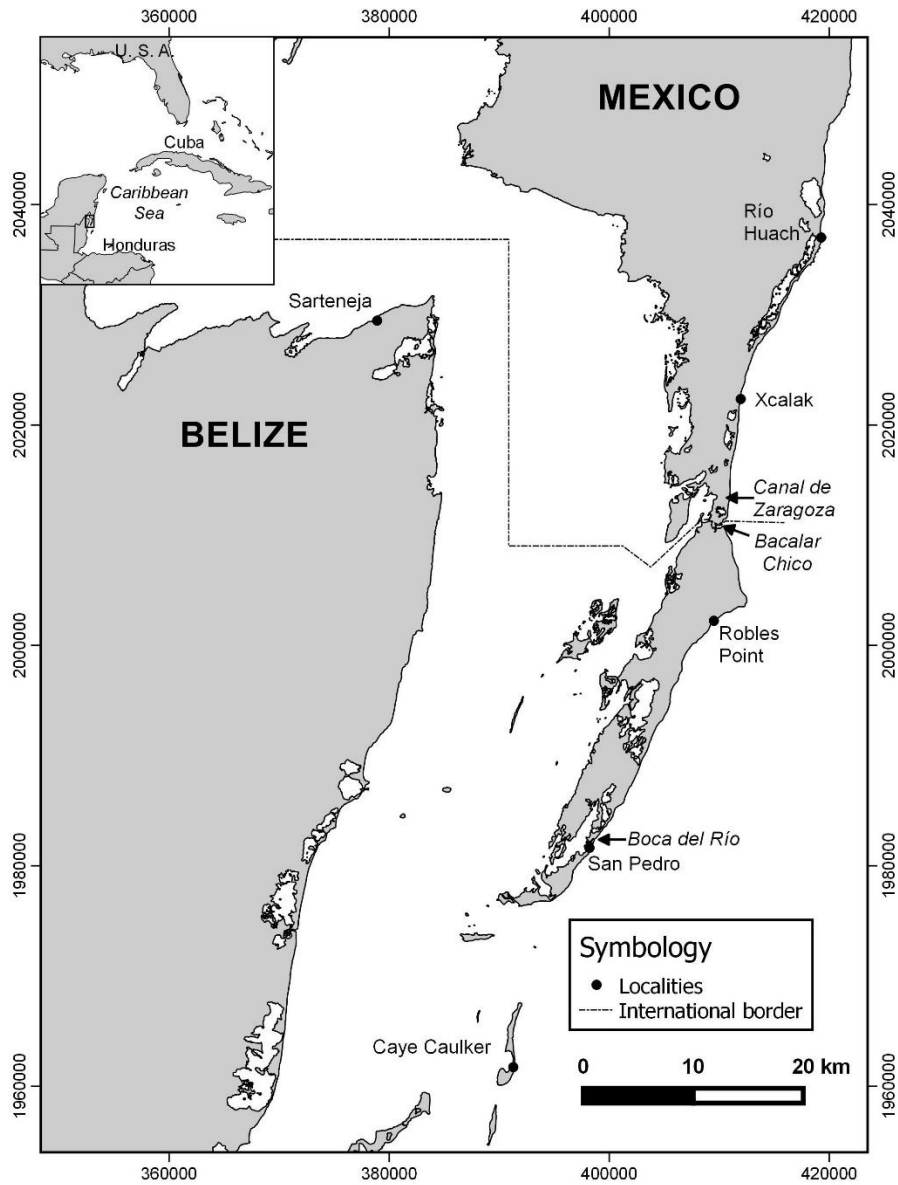
Fig. 1 Study area: Corozal-Chetumal Bay and Caribbean Coast, southern Mexico and northern Belize. Map processed by J. Padilla.

Table 1 Size of marked bonefish in Caribbean Coast (CC) and Corozal-Chetumal Bay (CB)

Region	Season	Minimum (cm)	Maximum (cm)	Mean (cm)	Std. Deviation	N
CC	Dry	23	50.8	34.988	4.8859	999
	Norths	23	56	34.925	4.3691	1191
	Rainy	22.2	56.4	35.226	5.9796	537
	Total	22.2	56.4	35.008	4.9108	2727
CB	Dry	22.1	48	28.098	3.5014	3454
	Norths	23.6	46.5	30.775	4.3554	804
	Rainy	22.2	50.8	28.707	4.6162	1831
	Total	22.1	50.8	28.635	4.0781	6089
Total	Dry	22.1	50.8	29.644	4.8087	4453
	Norths	23	56	33.253	4.8142	1995
	Rainy	22.2	56.4	30.186	5.6592	2368
	Total	22.1	56.4	30.606	5.2557	8816

Table 2 Size of recaptured bonefish in Caribbean Coast (CC) and Corozal-Chetumal Bay (CB)

Region	Season	Minimum (cm)	Maximum (cm)	Mean (cm)	Std. Deviation	N
CC	Dry	27.3	41.9	35.1	7.0	4
	Norths	30.4	37.3	35.6	2.6	6
	Rainy	33.4	49.4	40.4	4.8	18
	Total	27.3	49.4	38.6	5.2	28
CB	Dry	23.9	47.0	31.4	3.9	114
	Norths	24.5	41.0	29.8	5.1	8
	Rainy	22.7	42.3	30.5	3.5	419
	Total	22.7	47.0	30.7	3.6	541
Total	Dry	23.9	47.0	31.5	4.0	118
	Norths	24.5	41.0	32.3	5.1	14
	Rainy	22.7	49.4	30.9	4.1	437
	Total	22.7	49.4	31.1	4.1	569

Table 3 Seasonal minimum distance traveled by bonefish in Caribbean Coast and Corozal-Chetumal Bay

Region	Season	Minimum (km)	Maximum (km)	Mean (km)	Std. Deviation	N
CC	Dry	0	21.7	6.142	10.4715	4
	Norths	0	19.9	6.482	8.7356	6
	Rainy	0	2	0.242	0.642	18
	Total	0	21.7	2.422	5.9546	28
CB	Dry	0	45	3.441	8.1683	114
	Norths	0.1	77.1	12.858	26.4184	8
	Rainy	0	63.3	0.905	5.033	419
	Total	0	77.1	1.616	6.7517	541
Total	Dry	0	45	3.532	8.2154	118
	Norths	0	77.1	10.125	20.3932	14
	Rainy	0	63.3	0.878	4.9314	437
	Total	0	77.1	1.656	6.7122	569

4.0 CAPÍTULO III

Artículo sometido

Influence of environmental variables on abundance and movement of bonefish (*Albula vulpes*) in the Caribbean Sea and a tropical estuary of Belize and Mexico

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Summary
Bonefish (*Albula vulpes*) is a socio-economically important species that supports a data-poor recreational fishery in developing countries. Understanding how environmental variables influence its abundance and movement is important for better decision-making. This study used mark-recapture to examine the association between abiotic (temperature, salinity, wind speed, tides, moon phase and sediment coarseness) and biotic (presence of predators and vegatation) variables with bonefish movement and abundance in Corozal-Chetumal bay and the adjacent Caribbean coast of southern Mexico and northern Belize. We used seines to capture bonefish, marked 9,427, and recaptured 595 fish (6.1% recapture rate), during 16 sample periods between January 2016 and February 2018. Total abundance for each seine sample and distance between mark and recapture locations were used in two separate multiple stepwise regression analyses. Movement was negatively associated with temperature and predator presence, while sediment coarseness and moon phase were positively associated. Temperature increases were associated with short-distance movements. Temperature decreases and high-illumination lunar phases were associated with longer-distance movements and likely related to spawning migrations. Presence of predators, like barracuda, was associated with low bonefish abundances and was likely an adaptive response to form multiple schools of low density by bonefish to avoid predation. These spatio-temporal movement and abundance patterns are recommended to be used in fisheries and protected areas management and to inform the decision-making process in urban and tourism development in coastal habitats.

Keywords Mark-recapture, Albulidae, home-range, local movements, fish migration

Introduction

Recreational fisheries has gained importance in global fisheries (FAO 2012). Yet, there is paucity of information on recreational fisheries in developing countries (Gillet 2003; Cooke and Cowx 2004; Perez-Cobb et al. 2014) that hinders adequate decision making in fisheries management. In the Caribbean, bonefish (*Albula vulpes*) supports a socio-economically important catch-and-release (CR) sport fishery (Perez et al. 2018). Although much has been

learned in recent years about bonefish biology (Adams et al. 2018), data are still lacking on how environmental variables influence patterns of bonefish movement and abundance throughout their range.

Movement is a behavioral characteristic of living organisms that has consequences on population and community dynamics (Dingle 2014), and can be broadly characterized as local movement and migration. The former involves station keeping or foraging behavior and are repetitive responses to local resources (i.e. such as food) or other organisms (i.e. seeking cover from predation) that occur within home ranges (Dingle and Drake 2007; Thurow 2016). Migration however, is a specialized type of movement that involves individual behavior that displaces an organism from its home range (Dingle and Drake 2007). Both types of movement lead to changes in location but also lead to changes in abundance. Understanding how these dynamics are associated with biotic and abiotic variables has implications to current management strategies in protected areas of the Meso-American Barrier Reef System of Latin America.

Bonefish inhabit tropical and subtropical waters of the Western Atlantic region (Adams et al. 2008) and is a major target of a CR fishery in Belize and Mexico. In Mexico the bonefish fishery is unregulated, yet a voluntary ethic of catch and release allows an economically important fishery to thrive and provide employment to many flats fishing guides (Perez-Cobb et al. 2014). Although the economic impact of the bonefish fishery has not been quantified in Mexico, it is probably high; the annual economic impact of the flats fishery in neighboring Belize, which includes bonefish, permit (*Trachinotus falcatus*) and tarpon (*Megalops atlanticus*), exceeds $56 million (USD), and provides more than 2,100 full-time jobs (Fedler 2014). In Belize, bonefish, tarpon, and permit are regulated as catch and release only. Despite the socio-economic value of bonefish, major threats to this species are habitat loss and degradation due to coastal development (Zeller et al. 2011; Adams and Murchie 2015) that result in habitat fragmentation (Akçakaya 2000), abundance impacts (MacKenzie et al. 2006) and alters migration patterns (Begon et al. 2006).

The sustainability of the recreational bonefish industry relies upon the maintenance of abundant and healthy stocks (Danylchuk et al. 2007). This can only be achieved if management is informed by an understanding of environmental conditions that influence fish behavior and population dynamics. However, this information is lacking for Central America. Nearly all of the information on bonefishes is from studies in the Bahamas and Florida: feeding (Crabtree et al. 1998; Murchie et al. 2018), age and growth (Crabtree et al. 1996), maturation and reproduction (Crabtree et al. 1997), genetics (Adams et al. 2007; Wallace and Tringali 2010), movement (Haley 2009; Murchie et al. 2015a, b), searching for pre-spawning aggregation sites (Haley 2009; Danylchuk et al. 2011), larval studies (Pfeiler 1984; Mojica 1995), and fisheries and conservation (Ault et al. 2008; Fedler and Hayes 2008; Cooke and Philipp 2004; Danylchuk et al. 2007b; Adams and Cooke 2015; Frezza and Clem 2015; Adams et al. 2018). In contrast, the only studies in the Caribbean focused on species identification using genetic analysis in Belize (Adams et al 2008) and Mexico (Vásquez-Yeomans et al. 2009; Valdez-Moreno et al. 2010). Further, the single work that examined the influence of environmental variables focused on the effect of high temperatures and low dissolved oxygen levels that caused daily movements associated with tidal creeks in the Bahamas (Murchie et al. 2011). Additional factors thought to influence bonefish movements, such as salinity (Perez et al. 2018) and temperature changes produced by weather patterns, have not been examined.

Fluctuations in biotic and abiotic variables influence abundance and movement (Binder et al. 2011; Danylchuk et al. 2011; Thurow 2016). In estuarine systems, moon phase and seasonality produce salinity and temperature variations that influence fish abundance (Arévalo-Frías and Mendoza-Carranza 2014). For example, temperature triggers movements of juvenile common snook (*Centropomus undecimalis*), which result in predation and feeding competition that affect abundance (Barbour et al. 2014). The moon phase is mostly associated with gonadal development (Takemura et al. 2010; Ikegami et al. 2014) and spawning in broadcast spawners such as groupers, snapper (Heyman and Kjerfve 2008) and bonefish (Danylchuk et al, 2011). However, the influence of these environmental variables on abundance and movement patterns of bonefish has not been reported.

Modeling is a powerful tool for discerning the effects of often-correlated abiotic variables on animal movements (Mackenzie et al. 2006). Once the influence of abiotic variables is determined, the information is useful for guiding management strategies (Arévalo-Frías and Mendoza-Carranza 2014) and monitoring efforts (MacKenzie et al. 2006) and can be applied to bonefish management in the Caribbean. The goal of this study was to use mark-recapture data to model the influence of abiotic variables on bonefish movements in a tropical estuary (Chetumal-Corozal Bay) and the adjacent Caribbean coast of northern Belize and southern Mexico.

Methods

Study area

Our study area was comprised of two geomorphological regions: Chetumal-Corozal Bay (CB) and the adjacent Caribbean coast (CC) of the western Caribbean and Mesoamerican Barrier Reef System. This shared area, which is part of the southern Yucatan of Mexico and Ambergris Caye of northern Belize (Fig. 1), has vast estuarine and marine waters and ecosystems split by an international border. The regions are connected via the man-made Canal de Zaragoza in Mexico and the natural channels of Bacalar Chico (the international border between Belize and Mexico) and Boca del Rio in San Pedro, Belize (Fig. 1). Both regions generally include submerged aquatic vegetation of macroalgae (e.g. *Batophora* and *Chara*) and seagrass (*Thalassia testudinum* and *Halodule wrightii*), numerous coral species and coral rubble. Prevailing wind direction is generally from the southeast, except in November-January, when north winds predominate (Carrillo et al. 2009b). The mean air temperature is 26 °C (range = 14 °C to 35 °C), average annual precipitation is 1245 mm (range: 1000 mm-1500 mm), with mixed tides with semidiurnal predominance of a maximum height of 0.3 m (Carrillo et al. 2009a). The seasons are categorized as cold fronts ("nortes", but hereafter "norths") from November-January, dry from February-May, and wet (or "rainy") from June to October.

The Caribbean coast is characterized by a narrow continental shelf (< 10 km), where the reef area is parallel to the coast (Carrillo et al. 2015a). The coast is also comprised of a backreef lagoon system (Adams et al. 2006), approximately 1 km wide from the shoreline to the reef crest (Perez et al. 2018), with depth that ranges between 2 and 3 m, to a maximum of 6 m (Grimshaw and Paz 2004); it includes a mosaic of seagrass, mangrove, and coral reef habitats. Offshore (>1km) water salinity is <35.8 psu at 5 m, ranges from 34.5 to 36.6 psu, and maximum of 36.92 psu at 150 m, but it is generally lower (< 35.5 psu) closer to the coast (Carrillo et al. 2015b). The surface water temperature is >25 ℃, mean temperature is 26.5 ℃ at 93 m and 27.12 ℃ at 85 m, minimum is 16 ℃ at 150 m (Carrillo et al. 2015b). Recorded inshore (<1km from the shoreline) salinity and water temperature range from 34 to 36 ups (Perez et al. 2018) and 26.4 to 35.3 °C (pers. obs.), respectively.

The bay is a large and shallow tropical estuary, with depths of 0.5 m to 2.5 m in some areas (Hernández-Arana and Ameneyro-Ángeles 2011) and between 2 m and 5 m in others (Carrillo et al. 2009b). It consists of shallow flats with sandy and rocky bottoms, often with habitats of submerged aquatic vegetation and mangrove-lined creeks, wetlands and lagoons (Perez et al. 2018). The bay has freshwater inputs from the Rio Hondo, creeks and underground springs (Carrillo et al. 2009b) particularly during the rainy season. General salinities and water temperature can range from 8 psu to 18 psu and 24.5 °C to 31.0 °C respectively (Carrillo et al. 2009a). During the norths season, the salinity is 4 psu near the Rio Hondo but generally between 13 and 16 psu over most areas (Carrillo et al. 2009b). During the dry season, salinity is generally > 19 psu but there is stratification of less saline water at the surface (14 psu) and saltier water intrusion at the bottom (19 psu) (Carrillo et al. 2009b), likely produced by the change in wind direction from the southeast of the dry season. During the rainy season, as during the cold front and dry season, salinity is generally between 13 and 16 psu but there is a horizontal gradient of fresher water that ranged between 10 psu and 15 psu and dominates from the western side to the northern area of the bay by input from the Rio Hondo (Carrillo et al. 2009b). Salinity ranges were larger in CB (18-40 psu) than in CC (35-36) and seasonally in the dry (20-40 psu) than the rainy season (18-39 psu) and norths season (18-39 psu) (pers.obs). The mean water column temperature is the warmest in the rainy season (30.0 ℃ ± 0.48; max = 30.6 ℃), followed by the dry season (28.5 ℃ ± 0.75; max = 30.0 ℃) and the coolest in the norths season (25.7 ℃ ± 0.40; range = 25.2 ℃ – 26.8 ℃) (Legorreta 2018).

Mark-recapture sampling

A stratified random design was used to sample for bonefish in January, June, November and December 2016; January to July, August-September and December 2017; and February 2018. There were eight sampling days (four in Belize, four in Mexico) and per sample period. Sampling was conducted by a team of 4 persons. One of them was a professional guide, who targets bonefish as part of the CR fishery and selected sites for sampling based on local knowledge (Berkes 2008). Sites were <1.2 m deep, with sturdy sand, rock, or seagrass bottoms. The guide piloted the vessel (usually boats 8 m in length or smaller, with 15 to 60 HP motors) moved at 1-2 km/h by motor or poling approximately 500 m parallel from the shoreline. Bonefish schools were sighted and captured using two light-colored seine nets, each 45 m long, 1.2 m high, and 2.5 cm mesh. The fish were encircled with the seines and then taken out with hand nets and kept in a nearly submerged floating cage (1 × 0.5 × 0.25 m) until they were measured (fork length (FL) to the nearest mm) and marked with a dart tag (model PDS, Hallprint, Australia) in the left-side musculature between the first dorsal pterygiophores (Boucek and Adams 2011). Only fish ≥ 22 cm FL were tagged and the rest were released. At each site we recorded date, time, latitude and longitude, number of fish tagged, number of recaptures, number of fish released (< 22cm FL), bottom type (coarseness of sediment and density of vegetation), presence of potential predators (barracuda: *Sphyraena barracuda*, pelican: *Pelecanus occidentalis* and

osprey: *Pandion haliaetus*), moon phase and tide (from: http://www.tides4fishing.com). Salinity was measured using a refractometer (to the nearest psu) and water temperature using Hanna HI9812-5 (to the nearest 0.1 °C) below 1 feet of the water surface. Fish were handled for the shortest time possible, allowed to recover in another seine enclosure and then released *en masse* to reduce post-release mortality from predation (Adams et al. 2009). Because there are always unidentified and uncontrollable factors that influence detection of an animal (Conroy and Nichols 1996; Mackenzie and Royle 2005; MacKenzie et al. 2006) our effort was not controlled by the number of haul nets per month or region but by time. Hence, sampling ceased once: a) 4 days in each country had elapsed (8 days per sample period), b) or all sites in CB and CC of each country were sampled. Finally, a bonefish marked and recaptured during the same sample month was not considered as a recapture for that occasion.

Analysis

Abundance (*i.e.* capture per unit effort, CPUE) for each net haul was calculated by adding the number of fish marked, number of recaptures and number of fish < 22 cm FL released. Movement (*i.e.* distance between tagging and recapture sites to the nearest km) was measured using the shortest distance along the shoreline over water with Google Earth©. For some cases, the distance between a marked site in CC and a recapture site in CB (or vice versa) was measured either through the channel shoreline of Bacalar Chico in southern Xcalak (northern San Pedro) or Boca del Rio in San Pedro. Bonefish recaptured at the same site where marked were assigned a distance of 0 km.

Because ecological data, such as abundance, are often highly skewed and contain substantial presence of zeros (Fletcher et al. 2005), abundance data were log-transformed (x+1). Distance, however, was very skewed, but unlike other studies that used acrsine transformation (e.g., Schmitter-Soto et al. 2018) we used Tukey's Ladder of Powers to reduce skewness and increase power (Tukey 1977). Because continuous variables (salinity, temperature, and wind speed) were measured in different scales and varied significantly by season during our sampling, they were rescaled by normalizing the values between 0-1 to have similar weights, importance and reduce multi-collinearity in the modelling (Jongman et al. 1995). Ordinal variables were coded in the following manner: moon phase cycle (eight phases), predators (absence and presence) and tide (rising-high and lowering-low). Benthic habitat was split into two variables, sediment coarseness and vegetation density. Sediment, from fine to coarse, was ordered as muddy, sandy-muddy, sandy, sandy-rocky, and coral rubble. Submerged vegetation was ordered as no vegetation, sparse, medium, dense. All seagrass occurred on sandy bottom.

Multiple stepwise regression analysis was performed to understand how abundance and movement were influenced by abiotic (salinity + temperature + wind speed + moon phase + tide + sediment bottom) and biotic (predators + vegetation bottom) variables. The *lm* function was used to build a multiple linear regression model. Then, the *step* function was used to run a backward model selection in R (R Core Team 2017). The importance of variables in the model was assessed using Akaike Information Criterion (AIC) (Akaike 1973). Terms (variables) were retained if they reduced the model's AIC but were dropped if the AIC increased and the process was repeated until dropping any further terms did not reduce the AIC by more than 2 points (Burnham and Anderson 2002). Homoscedasticity was assessed with Bartlett's test and multicollinearity of variables was assessed using a variance inflation factor (VIF) from 1 to 2.5. All analyses were conducted in RStudio version 1.0.153 (Venables and Smith 2003) and significance was assessed at $p < 0.05$.

Results

Mark-recapture

There was a total of 16 sample periods that resulted in 122 net hauls. More hauls were made in CB (86) than CC (36). Seasonally, more hauls occurred in the rainy season (53), followed by the dry (40) and norths season (29). A total of 9,657 bonefish were marked, 6,474 in CB and 3,183 in CC. Seasonally, more were marked in the rainy season (447), followed by the dry and norths season (126). A total of 595 bonefish (6.1 % recapture rate) were recaptured, with more in CB (562) than CC (33). Seasonally, most recaptures were in the rainy season (432), followed by the dry (115) and norths season (48).

Abundance

Both, the mean number of marked and recovered bonefish ≥22cm was greater in CC and bonefish <22 cm was greater in CB (Table 1). Abundance changed seasonally, with the highest mean abundance in the dry season,

followed by the norths season, and the rainy season (Table 2). However, the interaction of season and region indicates that there were more bonefish <22 cm only during the dry and rainy seasons (Table 2) in CB only.

Movement

Overall, bonefish moved less in CB than CC (mean distance in CB = 0.9 km, SE = 0.2 km; mean distance in CC = 2.1 km, SE = 1 km). Bonefish were recaptured (82%) within 1 km of shoreline distance or at the same site in both CB (444 recaptures = 0 km; 22 recaptures = 0-1 km; 83 recaptures = 1-10 km; 12 recaptures = 10-46 km) and CC (22 recaptures = 0 km; 2 recaptures = 0-1 km; 6 recaptures = 1-10 km; 3 recaptures 10-21.7 km). Relative movement was greatest in the norths season (mean = 1.8 km, SE = 0.81, max = 31 km), followed by the dry season (mean = 1.7 km, SE= 0.42 km, max = 34 km) and the least during the rainy season (mean = 0.6 km, SE = 1.7 km, max = 46 km). Interestingly, interaction of season and region show bonefish moved more in the cooler dry (CB mean = 1.5 km, SE = 0.39; CC mean = 8.1 km, SE = 6.8) and norths (CB mean = 1.2, SE = 0.85; CC mean = 3.7 km, SE = 2.1) seasons than during the warm rainy season (CB: mean = 0.64 km, SE = 0.18; CC mean = 0.23 km, SE = 0.14) in both regions.

Modeling

Abundance. The final (i.e. reduced) abundance model consisted of predators (positive relationship) and sediment coarseness (negative relationship) (Table 3). VIF were reasonable for the full model (range = 1.10 to 1.29) and final model (range = 1.01-1.01).

Movement. The final movement model (model 1) consisted of all variables, except salinity, which was dropped: Distance ~ temperature + wind speed + lunar phase + predators + sediment coarseness + vegetation bottom + tide. However, the VIF for variables in the full model ranged from 1.34 to 3.90 and for the reduced model from 1.31 to 3.78. The VIF in the reduced model for sediment coarseness (3.27) and vegetation bottom (3.78) were high. This indicated that the sediment and vegetation co-varied. Thus, a second model was fit, leaving out salinity (since it was dropped) and vegetation bottom (since it had the highest VIF): Distance ~ + temperature + wind speed + lunar phase + predators + tide + sediment coarseness. Model 2 was reduced to sediment coarseness, temperature, moon phase and predators (Table 4). The VIF for the full model 2 (1.24-1.66) and reduced model (1.07-1.30) were reasonable. Models 1 and 2 were tested using ANOVA and there was a significant difference between them ($F_{-3,590} = 4.50$, $p <$ 0.05). Model 2 had a better fit without vegetation (Table 5). Temperature and predator presence had a negative relationship suggesting bonefish moved less with increased temperature and predator presence. Moon phase and sediment coarseness had a positive relationship (Table 4), suggesting movement behavior increased with moon phases with high illumination and sediment coarseness respectively.

Retained environmental variables

Predators. In a few of our samplings in CB, bonefish displayed a circular-rotation schooling behavior. Barracudas were the only predator present and close to bonefish schools before our seining. Other potential predators (pelicans and ospreys) were observed after the schools where seined. Overall, predator presence (45 out of 122 haul nets) was lower than absence in both regions (Table 5). However, regional and seasonal interaction show the presence was higher than absence in CB during the dry season (21 out of 40).

Sediment coarseness. CB uniquely consisted of muddy bottoms as opposed to CC with coral rubble. CB was comprised of four sediment types but more than half of our sampling occurred in sandy-muddy bottoms (45.3%) and sandy bottoms (32.6 %) with presence of vegetation (Table 6). Most of our sampling in CC occurred in sandy bottoms (55.6%) where seagrass was found and in sandy-muddy bottoms (36.1%) (Table 6). These habitats and proportions were also similar for all seasons (Table 6). However, the overall pattern was the opposite: sandy-muddy bottom (42.6%) followed by sandy bottom (39.3%).

Water temperature. The highest mean water temperature was during the rainy season (30.9 °C) and the dry season (29.9 °C), with the north season (mean = 28.5 °C) as the lowest (Table 7). Over all, temperature range (20-35 °C) was more important in the modelling than variables such as salinity.

Moon phase. Overall, high movement rate (> 1km) seems to be most associated to waxing gibbous in both CB (10.5% in waning crescent/after new moon, 15.1% in waning gibbous/right before full moon, and 50% in waxing gibbous/after full moon) and CC (22.2% in waning gibbous, 25% in full moon and 27.7% in waxing gibbous) (Table 8).

Discussion

This study examined the association between abiotic and biotic variables with seasonal and spatial variation in abundances and movements of bonefish.

An increase in movement was correlated with high predator presence. In fact, studies in the region indicate barracuda is a top predator that undergoes inter-habitat movements (Torres-Chávez et al 2018). This suggests that barracudas may follow bonefish movements. However, bonefish avoid predation using two adaptive behaviors. One, like sardines and anchovies in response to predation pressure (Kaltenberg and Benoit-Bird 2009), bonefish display a circling behavior. Two, and as indicated by local knowledge of fly-fishing guides and our observations, bonefish break into smaller schools, leaving a larger school a distance away. Similar behavior has also been reported in pre-spawning schools (Perez et al. 2018). This also explains why a decrease in abundance was associated with low predator presence; bonefish spread into less dense schools to avoid predation and increase survival.

Sediment:

High abundances were associated to finer sediment coarseness. This reflects that most of the Caribbean, as reported by Perez et al. (2018) is largely bare bottom. Particularly CB, where finer bottoms such as muddy and sandy-muddy bottoms are the dominant benthic cover. This is important information, as these habitats are seen less important than mangrove and coral reef habitats, but are likely offering feeding grounds for bonefish. In fact feeding marks produced by bonefish searching the bottom are very common throughout CB. CC however, was largely represented by sandy bottoms where seagrasses are the most common benthic cover in the reef lagoon. These findings also corroborates, that benthic habitats of the Caribbean are mostly bare bottom (Perez et al 2018) particularly in estuarine environments such as CB. Since seagrass habitats dominate CC, it is likely such habitats provide more prey diversity and quality (Colton and Alevizon 1983; Murchie et al. 2018). These differences in benthic cover also allows us to discern foraging and spawning movement behaviors, which are supported by modeling of high movement rates in association to larger sediment coarseness (i.e. higher in CC than CB).

Our models suggest temperature was more important than salinity, and it explained likely two patterns. First, a thermoregulation response that mostly likely occurred during the rainy season, when temperature was higher, associated with little movement. Usually bonefish would move to other areas in response to high temperatures and low levels of dissolved oxygen (Murchie et al. 2011), but here we present an alternative behavior and an adaptive response to survival in extreme environmental conditions. Second, a physiological-reproductive response that involved long-distance movements, that occurred during colder temperatures (i.e. norths season), which were likely associated with the spawning season and spawning migrations. Because weather is largely affected by climate change (Roessig et al. 2004; Centre et al. 2010), estuarine systems, in comparison to the Caribbean coast, are more susceptible to variations in weather patterns. Thus, temperature variation and evaporation and precipitation rates could impact distribution and disrupt local movements and spawning migration patterns of bonefish.

The spatio-temporal variation in abundance of small-sized and large-sized bonefish explain several important population dynamics. Bonefish population make a seasonal southward movement from the Mexican bay into the Belizean bay (Perez et al. 2018). Our models provide additional insights to a likely temperature-induced seasonal migration of small-sized bonefish from inner creek and lagoon to outer coastline habitats of the bay during the dry and rainy season. In marine, but also estuarine environments, temperature strongly influences fish seasonal movement, habitat use and abundances (Barbour et al. 2014 a,b). However, the population was balanced with large-sized bonefish that were likely intercepted during their spawning migration, which coincided during the norths season. Studies suggest that bonefish migrate during the norths season (Perez et al. 2018), when, as indicated by our models, temperatures were lowest. Our study suggests that creeks and lagoons are important recruitment areas for small-sized bonefish and the bay coastline may be an important thermal refuge zone for them. It also suggests there are areas in the bay which are important points where large-sized bonefish congregate. In these areas bonefish showed little movement, likely waiting for the right conditions before migrating to pre-spawning sites in Belize's barrier reef lagoons.

Increasing moon phase (i.e higher illumination) was correlated with longer distance movement. Bonefish spawn seasonally, and our results corroborate observations by Perez et al. (2018) that these movements occur days before the full moon. Lunar cycles cause changes in moonlight intensity and influence the physiological and behavioral activities in organisms (Ikegami et al. 2014). Many broadcast spawners reproduce in association with the full moon (Heyman and Kjerfve 2008; Takemura et al. 2010; Binder et al. 2011; Danylchuk et al. 2011) and

27

bonefish in the Caribbean seems to follow a simliar pattern (Adams et al. 2018). Our modeling also indicates high movement rates after full moon, suggesting, as indicated by Perez et al. (2018), a return to home ranges from spawning. Low movement rates (i.e. local movements) were associated with low illumination of moon phases, which further corroborates that bonefish have small home ranges and a high site fidelity to home ranges (Boucek et al. 2018; Perez et al. 2018) which in our case were mostly located in CB but a few in CC.

Organisms function, adapt, respond, and exploit their physical environment through physiological means and behavioral responses known as homeostasis (Pianka 1994). Both movement and abundance models did not retain salinity, likely because most sampling occurred in the southern and eastern parts of the bay, closest to the sea, where salinity ranges were adequate for bonefish presence. In fact the bay is very dynamic in that the eastern side is characterized by higher salinities driven by weather patterns (Carrillo et al. 2015b). It is also possible that evaporation was high, particularly in the rainy season, which kept salinity stable despite freshwater inflow. Thus, it cannot be refuted that bonefish movement patterns are associated with salinity changes during the rainy season (Perez et al. 2018), and we can speculate that part of their movements, especially in the upper parts of the bay, are likely an osmoregulation response which involved a southern movement (from Mexico to Belize).

Modeling using mark-recapture data was important to discern bonefish behavior in the eastern Caribbean. Our findings have major conservation implications. Future and similar studies in the Western Caribbean require a focus on connectivity of estuarine and marine environments as population dynamics are dependent on both. Such approaches are also of important in spatial management of fisheries resources. Another major implication is the importance of the eastern side of the bay that includes San Pedro and Xcalak, as seasonal refuge and spawning related congregating grounds. This suggests that nursery and recruitment data are needed to direct decisions on urban and tourism development that that directly impact benthic habitats. Resource managers are urged to use recreational data such as these (FAO 2009, 2012; Cook and Cowx 2004; Perez-Cobb et al 2014) in economic, tourism, urban and fisheries development and to create refuge, feeding and reproductive zones for sustainable recreational fisheries in Belize and Mexico.

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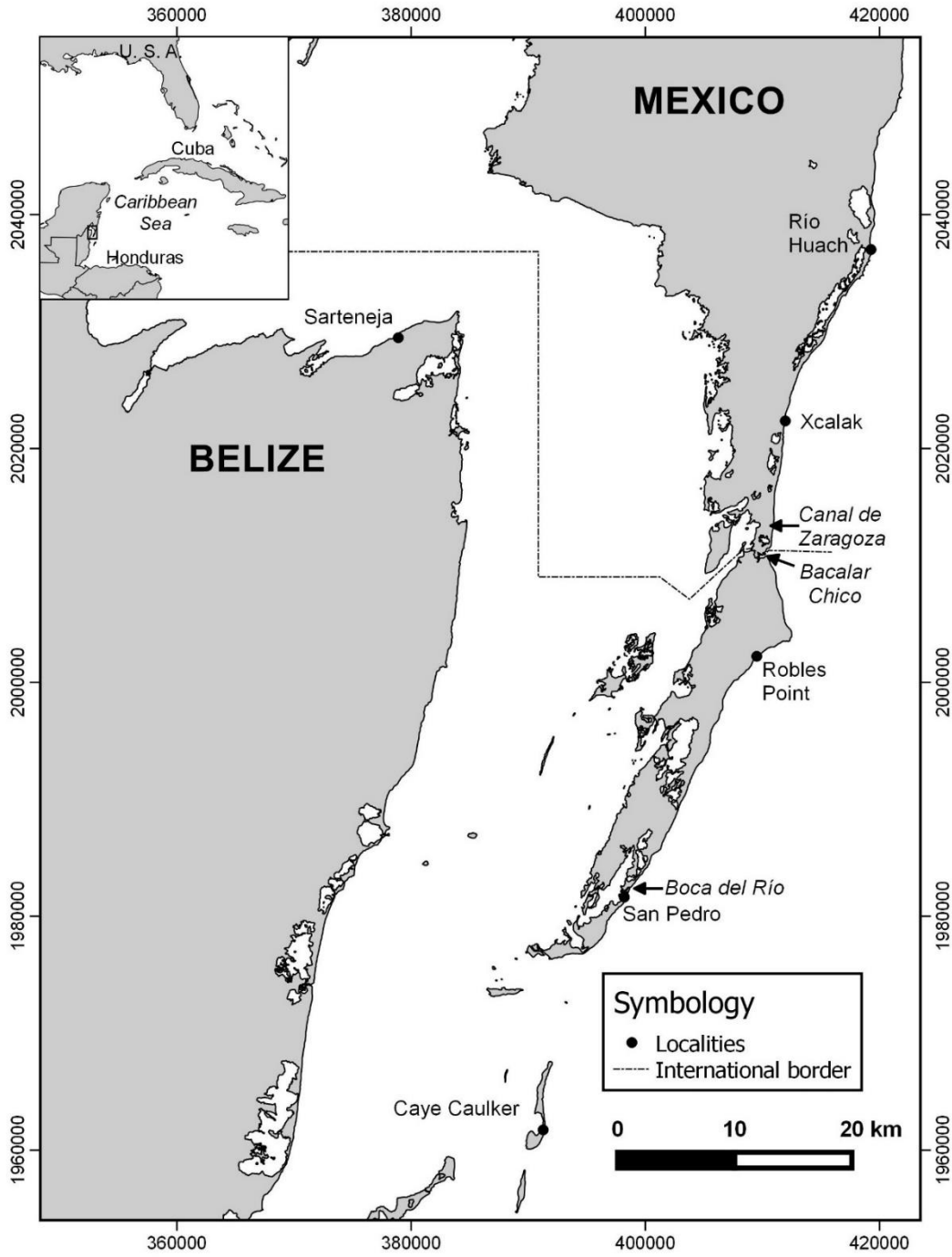
FIGURE. 1. Study area: Corozal-Chetumal Bay and Caribbean Coast, southern Mexico and northern Belize. Map processed by J. Padilla.

Table 1. Regional descriptive statistics of marked, recovered, released and abundance of bonefish in Corozal-Chetumal bay (CB) and Caribbean coast (CC).

Region	Descriptive statistics	Marked	Recovered	Released	Abundance
CB	Mean	69.84	7.14	87.41	164.38
	Std. Error of Mean	14.265	2.456	30.757	40.366
	Minimum	0	0	0	0
	Maximum	809	183	2465	3011
CC	Mean	74.97	1.03	52.26	126.81
	Std. Error of Mean	24.525	0.455	25.066	37.484
	Minimum	0	0	0	0
	Maximum	751	16	610	834
Total	Mean	71.35	5.34	77.24	153.3
	Std. Error of Mean	12.335	1.752	23.019	30.483
	Minimum	0	0	0	0
	Maximum	809	183	2465	3011

Table 2. Seasonal descriptive statistics of marked, recovered, released and abundance of bonefish in Corozal-Chetumal bay (CB) and Caribbean coast (CC).

Season	Descriptive statistics	Marked	Recovered	Released	Abundance
Dry	Mean	93.25	3.13	95.55	191.93
	Std. Error of Mean	25.127	.892	62.389	79.926
	Maximum	809	24	2465	3011
Norths	Mean	102.79	1.55	81.75	183.28
	Std. Error of Mean	30.065	.680	31.598	47.256
	Maximum	751	17	629	834
Rainy	Mean	37.62	9.08	61.04	107.74
	Std. Error of Mean	12.331	3.920	17.446	25.143
	Maximum	501	183	610	832
Total	Mean	71.35	5.34	77.24	153.30
	Std. Error of Mean	12.335	1.752	23.019	30.483
	Maximum	809	183	2465	3011

Table 3. Best linear model of variables and factors for bonefish abundance (CPUE ~ predators + sand bottom) from seining

Terms	Estimate	Std. Error	t value	Pr(>|t|)	2.50%	97.50%
Intercept	3.61	0.8467	4.264	4.05E-05	1.933427	5.286513
Predators	0.9228	0.4189	2.203	0.0296	0.09321	1.75233
Sand	-0.6418	0.2486	-2.581	0.0111	-1.13405	-0.14951

Residual standard error: 2.221 on 119 degrees of freedom; Multiple R-squared: 0.08071, Adjusted R-squared: 0.06526; F-statistic: 5.224 on 2 and 119 DF, p-value: 0.00669.

Table 4: Model 2; best linear model of variables and factors for bonefish movement (distance ~ temperature + predators + moon phase + sediment coarseness)

Terms	Estimate	Std. Error	t value	Pr(>|t|)	2.50%	97.50%
Intercept	0.05522	0.14291	0.386	0.69934	-0.22546	0.335903
Temperature	-0.84451	0.10051	-8.403	3.27E-16	-1.04191	-0.64712
Predators	-0.12639	0.04748	-2.662	0.00798	-0.21963	-0.03314
Moon phase	0.03019	0.01305	2.313	0.02109	0.00455	0.055826
Sediment coarseness	0.25839	0.04164	6.206	1.02E-09	0.176622	0.340165

Residual standard error: 0.4583 on 590 degrees of freedom; Multiple R-squared: 0.1524, Adjusted R-squared: 0.1467; F-statistic: 26.53 on 4 and 590 DF, p-value: < 2.2e-16.

Table 5: Regional and seasonal count of predator presence and absence 122 haul nets of mark-recapture in Corozal-Chetumal bay (CB) and Caribbean coast (CC).

Region	Predators presence	Season			
		Dry	Norths	Rainy	Total
CB	No	17	8	23	48
	Yes	20	5	13	38
	Total	37	13	36	86
CC	No	2	11	16	29
	Yes	1	5	1	7
	Total	3	16	17	36
TOTAL	No	19	19	39	77
	Yes	21	10	14	45
	Total	40	29	53	122

Table 6: Regional and seasonal count of sediment type in 122 haul nets of mark-recapture in Corozal-Chetumal bay (CB) and Caribbean coast (CC).

Region	Sediment type	Sediment coarseness	Season			
			Dry	Norths	Rainy	Total
CB	Muddy	1	1	3	2	6
	Sandy-muddy	2	17	6	16	39
	Sandy	3	10	3	15	28
	Sandy-rocky	4	9	1	3	13
	Total		37	13	36	86
CC	Sandy-muddy	2	1	7	5	13
	Sandy	3	2	9	9	20
	Sandy-rocky	4	0	0	1	1
	Coral rubble	5	0	0	2	2
	Total		3	16	17	36

Table 7: Regional and seasonal mean, standard error, minimum and maximum water temperature register during 122 haul nets of mark-recapture in Corozal-Chetumal bay (CB) and Caribbean coast (CC).

Season	Region	Temperature (^oC)			
		Mean	Std. Error of Mean	Minimum	Maximum
Dry	CB	29.88	0.278	26	34
	CC	30.27	0.669	30	32
	Total	29.91	0.261	26	34
Norths	CB	28.37	0.858	20	32
	CC	28.63	0.479	24	33
	Total	28.51	.0458	20	33
Rainy	CB	30.65	0.282	27	35
	CC	31.46	0.360	30	34
	Total	30.91	0.228	27	35
Total	CB	29.97	0.225	20	35
	CC	30.11	0.355	24	34
	Total	30.01	0.189	20	35

Table 8: Regional and seasonal count of moon phases in 122 haul nets of mark-recapture in Corozal-Chetumal bay (CB) and Caribbean coast (CC).

			Season			
Region	Moon phase	Moon phase order	Dry	Norths	Rainy	Total
CB	New moon	1	3	1	0	4
	Waning crescent	2	7	2	0	9
	Last quarter	3	4	0	0	4
	Waning gibbous	4	7	0	6	13
	Full moon	5	0	1	0	1
	Waxing gibbous	6	14	6	23	43
	First quarter	6	0	0	4	4
	Waxing crescent	8	2	3	3	8
	Total		37	13	36	86
CC	New moon	1	0	2	0	2
	Waning crescent	2	0	1	0	1
	Last quarter	3	0	0	0	0
	Waning gibbous	4	3	0	5	8
	Full moon	5	0	3	6	9
	Waxing gibbous	6	0	7	3	10
	First quarter	6	0	0	1	1
	Waxing crescent	8	0	3	2	5
	Total		3	16	17	36

5.0 CAPÍTULO IV

Articulo por ser enviado.

Using mark-recapture to estimate survival, recapture probability and movement of bonefish (*Albula vulpes*) in the Caribbean Sea and a tropical estuary in Belize and Mexico

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Abstract

Bonefish (*Albula vulpes*) are an important socio-economic resource species in coastal communities. Yet, the persistence lack of knowledge on population parameters of hinders its sustainable use from direct and indirect human impacts in the Caribbean region. Here we present a first multi-state modeling of bonefish to estimate survival, recapture probability and movement in the Corozal-Bay (CB) an adjacent Caribbean coast (CC) regions shared by Belize and Mexico. Mark-recapture method was used to mark 9657 bonefish and recapture 605 (5.9% recapture rate). A total of 64 multi-state models were run in MARK program. The best model with the lowest Akaike Information Criteria indicate: Survival was constant in CC but variable in CB, probability of recapture in CC and CB were both time-dependent, and movement between CC to CB and CB to CC were time-dependent. Our estimates of a lower survival rate in CC (63.6%) than CB (80.6%) indicate a higher exit rate through movement and mortality in CC than CB. These estimates were lower for CC to CB (1.3%) than for CB to CC (1.5%). Interestingly, there was a pattern of reduced survival for bonefish in the bay that is likely explained by their temporary migration from the bay to spawn in the Caribbean during the norths season. Although recapture probability in CC was also lower (1.3%) than CB (11.1%), recapture probability in CC was high only during norths and rainy season but highest in the dry season in CB, further corroborating migration movements related to spawning.

Key words:

Corozal-Chetumal Bay, fisheries management, conservation, habitat connectivity, multi-state models, Marine Protected Areas

Introduction

Mark-recapture studies are traditionally used to estimate abundance, birth rates, survival, and related demographic parameters to inform management and conservation of animal populations (MacKenzie et al. 2006). This method is commonly being used to determine movement and migration patterns of catch-and-release species in the Bahamas (Murchie 2010; Danylchuk et al. 2011; Adams et al. 2018; Boucek et al. 2018). Belize and Mexico in the Western Atlantic region (Perez et al. 2018). Yet, there is a persistent failure to recognize that although a fish population is considered catch-and-release, it is not immune to population decline. As a consequence, there is a paucity of fishery statistics (Perez-Cobb et al. 2014) such as fish population dynamics in an ecosystem context to predict effects of fishery management decisions (De Young et al. 2008). Developed countries such as the United States focus on fish population assessments on estimating mortality and maximum sustainable yield to guide policy making (Pauly et al. 2002), primarily because landing data for commercially important fish populations are most available, compared to data for species of the recreational fishery sector, and much less from catch-and release (Coleman et al. 2004). Therefore, it is important that fisheries research and management allocate efforts and funds to evaluate the catch-and-release fish.

Catch-and-release (CR) is a socio-economically important recreational activity in the Western Atlantic region (Adams et al. 2008). Caribbean countries such as Belize and Mexico use protected areas (PAs) as a precautionary approach to fisheries management (Pauly et al. 2002) due to many reasons, including the lack of data (Gillet 2003; Crowder et al., 2008). Mark-recapture studies show that both nations also share a bonefish (*Albula vulpes*) population (Perez et al. 2018). Bonefish, along with permit (*Trachinotus falcatus*) and tarpon (*Megalops atlanticus*) gained full protection as CR in Belize in 2009. Since then, CR fishing has become an alternative type of fishing to artisanal subsistence and commercial (ASC) fishing in almost every coastal community. CR fishing generates US $ 35 million in wages and salaries and provides over 2100 direct employment opportunities to Belize (Fedler 2014). In Mexico legislation still allows harvest of bonefish for subsistence and commercial use (Medina-Quej et al. 2009), but local fishers practice CR nevertheless, because of its greater economic value (Perez-Cobb et al. 2014). Unfortunately, CR and ASC fishing (hereafter bonefish fishery) face threats, both internal (i.e. by the same fishery) and external (e.g. tourism and commercial fishing).

The negative impact of CR fishing on the base resource and its habitat needs to be managed for the bonefish fishery to be sustainable. Fishing, even if CR, produces mortality, alters habitats and modifies fish behavior (Crowder et al. 2008). Recreational fisheries not only modifies system function and quality but also contribute to global fishery declines (Cooke and Cowx 2004), particularly because of the catch-and-kill practice. Catch and consume under recreational fishing has demographic and ecological impacts on fish populations (Coleman et al. 2004). Even though bonefish are returned to the water, CR still affects behavior and produces post-release mortality either through injury caused by the hook, exhaustion, and predation (Danylchuk et al. 2007a, b; Suski et al. 2007).

CR is also considered artisanal (Perez-Cobb et al. 2014) and as many other artisanal fishing it has access to many near-shore shallow habitats (Crowder et al. 2008) which are degraded by anglers and boat activities (Cooke and Cowx 2004). Estuarine habitats of the Corozal-Chetumal bay are feeding and refuge zones (Schmitter-Soto et al. 2009) and it seems the increase fishing pressure of CR (Perez-Cobb et al. 2014), ASC and recreational-tourism boats and water activities are having a toll on bonefish population.

Yet, a greater and more immediate threat to bonefish is the illegal, unreported and unregulated (IUU) harvest by ASC fishing. IUU is a worldwide problem that causes overfishing and significant stock declines of national, migratory and straddling stock populations (Pitcher et al. 2002; De Young et al. 2008; Meere and Lack 2008). The ASC use of gillnets and traps alter community structure and trophic relationships and can generate rapid declines of target and by-catch species (Crowder et al. 2008). In the 20th century the increase of human population on Christmas Island in Australia overfished bonefish populations during their spawning migration with gillnets (Jones and Balderamos 2011). Belize (Commonwealth Policy Studies Unit, 2009; Zeller et al. 2011) and Mexico (Herrera Pavón 2011) also have similar problems, but local governments and non-government organizations fail to recognize its negative impact. In 1910 an active spawning aggregation of Nassau grouper (*Epinephelus striatus*) in Mahahual, Mexico was gillnetted by fishers, leaving after 1999 less than 400 reproductive individuals (Aguilar-Perera and Aguilar-Dávila 1999). In the early 1980s Belize boasted a shark fishery, but by the end of that decade the use of gillnets reduced shark abundances along with their average size (Zeller et al. 2011). In the border area of Belize and Mexico, the exploitation of bonefish by ASC fishing with gillnets and traps (locally known as beach traps) was so quick that the fishery collapsed before any landings data were ever recorded (Caballero 2002). Only anecdotes from second-generation ASC fishers indicate in mid-1900s thousands of bonefish were captured daily while on their migration run and pre-spawning location, were salted and sold for local consumption (Arceo, pers. comm; Herrera-Pavón, pers. comm). Thus, there is a large perception that gillnets are causing a decrease in abundances of recreational fish species in Belize (Perez-Cobb et al. 2014).

Another major threat in developing and Caribbean countries, like Belize, that depend on coral reef ecosystems and associated ecosystems, are development activities that result in mangrove cutting and dredging (Gibson 2011; Jones and Balderamos 2011; Perez-Cobb et al. 2014). Studies have shown that mangroves are important nursery grounds where juveniles reef fish live and grown before making an ontogenic migration through seagrass ecosystems and then to coral reef ecosystems as adults (Mumby et al. 2004; Mumby 2006; Mumby and Hastings 2008). This means that nearly all fishery species require distinct juvenile, adult and reproductive habitats (Kaufman and Romero 2011).

Bonefish inhabit tropical and subtropical mangrove creeks and lagoons of estuarine ecosystems as well as sand, seagrass and coral reefs habitats of marine ecosystems. Studies in the Bahamas (Murchie 2010) and also in the border area of Belize and Mexico have shown that bonefish make a seasonal back and forth spawning migration between estuarine and marine ecosystems (Perez et al. 2018). Thus, bonefish also require multiple ecosystems to complete its lifecycle and survive. Unfortunately, in Belize, rural and urban development negative impacts are direct results of local government's economic goals and plans of tourism expansion (BTB and MTCAC 2011), these plans which often lack focus on environmental impacts and long-term economic loss. Habitat damage results in

habitat fragmentation (Akçakaya 2000) and affects population demographics (MacKenzie et al. 2006) such as survival, reproduction, migration and distribution, because environmental conditions (Begon et al. 2006) are easily modified. Thus, coastal development has the potential to impact ecosystems and in turn fisheries that people depend on as livelihoods (Zeller et al. 2011). Because of all the above-mentioned, it is uncertain whether the bonefish population is a resilient one, if it has recovered from harvesting and if it is recovering due to development impacts on their ecosystems.

   After many decades of bonefish extraction and fishing as a protected species, there is still a paucity on bonefish population parameters. The sustainability of the recreational bonefish industry relies upon the maintenance of healthy stocks (Danylchuk et al. 2007a). When the queen conch (*Strombus gigas*) fishery was in jeopardy, the CITES Authority requested assessment and management plans to increase regulations to establish size limits, non-fishing in spawning seasons and reliable data to reduce juvenile mortality and reproductive output to improve the fisheries (Taylor and Acosta 2011). Then, modeling population demographics to inform decision making (MacKenzie et al. 2006; White 2008; Converse et al. 2009) is necessary if the bonefish fishery is to be improved. With this in mind, the purpose of this study assess the bonefish population using mark-recapture data for multi-state models for recaptures (open population) to estimate survival, recapture probabilities and movement in the Caribbean Sea and a tropical estuary shared by Belize and Mexico.

Methods

Study Area

The study area comprises two strata: Chetumal-Corozal Bay (CB) and adjacent Caribbean coast (CC), both shared by Mexico and Belize (Fig. 1). There are three recognizable seasons, although their precise duration varies yearly: cold fronts, dry, and wet. The prevailing wind direction is mostly southeast, except during the cold front season. (For further environmental data see Carrillo et al. 2009). The bay is the estuary of the Hondo River and it also receives freshwater input from other minor tributaries. Bonefish habitats consist of shallow flats with sandy and rocky bottoms, often with submerged aquatic vegetation and mangrove-lined creeks, wetlands and lagoons (Perez et al. 2018). The Caribbean coast is comprised of a backreef lagoon system (Adams et al. 2006) approximately 1 km wide from the shoreline to the reef crest (Perez et al. 2018). And depth range between 2 and 3 m, to a maximum of 6 m (Grimshaw and Paz 2004). The habitat mosaic in CC consists of sand, seagrass and coral rubble. Both regions are connected in southern Belize via the wide opening of the bay, but the most direct access between the strata here studied is the man-made Canal de Zaragoza in Mexico and the natural channels of Bacalar Chico (the international border) and Boca del Rio in San Pedro, Belize.

Sampling

We used a stratified random sampling design of two strata, CC and CB, and seasonality. Our effort was controlled by time and consisted on monthly samplings of 8 days (4 days in each country). Sampling occurred on January, June, November and December 2016; January to December 2017 and February 2018 (Table 1). Sites were less than 1.2 m deep, with sturdy sand, rock, or seagrass bottoms. Bonefish were sighted and then captured using two light-colored seine nets, each 45 m long, 1.2 m high, and 2.5 cm mesh. The fish were encircled with the seines and then taken out with hand nets and kept in a nearly submerged floating cage (1 m x 0.5 m x 0.25 m) until they were measured (fork length, FL, to the nearest mm) and tagged with a dart tag (model PDS, Hallprint, Australia) in the left-side musculature between the first dorsal pterygiophores (Boucek and Adams 2011). Only fish > 22 cm FL were tagged, the rest only measured and counted. At each site we recorded the date, time, latitude and longitude, strata (CC or CB), tag number of recaptures. Fish were handled for the shortest time possible, allowed to recover in another seine enclosure and then released *en masse* to reduce post-release mortality from predation (Adams et al. 2009); for further details, see Perez et al. (2018). During our sampling very few, less than 10 bonefish had tags that disintegrated, had fallen or were cut by anglers.

Model structure

The multi-state or multi-strata model of Brownie et al. (1993) and Hestbeck et al. (1991) is an extension of the Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965). In "typical" open population mark-recapture models, the probability of an individual being seen (i.e. recaptured) is defined by 2 parameters: probability that the individual survived and remained in the sample area (φ) and probability that the individual is encountered, with the condition on being alive and in the sample area, (p). These parameters, are also defined as a *first-order Markov process*, where it is assumed there is a transition (i.e. moving from one state to another) probability (Arnason 1972, 1973; Brownie et al. 1993; Schwarz et al. 1993). Under such a process, the probability of a marked individual being recaptured in a given state and on a given occasion is defined by 2 parameters:

φ_i^{AB} = the probability that an animal is alive in state A at time i is alive and in state B at
time $i+1$

p_i^B = the probability that a marked animal is alive in state B at time i is recaptured or
resighted at time i.

Thus, φ represents the joint probability of both surviving and making a transition from one state to another. Therefore, probabilities of survival and movement, can be separated assuming survival from time i to $i+1$ is not dependent on the state at time i+1 as:

$\varphi_i^{AB} = S_i^A \psi_i^{AB}$

where

(i) S_i^A is the probability of survival from time i to $i+1$, given that the individual is in state A at time i, and

(ii) $\psi_i{}^{AB}$ is the conditional probability that an animal in state A at time i is in state B at time $i+1$, given that the animal is alive at $i+1$.

Thus, multi-state models provide estimates of probability of survival (S) and probability of capture during an encounter occasion (p) and probability of movement from state one state to another (ψ).

Analysis

We used maximum likelihood estimates (Lebreton et al. 1992) to estimate multi-state parameters using the logit-link in the program MARK (White & Burnham, 1999; Cooch & White, 2016). We first obtained an encounter history for each recaptured bonefish, for example: A000000000BA0000, which means that a bonefish was marked in CC (labeled A) in occasion 1, was not encountered from occasion 2 to 10, recaptured in CB (labeled B) at occasion 11, recaptured again in CC (labeled A) in occasion 12 and not encountered afterwards (occasions 13-16). We estimated time interval (Table 1) between sampling occasion by dividing the number of days between an end date (e.g. for sample occasion 1) and a start date (e.g sample occasion 2) by 31 (days) to get a ratio. Each encounter history consisted of 16 sampling occasions and 15 unequal time intervals (Table 1), was loaded in the program and specified respectively. Models were assessed using Akaike's Information Criterion (AIC) (Akaike 1973) to select the model with the lowest overall AIC (Burnham and Anderson 2002). We selected every possible combination of parameters (survival: S, probability of encounter: p, and movement: ψ), either constrained to be constant over time (.) or time-varying/time-dependent (t). Percentages of values of parameter estimates were added, then divided by 15 occasions, then multiplied by 100.

Results

A total of 9657 bonefish were marked and 605 were recovered (5.9% recapture rate). A total of 64 multi-state models were run in MARK. For each model we obtained 15 estimates of S and p for CC and CB. We also obtained 2 estimates of ψ, for movement from CC to CB and another for CB to CC. The best model (i.e., the one with lowest AIC) can be summarized as: S:CC(.), S:CB(t), p-CC(t), p:B(t), ψ: A to B(t), ψ:B to A(t). This model had an Akaike weight of 0.99991, where 37 parameters were estimated. The second top-ranked model had an Akaike weight of 0.00009 and was very unlikely to be the best model (Table 2).

Our results indicate bonefish survival in the Caribbean was constant (63.6%). However bonefish survival in CB (80.6%) varied through time. This suggests that bonefish in Caribbean (36.7%) have a higher exit rate from the population than in the bay (19.4%). Survival in the bay was below 50% (Figure 2) in 3 episodes (i.e. between occasions). Survival in CB seems to have been relatively high but constant from occasions 1 to 7 (6th January 2016-norths to 19th March 2017-dry), but there were 3 periods where survival reduced. First, survival was reduced in occasions 7 to 9 (20th March-dry to 10th June 2017-Rainy). It further reduced from occasion 10 to 12 (7th September-rainy to 6th October-rainy 2017). It also reduced from occasion 14 to 16 (29th December 2017-norths to 30th March-dry 2018).

On the other hand, the probability of seeing a tagged bonefish in the Caribbean (1.3%) and bay (11.1%) varied through time from one occasion to another (Figure 3). There were only two apparent periods when probability of getting a recaptured bonefish was high in CC: between occasion 2 and 4 (12th November 2016-norths and 9th January 2017-Norths) and 9 to 11 (10 June 2017-rainy to 6th September 2017-rainy). However, recapture probability in CB remained constant until occasion 7 (19th March 2017-dry) and since then there was a gradual; increase, with the highest in two occasions (30th February- dry to 30th March-dry 2018).

Finally, our estimates indicate bonefish movement CC to CB (1.3%) and from CB to CC (1.5%) was time-dependent (Figure 4). We observed a pattern of reduced survival for bonefish in the bay that was partly explained by their temporary migration to spawn in the Caribbean. Estimates of movement indicate there was a likely movement from CB to CC from occasion 2 (11th November 2017-norths season) to occasion 4 (9th January 2017-norths seasons). This was followed by a return movement between occasions 4 (10th January 2017-norths) to 6 (11th February 2017, dry season). There seems to have also been another movement from CB to CC between occasion 7 (19th March 2017-dry) to 9 (10th June 2017 Rainy) but followed by an immediate movement back to CB between occasion 8 (21st May 2017-dry) and 10 (30th July 2017-rainy). However, there seems to have been a back and forth movement between occasion 10 (31st July 2017-rainy) and 12 (6th October 2017-rainy). From occasion 12 to 14 (7th October to 28th December 2017) our mark-recapture effort was obstructed by 1) cold fronts that affected favorable conditions (visibility and wind) in CB, and 2) several thousands of bonefish in a site (Robles Point) at CC that made it impossible to seine to avoid obstructing a likely pre-spawning school. However, this period was followed by bonefish by movement from CB to CC between occasion 14 (29th December 2017-norths) to 16 (30 March 2018-dry).

Discussion

Our results on the survival changes produced by bonefish movement have management implications for a data-sparse bonefish fishery in the Bay and the Caribbean of Belize and Mexico. Although this study presents the likelihood of a healthy bonefish population, there is an alarming concern that migration solemnly does not explain the reduced survival of marked individuals.

Like many recapture-studies, these experiments are vulnerable to tag shedding or marked animals being missed or un-sampled (MacKenzie et al. 2006), which could have resulted in survival estimates lower than real. Migration for spawning seems to be a major cause of demographic changes of bonefish in the Caribbean and bay. Bonefish survival reduced periodically by less than 40% in the bay. This indicates more than 50% of bonefish exited our sampling area in the bay from one period to another. Individuals exit a population by migration or death. Our study suggests that the periodical reduction on bonefish survival in the bay was the result of bonefish migrating permanently or temporarily from the study site in CB to other areas of CB or CC. According to the little information on bonefish reproduction in the Western Atlantic region, migration in Florida could be between November and May-June (Crabtree et al. 1997), and spawning is likely in the Bahamas from September to March-April (Danylchuk et al. 2011).

We also found that during this period bonefish migrated multiple times to spawn in CC. In fact, bonefish in Belize and Mexico make a seasonal movement pattern from the bay to the Caribbean to spawn (Perez et al. 2018). However, this movement is temporary as they return to the bay after spawning. Then, it is also likely that bonefish migrated permanently to settle in CC, but studies from Perez et al. (2018) does not suggest any ontogenetic migration. Therefore, it also likely bonefish moved temporarily to other areas in CB.

The constant survival rate in CC is a good indication of a healthy population, even though nearly 36.7% of the fish exited the area. This can be explained by the fact that Belize's CC is a reproductive area, where the bonefish not only from Belize but also from Mexico congregate (Perez et al. 2018); this aggregation was sampled, but it is likely these individuals also exited and resulted in a low estimate of survival rate. However, if a species like bonefish is protected as catch and release, then survival in the bay should be relatively high and constant as in CC. Bonefish in the bay display a northward and southern movement pattern (Perez et al. 2018), which likely contributed to the low survival and recapture estimates. These movements, unlike those for spawning (Perez et al. 2018), are likely triggered by seasonal weather changes that result in temperature fluctuations (Perez et al. unpublished data). In fact, in some occasions our effort was affected during the norths season, as the north-western winds produced wave action that caused very turbid waters. In the Bahamas bonefish also make seasonal movements in response to temperature changes (Murchie et al. 2013).

The seasonal decline of bonefish survival can also be attributed to predation, fishing, tag and other human induced mortality. Bonefish studies suggest abundances are reduced and movement increases with presence of predators (Perez et al. unpublished data). Hence, predation is likely, producing high mortality and movement rates for bonefish in the bay. In fact, barracuda (*Sphyraena barracuda*) is a top predator that also makes seasonal inter-habitat movements to feed in the bay and Caribbean of Mexico and northern Belize (Torres-Chávez et al. 2018).

Bonefish could also be suffering by-catch mortality from fish traps in Belize and as target species with gillnets in Mexico. In fact, the migration run in the bay (Medina-Quej et al. 2009; Perez et al. 2018) also coincide with peaks of reduced survival, so these fishing methods could be contributing to mortality. The fact that bonefish is catch-and-consume in Mexico is a major concern for this recreational species. The primary reason why IUU are so common, is that both ASC and CR in Belize have undefined fisheries objectives (Medina-Quej et al. 2009). But for this to be resolved, information on the socio-economic and demographic characteristics of fishery systems are need to develop context-appropriate management approaches in developing countries (FAO 2009) like Belize and Mexico. Moreover, it cannot be refuted that habitat loss (Adams et al. 2014), increased fishing pressure from CR (Perez-Cobb et al. 2014) and boat traffic are contributing to low survival rates of bonefish. Finally, it is very unlikely tags resulted in low survival estimates because marked bonefish were recaptured two years later.

Our inferences on recaptured bonefish show the importance to fill-in gaps of knowledge of human impacts on bonefish populations. The Corozal-Chetumal Bay especially in Belize, faces increases in flats fishing boats, catch-and-consume fisheries, fishing traps, water sports, mangrove clearing and sediment dredging for filling private properties. Illegal, unreported and unregulated use of gillnets and traps in small-scale artisanal fisheries of Belize and Mexico require more attention by the scientific community, fisheries resource managers and governments.

Bio-economic models are largely applied to extractive fisheries to estimate quality/quantity, fishing effort, ecosystem availability to sustain fish species abundance of migratory and straddling stock populations (De Young et al. 2008). Resource managers, scientific community, and users of bonefish and its habits are encouraged to adopt such models to understand economic loss and gains in increase or reduced abundances in the bonefish fishery. Without more information of bonefish population parameters such as abundances, population size changes, natural mortality rates, reproductive ecology, the bonefish fishery will continue to be data-limited and received poor management and conservation decisions in developing Caribbean countries.

Table 1: Mark-recapture sampling design dates of bonefish at the Caribbean border of Belize and Mexico.

Start date	End date	Occasion	Estimate	Days	Time interval	Season
06/01/2016	15-06-16	1	-	-	-	Norths
09-11-16	11-11-16	2	1	149	4.8	Norths
02-12-16	05-12-16	3	2	21	0.7	Norths
08-01-17	09-01-17	4	3	33	1.1	Norths
26-01-17	29-01-17	5	4	17	0.5	Dry
10-02-17	11-02-17	6	5	12	0.4	Dry
07-03-17	19-03-17	7	6	27	0.9	Dry
16-05-17	21-05-17	8	7	59	1.9	Dry
07-06-17	10-06-17	9	8	17	0.5	Rainy
10-07-17	30-07-17	10	9	31	1.0	Rainy
29-08-17	06-09-17	11	10	30	1.0	Rainy
04-10-17	06-10-17	12	11	29	0.9	Rainy
03-11-17	28-11-17	13	12	28	0.9	North
27-12-17	28-12-17	14	13	30	1.0	North
20-02-18	30-02-2018	15	14	54	1.7	North
29-03-18	30-03-18	16	15	30	1.0	Dry

Table 2: Akaike Information Criterion (AICc), Delta AICc, AICc weights, model likelihood, number of parameters and deviance values for the top two ranked multi-state Cormack-Jolly-Seber models for bonefish in the Caribbean Sea and a tropical estuary shared by Belize and Mexico.

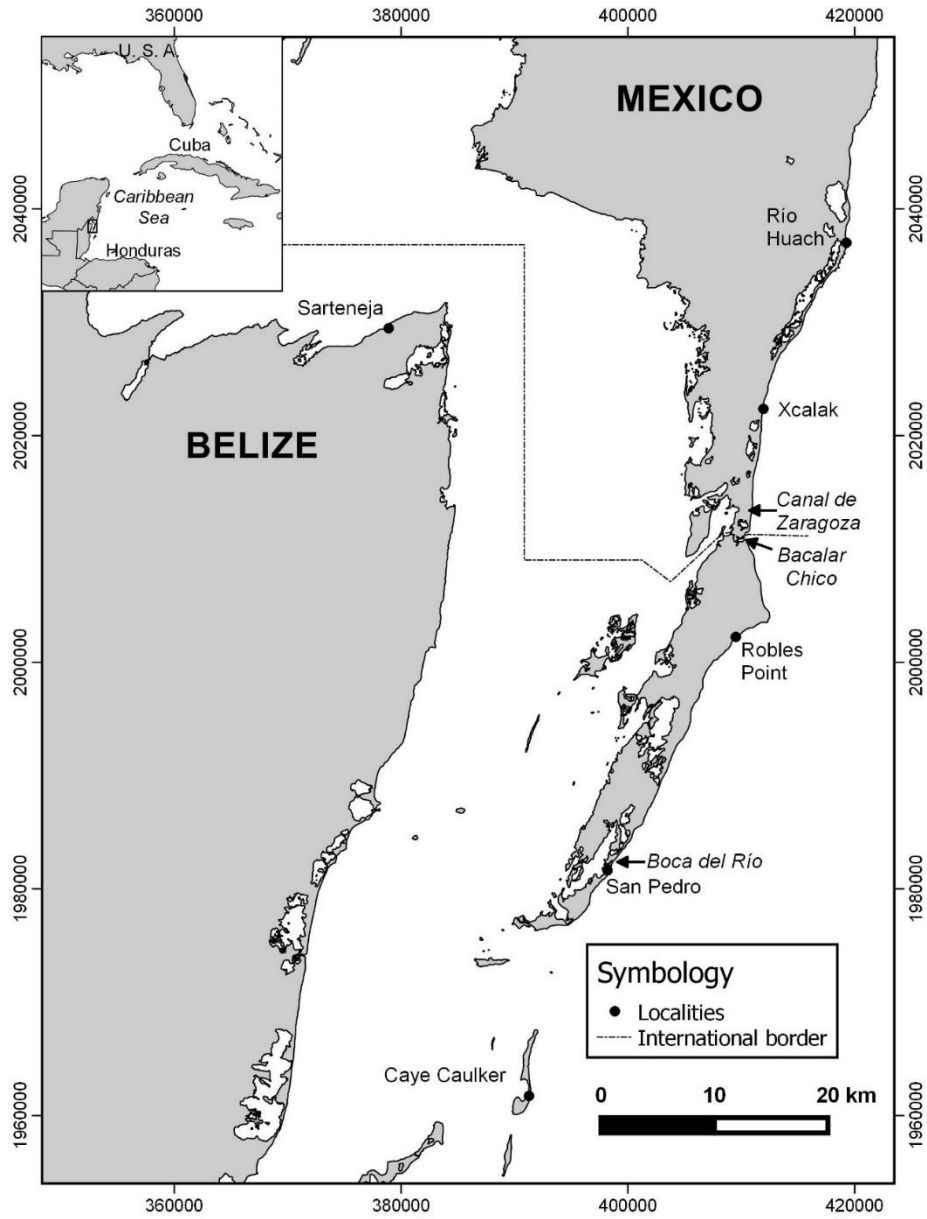| Model	AICc	Delta AICc	AICc weight	Model likelihood	No. Parameters	Deviance
S:CC(.), S:CB(t), p-CC(t), p:B(t), ψ: A to B(t), ψ:B to A(t)	11617.3861	0.0000	0.99991	1	37	1826.5323
S:CC(t), S:CB(t) p:CC(t) p:CB(t), ψ: A to B(.),ψ: B to A(.) PIM}	11635.9191	18.5329	0.00009	0.00001	34	1851.0867

Figure 1. Study area: Corozal-Chetumal Bay and Caribbean Coast, southern Mexico and northern Belize. Map processed by J. Padilla.
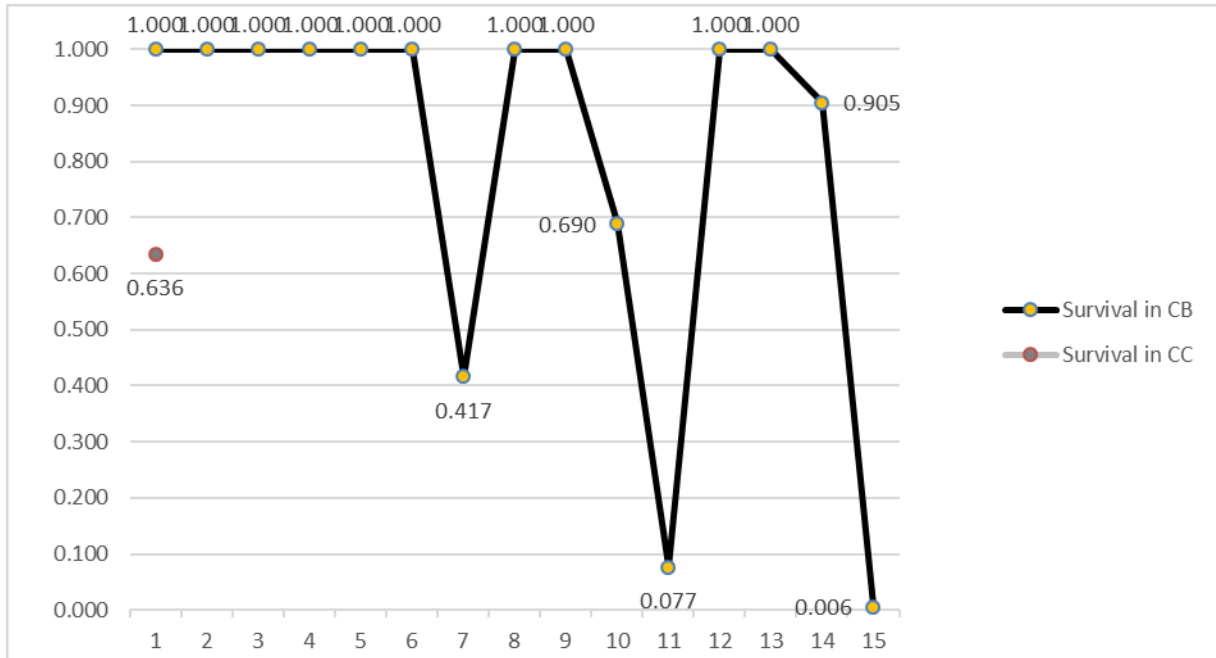
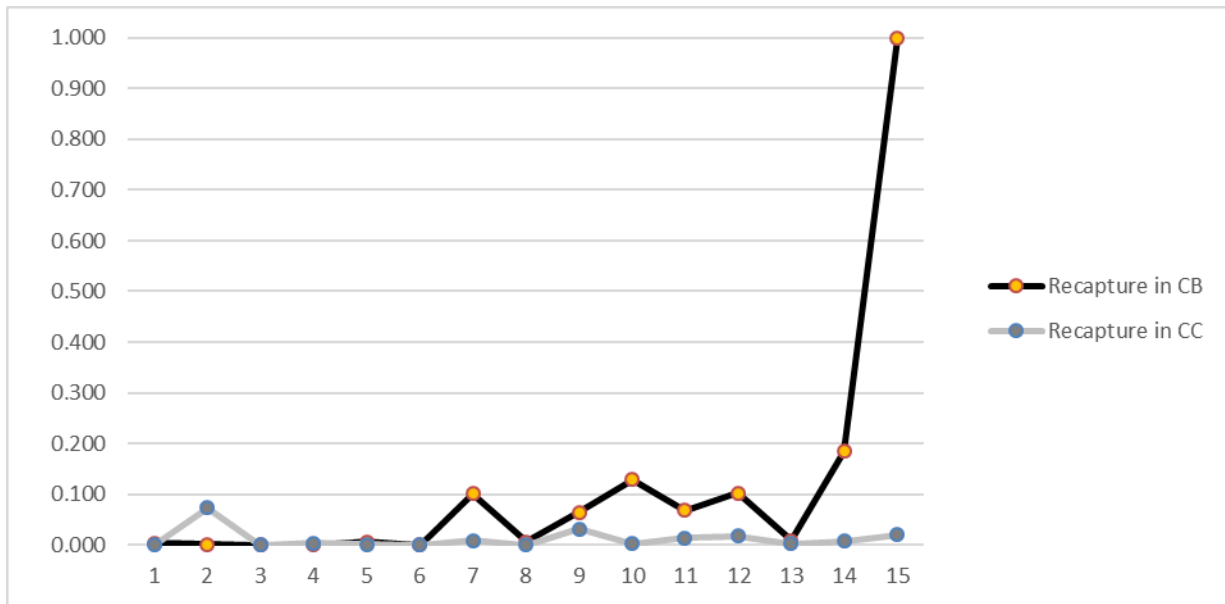Figure 2. Survival probabilities of bonefish in the Caribbean Coast (CC) and Corozal-Chetumal Bay (CB).

Figure 3. Recapture probabilities of bonefish in the Caribbean Coast (CC) and Corozal-Chetumal Bay (CB).
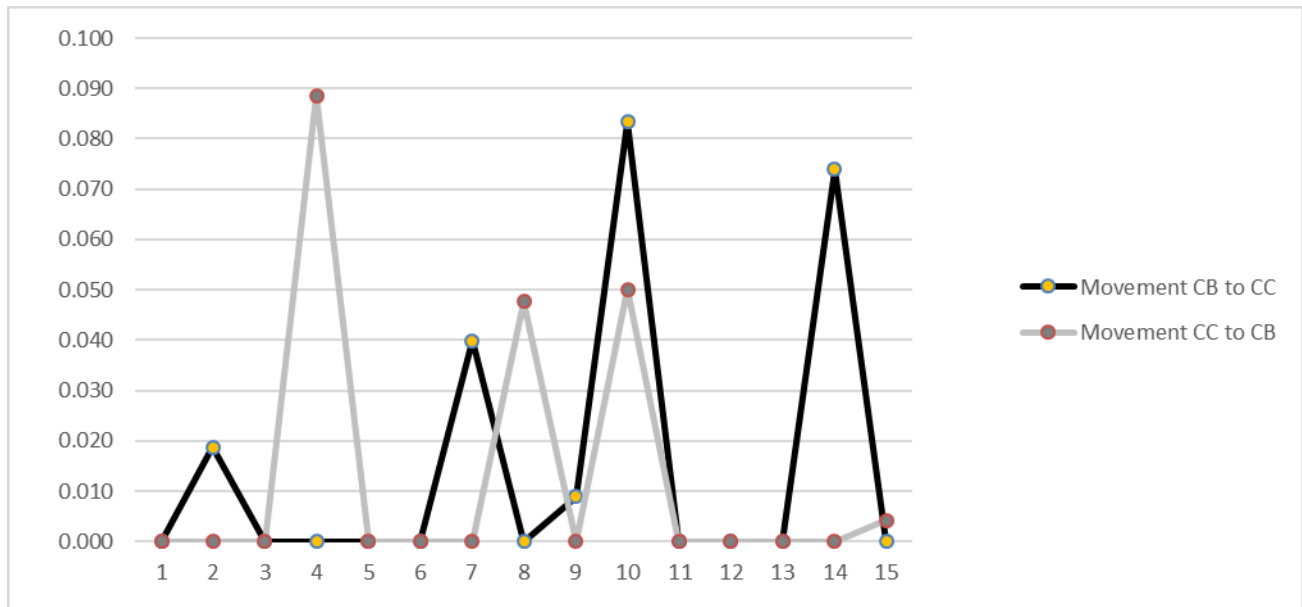
Figure 4. Movement probabilities of bonefish from the Caribbean Coast to Corozal-Chetumal Bay and viceversa.

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6.0 CAPÍTULO V

6.1 Discusión y conclusiones

Este estudio tuvo varias conclusiones. Primero, se detectó una conectividad estacional entre CC y CB relacionada con la reproducción del macabí. Segundo, los macabíes en CC fueron significativamente más grandes que en CB. Tercero, hubo varios patrones de migración relacionados con la reproducción: a) la migración desde los ámbitos hogareños a los sitios de pre-desove, b) la migración sincronizada desde el sitio de pre-desove al sitio de desove, c) la migración posterior al desove, como un retorno del sitio de desove o de pre-desove a los ámbitos hogareños. Por otra parte, se encontraron dos patrones de movimiento local: a) movimientos en los ámbitos hogareños relacionados al forrajeo, b) migración de refugio para buscar cobertura térmica en hábitats estarinos (esteros y lagunas) a las áreas costeras de CB, y c) un patrón putativo, probablemente una migración de alimentación o de exploración oportunista en asociación con variables bióticas y abióticas. Por último, se encontró que la temperatura es una variable importante asociada con los movimientos locales durante las estaciones seca y lluviosa así como la migración para la reproducción durante la temporada de nortes.

El macabí se distribuyó en ambas regiones del área de estudio. La tasa de intercambio (es decir, el movimiento) fue mayor dentro de cada región (96%) y en dirección norte-sur y sur-norte a lo largo de la costa. Sin embargo, el intercambio entre regiones (4%) dio lugar a una conectividad estacional que se produjo en las direcciones oeste-este y este-oeste a lo largo de la costa. Las diferencias significativas de tallas del macabí podría atribuirse a un cambio ontogenético desde los habitats estuarinos hacia los ambientes marinos (es decir, una migración hacia el mar a medida que crecen). Otra explicación razonable es la diferencia en los recursos alimenticios encontrados en ambas regiones. CB fue dominada por fondos fangosos y fangosos-arenosos, con pasto marino muy escaso, lo que probablemente ofrece menor cantidad y calidad de alimento, y una menor tasa de crecimiento. Los pastos marinos probablemente son escasos en CB dado que tienen poco crecimiento en los sedimentos inestables y

suaves; además están fisiológicamente estresados por la alta variabilidad de la salinidad producida por flujos de agua dulce, y el sedimento fino es frecuentemente suspendido por la acción de las olas y las corrientes, lo que reduce la luz disponible para la fotosíntesis (Hogarth 2015). Por otra parte, CC fue dominada por los fondos de pasto marino lo que explica que los macabíes fueran de mayor talla. El macabí consume una mayor diversidad de presas en los hábitats de pastos marinos (Murchie et al. 2018) y en los fondos arenosos (Colton y Alevizon 1983) que son comunes en la costa del Caribe. Por lo tanto, esto explica una tasa de crecimiento probablemente más rápida del macabí en CC.

El conocimiento local y el experimento de marca-recaptura indicaron una migración reproductiva de larga distancia. Ésta se produjo desde CB a dos sitios en la laguna arrecifal y arreciffe frontal de CC en dirección oeste-este durante la temporada de los nortes o frentes fríos (Fig. 1). Uno de estos sitios se localizó a 1 km al norte de la ciudad de San Pedro en Ambergis Caye, Belice, mientras que el otro está a más de 20 km de distancia en un área conocida como Robles Point, Belice. En este último sitio, durante el dia se observaron corridas de macabi hacia el norte en octubre y noviembre del 2016 y comportamientos reproductivas (es decir, rompiendo la superficie del agua) por un cardumen masivo (> 7,000 individuos) que migraban de forma sincrónica y en movimiento circular hacia el arrecife frontal entre noviembre y diciembre de 2017 y enero de 2018. Esta conducta se observó durante tres días después de la puesta del sol y se cree que fueron movimientos de práctica antes de migrar a desovar. Estas observaciones se realizaron entre 6 a 8 días antes de la luna llena por lo que el cardumen no fue visto otra vez y se cree que migraron a un sitio de desove cercano para reproducirse. Estas observaciones también son similares a las reportadas en las Bahamas (Danylchuk et al. 2018). Mientras el macabí de CB estaba experimentando estas migraciones de desove interregional (<13 km), el macabí dentro de CC experimentó migraciones de desove algo más cortas (+ 6 km), ambas durante la temporada de nortes. Por último, se registró otro patrón en dirección este-oeste a lo largo de la costa, como un movimiento de retorno a los ámbitos hogareños después del desove, probablemente después de la luna llena de enero de 2017 y 2018.

Por otra parte, los movimientos locales fueron en dirección norte-sur y sur-norte a lo largo de la costa (Fig. 1). Estos movimientos fueron de corta distancia y probablemente dentro de los ámbitos hogareños durante las estaciones de lluvias y secas. Durante estos periodos, la mayoría de los macabíes marcados fueron recapturados a 1 km de distancia a lo largo de la costa en ambas regiones. Lo que indica una alta fidelidad al sitio, similar a los hallazgos en las Bahamas (Boucek et al. 2018). Tambien, se encontró que los ámbitos hogareños del macabí varían según su tamaño, la región y la temporada. Por ejemplo, el macabí de tallas pequeñas presentó ámbitos hogareños más pequeños (media <1.6 km) en CB que los de mayor tamaño (media > 2.4 km) en CC. Además, estacionalmente, el macabí de la bahía cubrió distancias más largas durante la temporada de secas (<3.5 km) que en la estación de lluvias (<1 km). Por último, el macabí de CC tuvo un patrón similar, con ámbitos hogareños más pequeños durante la temporada de lluvias (media = 0.2 km) que la estación de secas (media = 6.1 km) y la estación de nortes (media = 6.4 km).

La modelación permitió identificar la temperatura como el factor abiótico más asociado con la variabilidad de la tasa de movimiento (es decir, la distancia). Esto indica que los movimientos probablemente fueron una respuesta de comportamiento a los cambios de temperatura estacional. En CB, se plantea una migración de refugio de corta distancia (esteros y lagunas de CB hacia áreas a lo largo de la costa este de CB) que habría ocurrido antes de que se registraran los movimientos cortos (<1 km) y una gran abundancia de macabíes de tallas pequeñas (< 22 cm) en lluvias y secas. Un patrón similar se observó en CC y en asociación con la alta temperatura o el flujo de agua dulce en secas y lluvias así como a las bajas temperaturas en nortes (relacionado con la reproducción). Los estudios en las Bahamas también indican movimientos asociados con el aumento de la temperatura (Murchie et al. 2011), pero no con bajas temperaturas y este comportamiento se clasifica de forma general como un movimiento. También se confirma que los varaibles bióticas como la presencia de barracuda como depredador así como variables abióticas como el tipo de fondo y la fase lunar están asociados con los patrones de movimientos. Por lo tanto, los movimientos locales fueron en su mayoría comportamientos de forrajeo para evitar la depredación, lo que también pudo haber afectado la abundancia espacio-temporal del

macabí. Sin embargo, la influencia de las tres variables se correlaciona con una migración hipotética de alimentación y evasión de depredadores así como un comportamiento de exploración en el que se registraron largas distancias (+6 km) en fases lunares con alta iluminación.

Se realizó una combinación de métodos de las ciencias sociales y biológicas para generar información que pueda ser utilizada por los administradores de recursos naturales en el manejo del macabí como un recurso compartido entre México y Belice. Es importante realizar esfuerzos similares en otros sitios de ambos países. Las técnicas de las ciencias sociales (aplicación de cuestionarios, observación participante, talleres, entrevistas y notas de campo etnográficas) fueron relevantes para desarrollar un mejor diseño de muestreo e interpretar los patrones de los datos de marca-recaptura. También fueron importantes para identificar las amenazas de conservación asociadas con el desarrollo costero. Dichos impactos obstaculizan directa e indirectamente el uso sostenible de los recursos en particular del macabí y sus hábitats en la región del Caribe occidental. Es importante que ambos países desarrollen estrategias de cooperación, así como estrategias de soluciones y acciones para encontrar un equilibrio entre el desarrollo y el uso sostenible y conservación de los recursos.
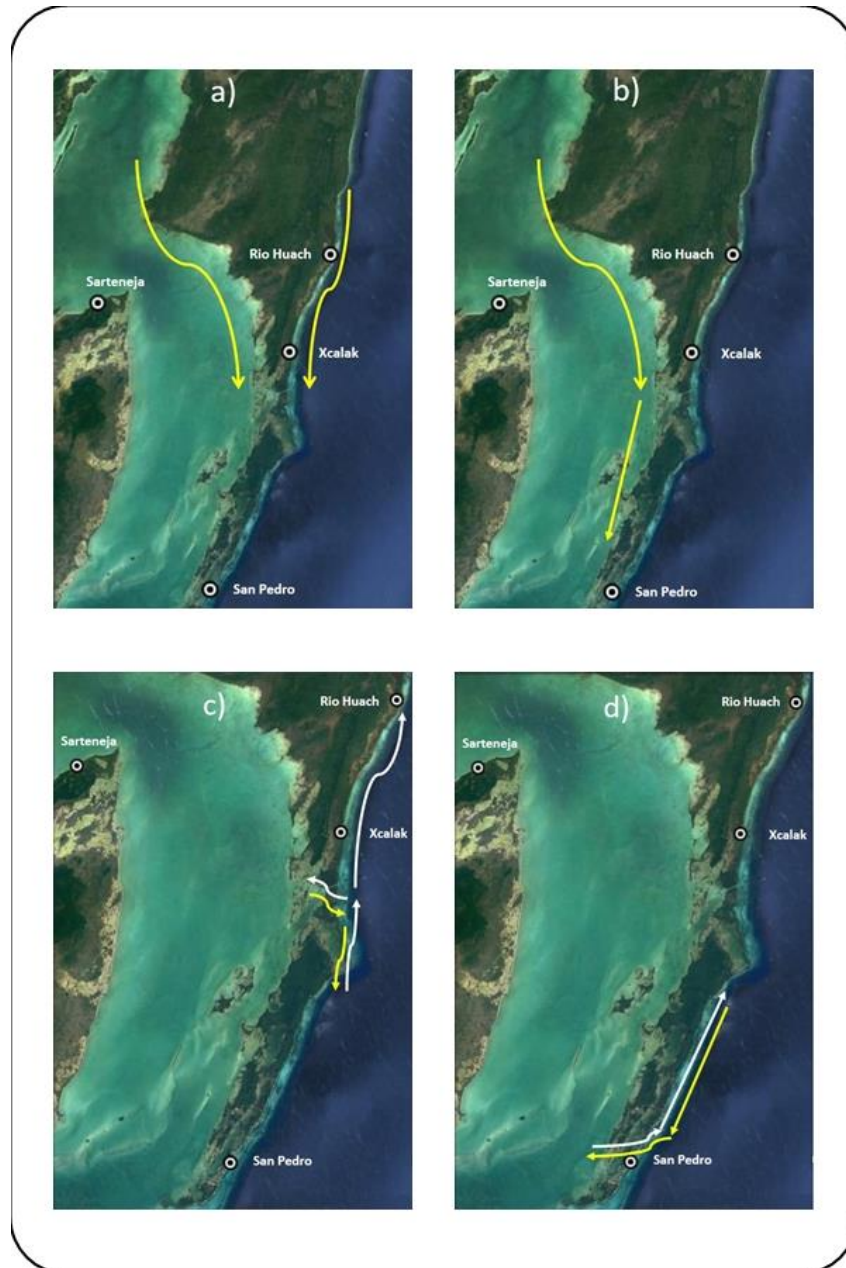
Figura 1. Patrones de movimiento en la Bahia de Chetumal-Corozal y la costa adyacente del Caribe. a) Hacia el sur a lo largo de CB y CC de México y Belice de acuerdo con LK (septiembre a noviembre); b) Hacia el sur a lo largo de CB de México de Belice (marcado en octubre y recuperados en enero); c) occidental desde el CB de México hasta el CC de Belice y hacia el sur a lo largo del CC de Belice (marcado en junio de 2016 y recuperado en diciembre de 2016), y movimiento hacia el norte a lo largo de CC de Belice, y luego hacia el este hasta CB de México (marcado en un día de enero y recuperado al día siguiente) y hacia el norte a lo largo de CC de México (marcado a principios de enero de 2016 y recuperado a finales de enero de 2016); d) al este desde CB a CC de Belice y luego hacia el norte a lo largo de su CC (marcado a principios de noviembre de 2016 y recuperado en diciembre de 2016) y una ruta de retorno similar, sur y luego al oeste (marcado en diciembre de 2016 recapturado en junio de 2017). Imágenes de Google Earth ©.

6.2 Recomendaciones

Conservación y manejo

La conectividad estacional mediada por la migración de macabí tiene implicaciones importantes para sus pesquerías en México y Belice. Ambas naciones, así como los estadounidenses que participan en la pesca de captura y liberación (CR), deben continuar colaborando en la investigación y gestión de las pesquerías del macabí en la región.

El área de Robles Point, en la costa caribeña de Belice es un sitio importante de agregación de pre-desove para ambos países (Fig. 2). Este este estudio recomienda declarar el área desde Basil Jones hasta Robles Point, Ambergris Caye, al norte de SP, Belice, como una zona especial de conservación con regulaciones particulares:

• Las guías de pesca de CR deben considerar acuerdos de manejo local que minimicen los impactos pesqueros durante la temporada reproductiva (este estudio sugiere: octubre-febrero). Auqnue se recomenda más estudios para una mejor definición.

• Los administradores locales, el gobierno y también las ONG internacionales deben: 1) considerar la educación y la concientización, el monitoreo (o más investigación) del pre-desove y la aplicación de las regulaciones de las áreas protegidas, así como las relacionadas al macabí y sus hábitats, 2) asignar el área como un área de no-desarrollo para que no se construyan muelles y se realice actividad relacionada con el agua, como el dragado que impacta los hábitats bénticos (arena, lodo, pastos marinos y corales) y la estructura y geomorfología (tala de manglares) de la línea costera, y 3) considerar la visita a través de carritos de golf y actividades acuáticas, como la natación y el esnórquel, como actividades que también podrían tener un impacto en el comportamiento del macabí durante la temporada de desove.

Figure 2. Área de Robles Point, propuesta como un área de manejo especial del macabí en Belice.

En la bahía, se recomienda que ambos países regularicen la pesca con trampas de atajo y redes agalleras, considerando:

  • caracterizar las pesquería en relación con la base de recursos y su hábitat, usuarios, artes de pesca y manejo;

  • una temporada de pesca de abril a septiembre, con octubre a febrero como un período en que se remuevan las trampas, para que no afecten la migración del macabí durante su periodo reproductivo; e

  • involucrar a los pescadores artesanales en oportunidades comunitarias, programas de modos de vidas alternativas e iniciativas de investigación para un manejo participativo.

Finalmente, se insta a los administradores de los recursos naturales y a los gobiernos de ambas naciones a:

  • definir con claridad los objetivos de pesca que incluyan la protección del macabí y sus hábitats en México y Belice;

  • prohibir el uso de redes de enmalle en todas las áreas costeras poco profundas, incluida la laguna arrecifal y el arrecife frontal en ambas naciones,

para evitar la captura incidental de peces arrecifales y en sitios de pre-desove y desove;

• actualizar las regulaciones y los planes de manejo de los santuarios de vida silvestre y las áreas marinas protegidas, e incluir una organización local que haga cumplir las regulaciones actuales relacionadas con los artes y métodos de pesca, el recurso base y sus hábitats (fondos de pastos marinos y sedimentos), la calidad del agua (es decir, fuentes de contaminación) y acuerdos regionales e internacionales de biodiversidad;

• desarrollar estrategias de formación y sensibilización bi-nacionales que se centren en los departamentos gubernamentales responsables de la administración de actividades humanas (turismo, pesca e institutos educativos) y la comunidad de usuarios; y

• por último, que las áreas protegidas en CB de Belice formen parte del Corozal Wildlife Sanctuary, para que reciban un manejo como una sola bahía.

Investigación

Se necesitan más esfuerzos de investigación para:

• caracterizar el tiempo, la ubicación y la dinámica de desove del macabí en los dos sitios identificados mediante el marcaje y telemetría acústica, así como con video subacuático;

• definir la migración estacional y los movimientos de forrajeo en una escala espacial mayor y cuáles son los detonantes ambientales relacionados a los movimientos;

• determinar la edad, el crecimiento y la madurez sexual de las subpoblaciones del macabí en ambas regiones;

• determinar los sitios de refugio y alimentación (es decir, las áreas de reclutamiento); y

• realizar investigaciones similares en otras áreas de ambos países para identificar otros sitios de pre-desove.

Con respecto a los usuarios, la importancia de la pesca de captura y liberación en México y Belice debe justificarse mediante la:

- determinación del impacto socio-económico de estas pesquerías , redes de enmalle y trampas de atajo;
- caracterización de la pesca con redes de enmalle y trampas de atajo; y
- realización de programas de educación y sensibilización.

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8.0 ANEXOS

8.1 ANEX0 1

Tabla 1. Diversidad de *Albula* spp. en la región del Atlántico Oeste y la región del Indo-Pacífico.

Especies del complejo Albulidae, genero *Albula*	Región del Atlántico Oeste (Caribe y Atlántico oeste)	Región del Indo-Pacífico (Océano Índico y Pacífico occidental)
Complejo: Albula vulpes		
A. vulpes	X	X
A. goreensis (Concido como: A. sp. B, A. garcia and A. nova sp.)	X	
A. sp. cf. vulpes	X	
A. esuncula		X
A. gilberti		X
A. glossodonata		X
A. koreana		X
Complejo: Albula argentea		
A. argentea		X
A. oligolepis		X
A. virgata		X
Complejo: Albula nemoptera		
A. nemoptera	X	
A. pacifica		X

Fuentes: Adams et al. 2013; Wallace 2014, 2015; Wallace y Tringali 2010)

8.2 ANEXO 2

Formatos de campo

Bonefish migration, habitat use, feeding and reproduction

Data Collection Form 1: Questionnaire

Kindly fill in the questions to the best of your knowledge. Your input will be helpful in ensuring a long-term sustainable management of bonefish in Belize.

Date: _____   Interviewer: _____ Place: _____

Activity: Tournament organizer ☐   Establishment owner ☐ Independent Tour-guide ☐

Sport Fisher   ☐   Establishment's Tour-guide ☐

1. GENERAL INFORMATION

1. Age:

2. Gender:

3. Owner's nationality:

4. Years in business:

5. Name of establishment:

6. Location of establishment

TAG-RECAPTURE DATA

1. Fishing Province:

Northern Belize ☐   Central Belize ☐   Southern Belize ☐

2. Main type of fishing:

Catch and release ☐   Commercial ☐   Subsistence ☐   Traditional

3. Fishing gear used_____

4. Time spent fishing: _____

5. Fish caught with tag_____ (Use separate sheet to fill in G.P.S coordinate & tag #)

6. Fish caught without tag_____

7. Based on geomorphology, the fishing was conducted in the:

Fore reef ☐   Between channels of the reef crest ☐

Back reef ☐   Close/around patch reefs ☐

Lagoon floor, less than 1.5 m ☐   Around cayes and close to mangroves ☐

Lagoon floor, deeper than 1.5 m ☐   Other: _____

Does not apply ☐

LOCAL KNOWLEDGE

1. What is the first consideration when going fishing?

Wind ☐   Sun (few cloud) ☐   Moon ☐   Tide ☐   Other:_____

Why? _____

What does it cause? _____

2. If the answer to question 1 is wind or tide go to question 3-9, if not go to question 10:

3. Where do you go to fish when the wind or tide is from a cold front?

Inside the lagoon ☐ West coastline ☐ East coastline ☐   Other: _____

4. What do you observe bonefish doing in the area mentioned?

_____

5. Are there predators during cold front?

Yes ☐   No ☐

6. Which predators are there during cold front?

Barracuda ☐   Osprey ☐   Other: _____

7. Where to you go when the wind or tide is from the south east wind?

Inside the lagoon ☐ West coastline ☐ East coastline ☐   Other: _____

What do you observe bonefish doing in the area mentioned?

_____

8. Are there predators during a south east wind?

Yes ☐   No ☐

9. Which predators are there during a south east wind?

Barracuda ☐   Osprey ☐   Other: _____

10. Have you observed fish moving fast?

Yes ☐   No ☐

Where they single or groups? _____

If yes go to go to question 6 in no go to question 9.

11. In which direction?

East towards the reef ☐   South ☐   North ☐   West towards to bay ☐

12. Which time of the year? _____

13. Is it moon related?

Before the moon ☐   After full moon ☐   Other (days): _____

14. Do you know if bonefish aggregate to spawn/reproduce?

Yes ☐   No ☐

If yes go to questions where and what time of the year?

_____ _____

Data Collection Form 2: Informal interviews

This guideline will be conducted on guides and fishers of large experience, which will be based on information from key informants. First, open interviews will be applied, but based on the situation (attitude and knowledge), closed interviews will be chosen to be applied.

Guideline to open interviews:

1. What can you tell me about bonefish reproduction?

2. What can you tell me bonefish feeding predator evasion?

3. Where (area and habitat) to do you normally fish for bonefish?

4. When you go there what do you observe bonefish doing, are they feeding, cruising or resting?

5. When you go to a place and there is no bonefish, where do you think it went?

6. What do you think caused bonefish to be absent from the area/habitat?

7. What do you think cause bonefish to be absent from the area/habitat?

8. Tell me a little about what you think of bonefish reproduction?

9. Have you observed bonefish moving single or in groups in a certain direction?

10. Where were you when you observed that and what time of the year?

11. In which direction and what do you think caused such movement?