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El Colegio de la Frontera Sur

Estrategias de vida y relaciones interespecíficas del pez león en el Caribe mexicano

Tesis
presentada como requisito parcial para optar el grado de
Doctora en Ciencias en Ecología y Desarrollo Sustentable
Con orientación en Conservación de la Biodiversidad

Por

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para obtener el grado de **Doctora en Ciencias en Ecología y Desarrollo Sustentable**

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Trabajo dedicado a la mar y a quienes la conservan

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Índice

RESUMEN

La invasión del pez león, *Pterois volitans* (L., 1758) (Scorpaeniformes, Scorpaenidae) en el Atlántico se considera una de las más dañinas para el arrecife. Las medidas actuales de control de la especie se basan en capturas directas por buzos y pescadores que deben mantenerse continuamente para obtener resultados, los cuales son efectivos sólo de manera local. En general, la elaboración de estrategias eficientes para el control de organismos no deseados se basa en el conocimiento de la historia natural y conducta de dichas especies. El presente trabajo relaciona el comportamiento del pez león con las características del hábitat y describe sus interacciones con organismos coexistentes. El estudio se enfoca en: 1) relacionar la talla de los peces león con las características ambientales y su conducta, 2) describir y estudiar los organismos que se asocian con los peces león en sus refugios y 3) reportar nuevos depredadores y consumidores del pez león en el Caribe. Los registros se realizaron en tres localidades del sur de Quintana Roo (el Parque Nacional Arrecifes de Xcalak, la Reserva de la Biosfera Banco Chinchorro y Mahahual), mediante observaciones directas subacuáticas. Las registros de depredación de pez león se hicieron en todo el Caribe de manera directa, por encuestas a manejadores, búsqueda de literatura y videos por internet. Los datos se analizaron de manera descriptiva y mediante la aplicación de un mapa de organización. Se realizaron pruebas de Mann-Whitney para evaluar si la presencia de peces león se relaciona con la presencia de otros peces. Se observaron un total de 793 peces león y se consideraron tres tipos de comportamiento: descanso, desplazamiento y cacería. Se encontró que los peces león pequeños cazan menos y durante la noche, mientras que los medianos y grandes cazan durante el día y en cualquier tipo de hábitat lo que se puede asociar a una baja depredación. También, se observaron varias especies de peces que coexisten en los mismos refugios que el pez león sin relación alguna siendo las más frecuentes *Gramma loreto, Chromis cyanea y Canthigaster rostrata.* *Gramma loreto* es la principal especie asociada al pez león se observó en grupos y asociada con agregaciones de pez león de gran tamaño. Se reportan 24 especies de depredadores/consumidores del pez león cambiando el paradigma del pez león como inmune a depredadores gracias a sus espinas venenosas y bajo número de depredadores en las áreas invadidas. La presencia de pez león puede generar asociaciones más complejas en la comunidad de peces que una simple relación de depredador-presa, actuando tal vez como cliente de peces limpiadores, o bien representando una defensa ante otros depredadores.

Palabras clave: *Pterois volitans*, especies invasoras, flexibilidad conductual, depredación, agregaciones, interacciones.

CAPÍTULO 1

INTRODUCCIÓN GENERAL

Entre las amenazas más importantes para la conservación de la biodiversidad se encuentran las invasiones biológicas (McNelly 2001). En el medio marino se han extendido ampliamente reportándose especies invasoras en el 84% de las ecorregiones del mundo (Molnar et al, 2008) Entre estas especies se incluyen algunos peces (carpas, tilapias, lobinas, plecos) que pueden causar la extinción de especies nativas, disminución de los recursos pesqueros, destrucción del hábitat y daño a las artes de pesca, lo que provoca desempleo y pérdidas económicas (Wakida-Kusunoski et al. 2007).

Entre los factores qué promueven que especies exóticas se vuelvan invasoras está la flexibilidad conductual, que permite a los organismos encontrar nuevos nichos ecológicos, y competir activamente por los recursos: alimento, refugios, o hábitats (Wright et al. 2010). Los estudios de comportamiento de peces invasores en los ecosistemas afectados permiten determinar y conocer las conductas clave para poder elaborar estrategias para su manejo, por ejemplo, diseñar trampas específicas (Thwaites et al. 2010). En México, los estudios etológicos se han aplicado en algunos casos, como el del control de insectos en cultivos de café (Hénaut et al. 2001), el control de la palomilla del nopal *Cactoblastis cactorum* en la península de Yucatán (Soberón et al. 2001; Hénaut et al. 2010) y para el control de ratas y gatos ferales en diferentes islas del Golfo de California (Aguirre-Muñoz et al. 2008).

Una de las invasiones biológicas que se ha establecido con mayor rapidez y éxito es la del pez león, *Pterois volitans (*Linnaeus, 1758) y *P. miles* (J.W. Bennett, 1828) (Scorpaenidae) en el Atlántico occidental (Schofield, 2009). Debido a que su erradicación es poco probable, a que el pez león es un depredador voraz, que en áreas invadidas consume una diversidad mayor de peces y peces de mayor tamaño que en su área nativa (Morris, 2009), desplaza a competidores por alimento (Albins, 2013), interrumpe a limpiadores (Côté y Maljković 2010) así como los posibles efectos en cascada (Albins y Hixon, 2011), la invasión del pez león en el Atlántico se considera una de las invasiones marinas más importantes (Albins y Hixon, 2013; Hixon et al. 2016)

Los primeros avistamientos de *P. miles* y *P. volitans* en el Atlántico ocurrieron en 1985 en Florida (Morris y Akins, 2009). En 2001 se reconocieron como especies invasoras establecidas en aguas aledañas a Carolina del Norte y en ese mismo año se registró al género en Bermudas (Whitfield et al*.* 2002*).* De acuerdo con lo pronosticado por Morris (2009, 2012), considerando entre otros factores su tolerancia térmica de 10º C (Kimball et al. 2004) la dispersión (de *P. volitans*) continuó hacia el golfo de México y más al sur del océano Atlántico, hasta las costas de Brasil (Ferreira 2015) En el Caribe, *P. volitans* ha ido progresando paulatinamente (Snyder y Burgess, 2007; Chevalier et al. 2008; Guerrero y Franco 2008; Freshwater et al. 2009; Claydon et al. 2009; González et al. 2009; Aguilar-Perera y Tuz-Sulub 2010; Lasso-Alcalá y Posada 2010). En nuestro país, el primer registro ocurrió en Cozumel en 2009, seguido en ese mismo año por otras localidades de Quintana Roo; un año después se reportó en Yucatán (Aguilar-Perera y Tuz-Sulub, 2010), y posteriormente en Veracruz (Santander-Monsalvo et al. 2012), Campeche (Aguilar-Perera et al. 2013), y Tabasco (Wakida-Kusunoki y Amador, 2015). En el sur del Caribe mexicano, en el Parque Nacional Arrecifes de Xcalak, se ha estimado que *P. volitans* se estableció en tan sólo tres años (Sabido-Itzá et al. 2016), y recientemente se ha reportado el primer espécimen de *P. miles* colectado en Banco Chinchorro e identificado mediante ADN mitocondrial (Guzmán-Méndez et al. 2017).

Además de su amplia y rápida dispersión geográfica, el éxito invasor del pez león se refleja en densidades más altas en la zona invadida que en su hábitat natural (0.8 ind/ha, Green y Côté, 2009) con valores, por ejemplo, de hasta 450 ind/ha en Carolina del Norte (Morris y Whitfield, 2009). En Xcalak y Banco Chinchorro se han registrado hasta 333 ind/ha (datos no publicados).

El éxito del pez león como especie invasora se debe a su alta tasa de crecimiento y reproducción (Morris, 2009), en la zona invadida el pez león crece dos veces más rápido que en su ámbito nativo (Pusack et al. 2016). Las hembras maduran alrededor de los 180 mm de longitud total (LT) y los machos a los 100 mm de LT, el desove ocurre durante todo el año aproximadamente de 2.5 a 4 días, lo que equivale a más de dos millones de huevos al año, y con un potencial de reproducción de siete años (Morris, 2009; Morris y Whitfield, 2009; Fogg et al. 2017). Las larvas se desarrollan en la superficie del océano dentro de la masa de huevos gelatinosos (Fishelson, 1975) y posteriormente entran a una fase pelágica de 25 a 40 días (Hare y Whitfield, 2003; Ahrenholz y Morris, 2010). En el golfo de México y sur de Florida la corriente de Yucatán es un factor potencial de rápida dispersión de larvas en dirección al Oeste y NO (Vásquez-Yeomans et al. 2011).

Otra característica del pez león que ha facilitado el éxito en la invasión, es la diversidad de hábitats ocupados. En su hábitat natural, Fishelson (1975) reportó a los peces león como solitarios, territoriales, dispersos en el arrecife en profundidades hasta de 170 m. Sin embargo, para el Caribe se han encontrado desde hábitats someros (Claydon et al. 2009; Barbour et al. 2010; obs pers), hasta profundos a 300 m (Bouchon y Bouchon-Navarro, 2010; Albins y Hixon, 2013). En zonas invadidas, su presencia es también común en manglares, pastos marinos, parches arrecifales (Claydon et al. 2009; Barbour et al. 2010; Biggs y Olden, 2011; obs. pers.), sistemas estuarinos (Jud et al. 2011), ojos de agua dulce en el mar (obs. pers.) y en artefactos o estructuras artificiales (Smith, 2010). No se ha encontrado relación entre la abundancia del pez león y la cobertura de coral (Lee et al. 2011), pero si se relaciona con la complejidad del arrecife (Bejarano et al. 2015) Para las Bahamas se demostró que el pez león prefiere sitios con poca energía de oleaje, además que en el día se refugian en oquedades (Anton et al. 2014). Cure y colaboradores (2012) relacionaron variables como temperatura, nubosidad, tipo de sustrato y visibilidad con la abundancia de pez león tanto en áreas nativas como invadidas, y encontraron que la visibilidad y la presencia de congéneres está relacionada positivamente con su abundancia. También identificaron que en poblaciones nativas los peces león prefieren áreas de menor complejidad y sitios artificiales. Posteriormente, se analizó en el ámbito nativo la relación entre distribución y abundancia de cuatro especies de pez león con diez parámetros ambientales, y se encontró que *P. volitans* tiene mayor plasticidad para ocupar diferentes hábitats, incluso sitios de baja salinidad y sedimentación, característica que ha favorecido su rápida invasión (Cure et al. 2014). Igualmente, este estudio mostro agrupaciones mono y pluriespecíficas para

P. volitans P. antennata, Dendrochirus zebra y D. brachypterus así como diferencias entre localidades. Por su parte McTee y Grubich (2014) informaron de agregaciones de *P. miles* en su distribución natural, mientras que *P. radiata* se describió como solitario.

No se conoce si hay variaciones del uso del hábitat y comportamiento gregario en relación a la talla (edad) del pez león. Tal información ayudaría a entender la historia natural y la estrategia de vida de la especie, por lo que en el Capítulo 2 trataremos de contestar a esas preguntas.

Otra de las características que han propiciado el éxito del pez león como invasor es su alimentación generalista (Morris y Akins 2009). Adicionalmente puede expandir su estómago hasta 30 veces su tamaño y tiene una resistencia al ayuno de 12 semanas (Fishelson 1975, 1997; Matsumiya et al. 1980). Por otro lado, en las zonas invadidas el pez león consume mayor cantidad de presas, y presas más grandes (Morris, 2009). En el Caribe mexicano se reportaron más de 40 especies de presas usando métodos genéticos (Valdez-Moreno et al. 2012). Los peces de cuerpo estrecho, solitarios, que habitan cerca del fondo, son más susceptibles a la depredación por parte del pez león que los peces pelágicos, los limpiadores o aquellos de estrategia grupal (Green y Coté, 2014). Se demostró en laboratorio que el pez león prefiere *Gramma loreto* sobre *G. melacara* (Kindinger y Anderson, 2016), aunque *in situ* es al contrario (Cobián et al. 2016). Sus estrategias de alimentación son variadas, se alimenta todo el día, pero tiene mayor actividad al amanecer (Côté y Maljković 2010), puede también cazar en emboscada, acorralando peces (Morris y Akins, 2009) o bien, descontrolando a sus presas mediante la expulsión de chorros de agua por la boca (Albins y Lyons, 2012). Por otro lado, el pez león parece ser difícil de detectar por sus presas. Lönnstedt y McCormick (2013) demostraron experimentalmente que las damiselas *Chromis viridis* no detectan a los peces león, en comparación con otros depredadores, y una respuesta similar se ha observado en situaciones experimentales e *in situ* en otras ocho especies de peces del Caribe: (*Abudefduf saxatilis, Haemulon plumierii, Halichoeres bivitattus, H. garnoti, Scarus taeniopterus, Sparisoma aurofrenatum, Stegastes leucostictus* y *Thalassoma bifasciatum)* (Anton et al. 2016). También, *Coryphopterus glaucofraenum* y *Gnatholepis thompsoni* muestran diferencias en la identificación de depredadores nativos y del pez león, siendo las señales visuales más importantes que las químicas (Marsh-Hunkin et al. 2013). No existen estudios sobre los peces león y sus presas potenciales en relación al uso de hábitat, ni sobre otras interacciones además de la depredación por lo que en el Capítulo 3 nos enfocamos sobre conocer la coexistencia entre otras especies de teleósteos y el pez león así como sus posibles relaciones.

Otro factor de éxito como especie invasiva es la ausencia de depredadores nativos debido posiblemente a que rechacen la forma inusual del cuerpo del pez león, sus espinas venenosas que cubren su cuerpo y/o que el pez león no sea visto por su coloración criptica. El único registro documentado del pez león como presa ha sido en estómagos de serránidos, *Epinephelus striatus* y *Mycteroperca tigris*, (Maljković et al. 2008). No obstante, los estudios en laboratorio indican que los meros evitan activamente a los peces león, incluso durante periodos de hambre extrema (Morris, 2009). Leung y colaboradores (2011) y Mumby y colaboradores (2011) sugieren que los meros pueden servir de agentes de biocontrol del pez león. Sin embargo, salvo la referencia antes mencionada, no hay evidencia de depredación y ésto ha sido un tema controversial (Hackerott el al. 2013; Valdivia et al. 2014) No obstante, hay información anecdótica en internet (videos); además del conocimiento local de pescadores en el sur de Quintana Roo que al bucear langosta, han presenciado que los meros consumen pez león. Por ello, en el Capítulo 4, nos propusimos sintetizar la información disponible sobre posibles depredadores y consumidores del pez león en las zonas invadidas incluyendo observaciones personales.

En relación con los posibles competidores nativos por alimento o por refugio en Xcalak se ha sugerido (Murillo Perez, 2016) que el pez león puede competir con la cabrilla *Cephalopholis cruentata* (Serranidae) por la alimentación; en la bahía de Florida se identificó que el mero *Epinephelus morio* puede interferir con el consumo de presas del pez león al presentar una conducta de defensa de refugios (Ellis y Faletti, 2016). No obstante, se requiere mayor información sobre el comportamiento y las interacciones entre presas y depredadores nativos y pez león para conocer el impacto de la especie invasora en la comunidad arrecifal.

Los estudios y las estimaciones de los efectos del pez león sobre los arrecifes en áreas invadidas apuntan a disminuciones importantes en la abundancia de la ictiofauna y efectos graves sobre la condición de los arrecifes (Albins y Hixon, 2013; Hixon et al. 2016). En el presente estudio se eligieron tres localidades arrecifales asociadas a sitios de menor densidad humana, dos de ellas áreas naturales protegidas, en la hipótesis de que al ser sitios menos perturbados puedan reflejar mejor los efectos reales del invasor.

El comportamiento del pez león es menos conocido en su ámbito de origen que en ciertas zonas del Caribe (Cure et al. 2012). Su mayor actividad la desarrolla en horas de poca luz y durante la noche, y por el día generalmente descansa en oquedades y bajo cornisas (Green et al. 2011). Cabe señalar que su visión es buena en condiciones de penumbra (Karpestam et al. 2007). La luminosidad parece ser un factor importante en el comportamiento, ya que en días nublados hay mayor actividad y búsqueda de alimento en las Bahamas. Así mismo, Cure y colaboradores (2012), identificaron mayor actividad durante horas con poca luz, aunque no vieron relación entre tiempo y éxito en la depredación del pez león por localidad, lo cual muestra que *P. volitans* tiene variaciones regionales considerables. Se desconoce si el comportamiento del pez león varía en relación a la edad, a las condiciones ambientales, a la presencia de otros organismos, o bien si existe un uso diferenciado al hábitat.

No existe hasta la fecha una descripción detallada de los refugios usados por el pez león, ni sobre su comportamiento en relación con factores ambientales o con otras especies en la región del Arrecife Mesoamericano.

Considerando el éxito y la rapidez de dispersión del pez león, se inició una estrategia de control para el Atlántico desde el 2009 (Morris, 2009). Hasta ahora la única medida posible de control es la captura directa de organismos por buzos y pescadores a, través de torneos o campañas de pesca periódicas. Los efectos solo se reflejan localmente, el esfuerzo es grande y con riesgos de picaduras de pez león (Arias-González et al. 2011; Frazer et al. 2012; Hackerott et al. 2013; Valdivia et al. 2014).

En México, desde el primer registro, la Comisión Nacional de Áreas Naturales Protegidas implementó una estrategia temprana, cuyas actividades se centraron en la difusión del problema y la captura de individuos. Posteriormente, las acciones se desarrollaron dentro del marco regional del Caribe con nueve ejes fundamentales incluida la investigación aplicada (Gómez-Lozano et al. 2013).

De 2009 a 2014, en las tres localidades en donde se desarrolló este trabajo se efectuaron capturas continuas por los pescadores, prestadores de servicio, y guarda-parques, enfocando los esfuerzos en las zonas de pesca y de manera ocasional también en las zonas prohibidas para la pesca, a profundidades máximas de 30 m, Se calcula que en cinco años se extrajeron más de 7000 peces en Banco Chinchorro (García-Rivas, 2015).

Si bien las predicciones y los modelos pronosticaban un panorama desalentador con disminuciones importantes en la producción pesquera, los efectos a cinco años no fueron evidentes sobre la producción de langosta espinosa *Panulirus argus* de Banco Chinchorro (Sosa-Cordero et al. 2014). Tampoco sobre la ictiofauna de este sitio el efecto es claro, ya que las áreas de mayor densidad de peces león fueron impactadas por el huracán “Dean” dos años antes a la llegada del invasor (Priego, 2014).

Considerando lo anterior, en este trabajo, desarrollamos tres aspectos relacionados con las estrategias de vida del pez león: 1) el estudio de las variaciones del uso del hábitat y comportamiento gregario en relación a la edad (tamaño) del pez león, 2) el estudio de sus interacciones con otros organismos en sus refugios y 3) sus posibles nuevos depredadores.

OBJETIVO GENERAL

Conocer las estrategias de vida del pez león y sus interacciones con otros organismos en el arrecife.

OBJETIVOS PARTICULARES

1. Describir la conducta del pez león en relación con la elección y uso del hábitat en Mahahual, en la Reserva de la Biosfera Banco Chinchorro, y en el Parque Nacional Arrecife de Xcalak, Quintana Roo, México.
2. Conocer los horarios de actividad del pez león en relación con características bióticas y abióticas del medio, el hábitat y su uso.
3. Identificar los organismos que ocupan el mismo hábitat y pueden interactuar con el pez león.
4. Explorar la existencia de posibles depredadores de pez león.
5. Hacer recomendaciones de manejo basadas en la información etológica de la especie.

CAPÍTULO 2

Age-dependent strategies related to lionfish activities in the Mexican Caribbean

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SOMETIDO A

Environmental Biology of Fishes

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Abstract

Lionfish are successfully invasive predators that inhabit a large range of habitats in the Caribbean region. Our study in the Caribbean has focused on the relationship between the biological characteristics of lionfish particularly their age and their activities and the use of those in the different habitats. In this study, we observed a high number of lionfish individuals, focusing on the behavioural activities and biological traits in relation to the different habitats and environmental characteristics. We monitored 793 individuals, recorded their activities, biological traits, and habitat characteristics. Our results demonstrate that lionfish are not solitary and frequently form groups for many activities. For the first time, we have provided evidence for the differences of lionfish habitat use according to activity, and age of individual fish. Coral reefs appear to be the preferred habitat of older and larger individuals, whereas the younger lionfish use a diversity of habitats, ranging from mangroves to coral reefs. In addition, this study suggests that predation of lionfish is an age-dependent strategy, that also depends on the time and the tone of the environment. Lionfish use not only the head-down posture to catch prey but also horizontal and head-up postures. It was observed that the smaller lionfish hunt mainly in dark areas and during the night while the larger fish hunt mainly during the day and in clear areas. These new aspects of lionfish ecology and behaviour are discussed in light of their invasive success.

Keywords: invasive, group, habitat characteristics, hunting behaviour, refuge, Scorpaenidae

Introduction

Lionfish, *Pterois volitans* L. 1758 (Scorpaeniformes, Scorpaenidae), is an invasive species in the Caribbean that can cause serious damage to reef ecosystems (Albins and Hixon 2013). It occupies a wide range of habitats such as mangroves, sand, barrier reefs, lagoons, and has also been reported in man-made structures and docks (Jud et al. 2011). These carnivorous fish eat small reef crustaceans and fish (Valdez-Moreno et al. 2012). The importance of crustaceans in their diet is inversely proportional to the size of the fish, where the larger lionfish prey almost exclusively on teleost fish (Morris and Akins 2009). Lionfish represent an important competitor for native carnivores (O'Farrell et al. 2014; Raymond et al. 2015), reducing the recruitment of reef fish by up to 79% (Albins and Hixon 2008) as well as the invertebrate population (Albins and Hixon 2013). Recent studies on the relationship between lionfish and its possible predators suggest that they are not efficiently controlled by sharks or large groupers, and that direct capture by fishing remains the best control measure to decrease its abundance (Hackerott et al. 2013; Valdivia et al. 2014). Currently, direct capture by divers and fishermen is the basic control method, which has resulted in great effort with poor results (Barbour et al. 2011; Frazer et al. 2012).

In their original environment, lionfish are able to adopt to a wide range of habitats (Albins and Hixon 2013). For example, Cure et al. (2014) showed the plasticity of lionfish to water visibility in Guam Island (US territory in the western Pacific Ocean), *P. volitans* is associated with low water visibility, while in the Philippines it is more often found in clear water in reef-associated habitat. Bejarano et al. (2014) showed that reef complexity may influence the abundance of lionfish which tend to choose sites with high density of prey when they hunt. Anton et al. (2014) show that in the Bahamas, the lionfish prefer sites that have a low degree of exposure to wave energy, and during the hours of strongest daylight they take refuge in protected shelters. Lionfish is also an opportunist and generalist hunter (Layman and Allgeier 2011) that seeks its prey during hours of low light intensity (Green et al. 2011). Even if lionfish are generally considered as solitary (Fishelson 1975), they may predate in groups during cooperative hunting (Lönnstedt et al 2014). Many authors mention that lionfish hunt preferably at low light intensity (Green et al. 2011). Fishelson (1975) mentioned that in the Red Sea, predation is a nocturnal activity for lionfish. In the Caribbean, other authors observed that the foraging activity occurs around sunrise and sunset, and that lionfish are inactive the rest of the time (Green et al. 2011; Green and Côté 2014). Fishelson (1975) describes that lionfish use their pectoral fins to flush fish and benthic invertebrates into their mouths. Lionfish also blow a jet stream of bubbles to mimic a current, tricking fish into swimming headfirst into their mouths (Albins and Lyons 2012). Jud and Layman (2012) investigated lionfish in an estuary in Florida, finding a pattern of site fidelity.

In a large variety of fishes, differences in use of habitats are related to the size of the fish, which generally reflect the age and activities, principally for reproduction, feeding and predation. For example, in the Caribbean, several species of fishes use mangrove and seagrass beds as nurseries mainly because it provides better protection against predators (Nagelkerken et al. 2001). However, according to the same authors, the dependence for a specific kind of habitat (e.g. seagrass bed, mangrove) may differ according to species. In this context, Dahlgren and Eggleston (2000) demonstrate, in the Nassau Grouper, the existence of a trade-off between growth and being predated that provokes a shift between habitats according to fish body size. Furthermore, when there is a separation between day and night activities, these can occur in different habitats or microhabitats. For example, Jadot et al. (2006) tracked the *Salema* species (*Sarpa salpa* L. 1758; Perciformes, Sparidae) and demonstrated that this fish used different habitats according to their resting or displacement activities that, to a large extent, depend on whether it is night-time or daytime.

According to Edwards et al. (2014), the size of lionfish reflect their age. Since the smallest individuals are more vulnerable when faced with predators, small lionfish may have different strategies than older and larger individuals in regard to their choice of habitats, daily activities, and social and predation behaviour.

The literature provides contradictory evidence regarding the time predation occurs, solitary or grouping behaviour, and the use of different habitats by lionfish. In order to develop adequate control strategies, it is important to identify lionfish behaviour in relation to their biological traits, particularly their size (or age), habitat characteristics and behavioural activities. To understand these relationships, we used a large variety of factors in different habitats to allow us to clarify lionfish life strategies in the southern region of the Mexican Caribbean. Furthermore, we hypothesise that behavioural activities used in a large range of habitats where lionfish were observed, may differ according to age, determined by the size of these fish, the time of day and microhabitat characteristics.

Material and methods

Collecting sites

We conducted lionfish observations between May 2013 and May 2014 in three localities in Quintana Roo State, in the Mexican Caribbean (Fig. 1): Mahahual (18°42'N-87°42'W), Banco Chinchorro Biosphere Reserve (18°44'N-87°19'W), and Xcalak Reef National Park (18°21'N-87°48'W). We recorded lionfish through direct observations by focal observation and *ad libitum* records (Altmann 1974) during one-hour SCUBA dive sessions (fins and mask were used in mangroves). We also made recordings with a GoPro Hero III ™ camera. As previous observations (personal observation, MCGR) indicated higher lionfish abundance on the barrier reef, our surveys were focused in this type of habitat, rather than on the lagoon reef, piers, mangroves and sea grasses. Dives took place between 7:00 a.m. to 21:00 p.m., to record variations throughout the day. Depth varied from 1 m to 30 m.

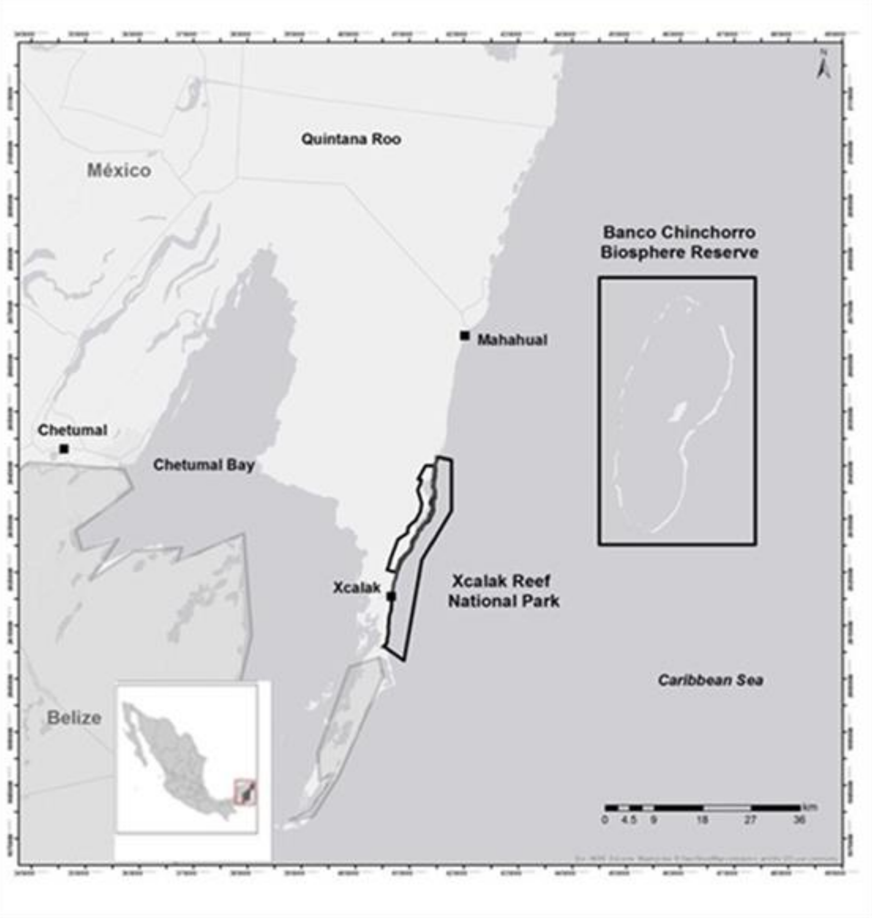

Fig. 1 Study sites used in this study in the Southern Mexican Caribbean: Mahahual, Banco Chinchorro Biosphere Reserve and the of Xcalak National Park reef.

Data collection

To optimize data collection, three observers recorded lionfish information. For each lionfish, we recorded the following behaviours and characteristics: **1)** total length of fish considering three class of sizes (small: < 15 cm, medium: from 15 cm to 25 cm, and large: ≥ 25 cm; according to Edwards et al. (2014), these sizes correspond to a fishes age where small individuals have ≤ one year , medium individuals have around two years, and large individuals have ≥ three years); **2)** coloration of fish considering three classes (dark: predominantly red, medium: equal red and white colours, and light: predominantly white); **3)** fish posture considering five categories (horizontal, sideways, head-up, head-down and inverted; see details in Table 1 and illustrations Fig. 2); **4)** behaviours at the moment of observation considering three kind of behaviour (motionless, moving and hunting; see details in Table 1); **5)** group composition considering solitary fish (when only one individual is present in a 1.5 m radius circle, or in a cave) *vs* group of individuals.

Table 1. Complete description of the lionfish behaviours and postures used in this study.

Behaviours	**Descriptions**
Motionless	Characterized by the lack of displacement, the eyes can be open or closed and the pectoral fins are relaxed
Moving	The fish swim by moving the tail with lateral movements and the pelvic fins are deployed. The fish can move along the seafloor, leaning with their pelvic fins.
Hunting	Lionfish is in head-down position, quiet and moving slowly, using the wide open pectoral fins as a shield, the caudal fin undulating, and sucking the prey with the mouth wide open

Postures	**Descriptions**
Horizontal	The fish lies prone on the floor, the pectoral fins held almost against the flanks and the body supported by the pelvic fins, or when the fish is floating on the substrate
Sideways	The fish is in lateral position, the pectoral and pelvic fins hold the walls of the natural or artificial structure
Head-up	The fish is vertical, with its head up
Head-down	The fish is also in vertical position its head down
Inverted	Used when the fish is at the top of a cavern, or any structure, in a horizontal inverted posture, with the pectoral and pelvic fins touching the ceiling

Lionfish were observed in different environments: mangrove, under docks, reef patches, and barrier reef (see details in Table 2). For each lionfish observed, we recorded the type of environment and characteristics of the microhabitat in where each fish was observed (all details were given in Table 2). Temperature, observation depth, and time were recorded using a TUSA™ IQ-800 computer.

Table 2. Complete descriptions of habitat and environmental characteristics considered in this study. Information were considered by personal dive appreciation or using a dive computer Tusa (TUSA™ IQ-800).

Features	Descriptions	Measurement method
Type of Shelter		
Simple	Open and light-toned areas in the reef (walls)	Dive appreciation
Dome or cave	Structure with a roof and two walls	
Complex	Structure with at least three walls	
Depth categories (m)		
Low	< 10	Dive computer
Middle	From 11 to 20	-
High	From 21 to 30	
Current		
Soft	When the current does not move soft coral	Dive appreciation
Medium	Soft corals leaning slightly	
Strong	Soft corals bent to 90°	
Visibility		
Low	< 2 m	
Medium	From 3 to 10 m	Dive appreciation
High	> 10 m	

Time of day		
Morning	7:00 to 13:00	
Midday	13:00 a 18:00	Dive computer
Night	18:00 a 21:00	
Light exposition		
Light	Lionfish is in area with sunlight	Dive appreciation
Shadow	Lionfish is in a shaded area	
Light along day		
Light hours	with sunlight	
Crepuscular	twilight	Dive appreciation
Dark	without sunlight	
Tonality of the substrate		
Light	the support is clear	Dive appreciation
Dark	the support is dark	
Temperature	Measured in degrees Celsius	Dive computer
Habitats		
Wall reef	Wall in frontal reef	
Lagoon	Reef formation isolated in lagoon	
Dock	Concrete piers	
Sand	Patches of sand	Dive appreciation
Rock	Rocks not covered by coral	
Mangrove	Mangrove	
Seagrass	Beds of seagrasses	

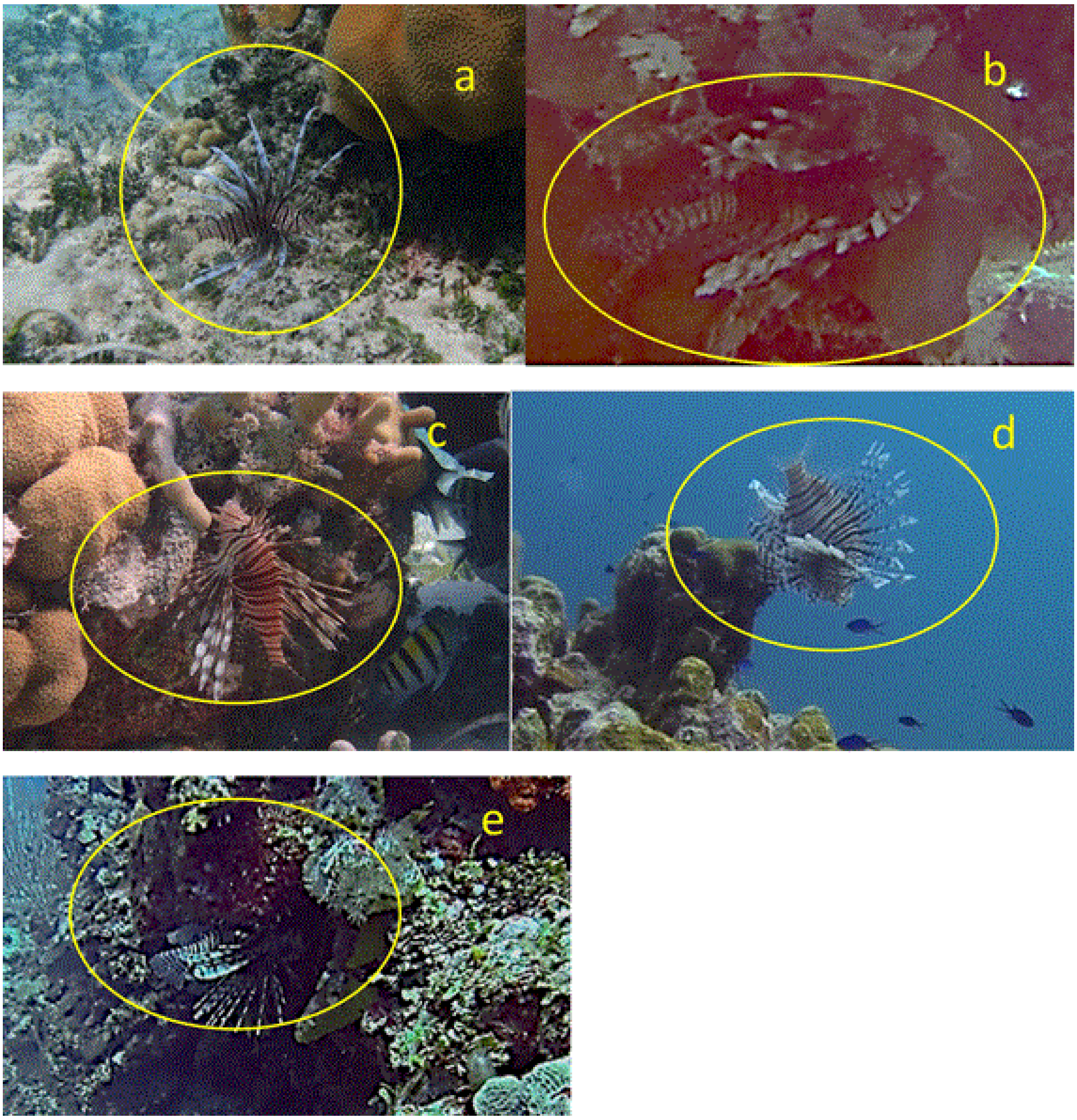

Fig. 2 Illustrations of five postures identified in this study. Horizontal (a), sideways (b), head-up (c), head-down (d), and inverted (e) (photos by Maria Del Carmen García Rivas)

Statistical analysis

A *G*-test (maximum likelihood ratio test) was used to test significance in frequencies for the following comparisons: 1) postures for each behaviour, 2) solitary *vs* group for each behaviour, 3) behaviour for each size of fish category, 4) behaviour for each fish colour. In addition, to ascertain possible relationships between activities, postures, biological traits, and environmental characteristics, we used the Self-Organizing Map algorithm (SOM, neural network).

The Self-Organizing Map algorithm (SOM; see Kohonen 2001 for details) was used to analyse non-linear data and/or variables that have skewed distributions, without an *a priori* transformation. Additionally, the SOM algorithm averages the input dataset using weight vectors and thus removes noise. These features were relevant in our study because we analysed a binary dataset with many zeros. The SOM Toolbox (version 2) for Matlab® developed by the Laboratory of Information and Computer Science at the Helsinki University of Technology (http://www.cis.hut.fi/projects/somtoolbox/) was used. The structure of the SOM for our study consists of two layers of neurons connected by weights (i.e., connection intensities): the input layer comprises 38 neurons (one per variable, but see below) connected to the 793 samples (fish), the output layer is composed of 140 neurons (visualized as hexagonal cells) organized on an array with 14 rows and 10 columns. In the output layer, the neurons act as virtual sites and approximate the probability density function of the input data. During the training, we used a mask function to give a null weight to 24 environmental variables (habitat type, habitat characteristics, time), whereas 14 biological variables or "traits" (e.g., fish activities, postures and tones) were given a weight of 1 so that the ordination process was based on the 14 biological variables only. Setting the mask value to zero for a given component removes the effect of that component on organization. The occurrence probability of a fish trait in a given area in the form of the connection intensity was visualized on the SOM map by a scale of grey, and therefore allowed us to analyse the effect of each environmental variable on the patterning input dataset (fish behaviour, traits). The map size is important in detecting the deviation of the data. Therefore, the network was trained with different map sizes (from 10 to 200 units), and the optimum map size was chosen based on local minimum values for quantization and topographic errors (for a practical example see Céréghino and Park 2009). At the end of the learning process, each individual fish was set in a SOM hexagon. Neurons that are neighbours on the grid are expected to represent neighbouring clusters of fish; consequently, fish separated by a large distance from each other, according to biological variables, are expected to be distant in the output space. A k-means algorithm was applied to cluster the trained map. The SOM units (hexagons) were divided into clusters according to the weight vectors of the neurons, and clusters were justified according to the lowest Davis Bouldin Index, i.e. for a solution with low variance within clusters and high variance between clusters.

Results

A total of 793 fish were recorded over a period of one year, of which 62 came from Mahahual, 357 from the Banco Chinchorro Biosphere Reserve, and 374 from the Xcalak Reef National Park. The great majority of individuals (81%; n = 644) were recorded during hours of daylight, 12% (n = 92) at dusk, and finally 8% (n = 57) during the night. Sixty-seven percent of fish (n = 530) were observed at low depths, 27% (n = 216) were found at intermediate depths, and only 6% (n = 47) at high depths. The visibility at day was always greater than 10 m, and the average water temperature was 28.5±1.5°C.

Relationship between behaviours, postures and lionfish characteristics

The most common and significant ($G = 606.2$, $DF = 2$, $P < 0.001$) behaviour of the lionfish was “motionless” which was observed for 75% of individuals. The “moving” behaviour was observed for 18% (n = 139) of individuals, and the “hunting” behaviour was observed for only 7% of individuals. Out of the five postures observed, the most common is the horizontal position (75% of individuals; Fig. 2a), principally observed for “motionless” and “moving” fish (Fig. 3). The sideways posture (Fig. 2b) is only observed for “motionless” fish (Fig. 3). The head-up posture (Fig. 2c) is observed for all behaviours (Fig. 3), and although the head-down posture (Fig. 2d) is observed for all three behaviours, it was generally more associated with “hunting” fish (Fig. 3). Finally, the inverted posture (Fig. 2e) is predominantly observed for “motionless” fish (Fig. 3). Our study shows that all three postures were used by lionfish while hunting; however, the head-down posture was dominant. We did not observe a significant difference (*G* = 0.2, *DF* = 1, *P* > 0.05) between the number of solitary individuals (n = 224) and lionfish moving in groups (n = 235). The number of individuals found in groups varies from two to a maximum of eight lionfish (Fig. 4). Groups of two individuals were the most frequently observed (57%). There is a significant preference to conduct hunting behaviour solitarily (66%; 31 individuals of 47) (Fig. 5). With respect to the other two behaviours, although there is a tendency for "moving" behaviour to be conducted solitarily and “motionless” behaviour to be conducted as a group, none of these tendencies is significant (Fig. 5). Even if all fish size categories present all behaviours (Fig. 6), our results show that for all size categories, all fish were observed significantly more frequently conducting “motionless” behaviour, while hunting was the least frequent behaviour.

In relation to the tone of lionfish, the majority (54%; n = 424) presented a medium tone, 25% a dark tone (n = 191) and 21% a light tone (n = 162). There is a clear dominance of medium tone fish for all behaviours (Fig. 7). However, during hunting behaviour light colour individuals were more frequent than dark ones (30.4% and 17.8 % respectively) while there were no differences between the proportion of individuals with light and dark tones for moving (26.3% and 20.5% respectively) and motionless (20.6% and 16.9% respectively) behaviours (Fig. 7).

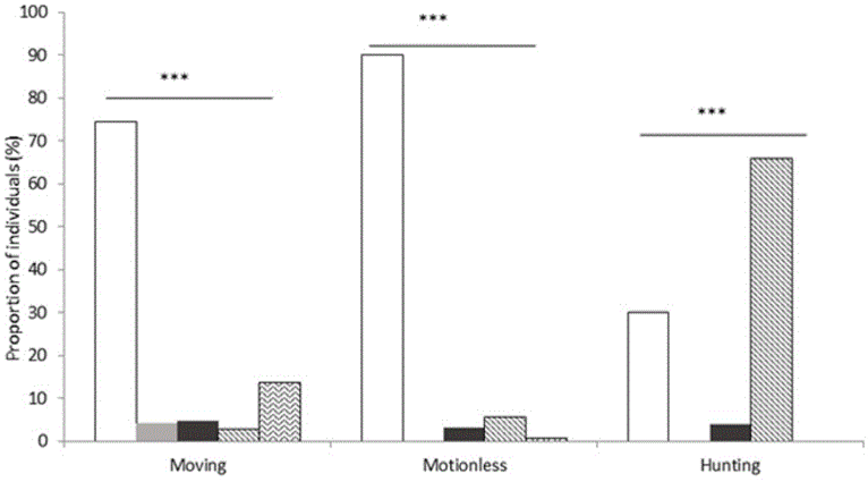

Fig. **3** Percentage of the five postures described for lionfish for each behaviour observed in the south of Quintana Roo, Mexico. Horizontal (white), sideways (grey), head-up (black), head-down (hatched), inverted (waves). Results from *G*-test for each behaviour: “motionless” (*G* = 238, *DF* = 3, *P* < 0.001), “moving” (*G* = 882, *DF* = 4, *P* < 0.001), and “hunting” (*G* = 33, *DF* = 2, *P* < 0.001)

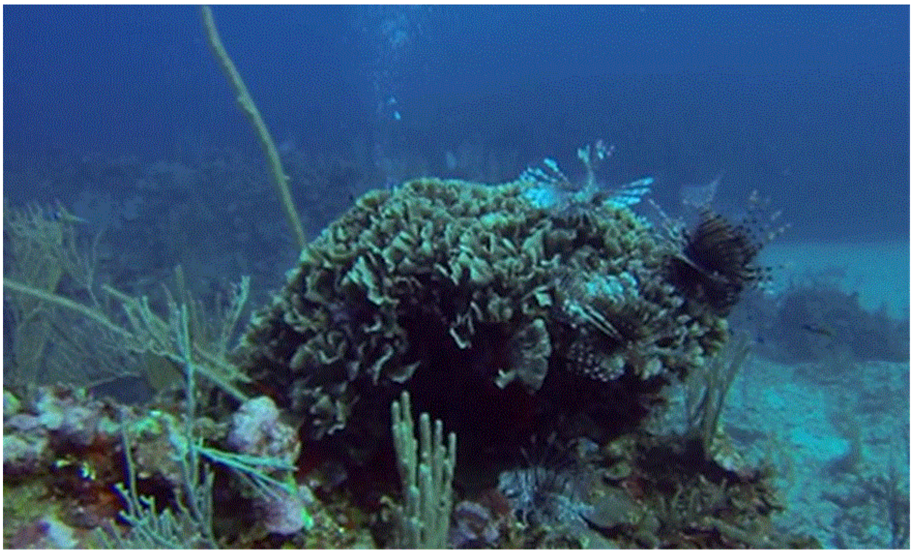

Fig. 4 Illustration of a group of four lionfish gathered around a coral head (photo by Maria Del Carmen García Rivas)

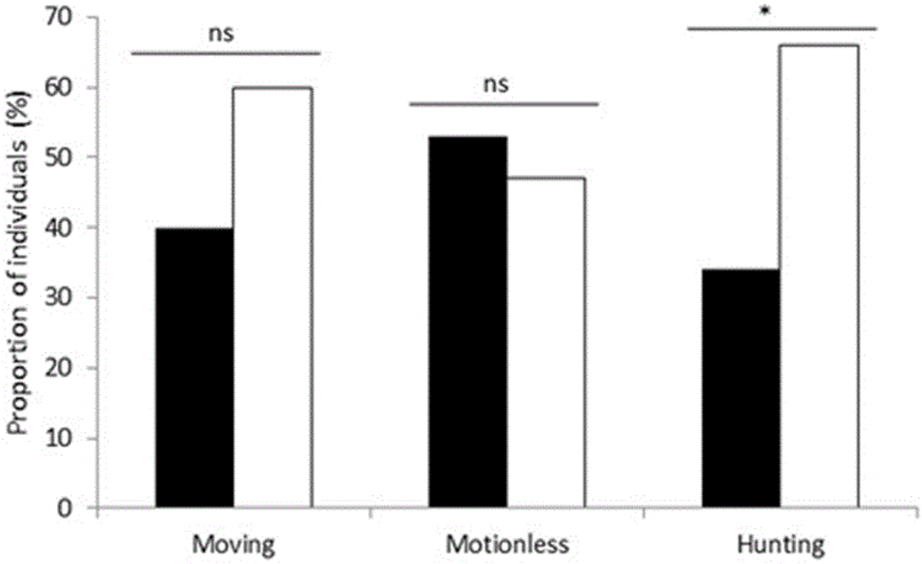

Fig. 5 Percentage of the group composition of lionfish for each behaviour. Solitary (white) and group (black). Results of *G*-test for each behaviour: moving (*G* = 3.3, *DF* = 1, ns), motionless (*G* = 1.2, *DF* = 1, ns), and hunting (*G* = 4.8, *DF* = 1, *P* = 0.002)

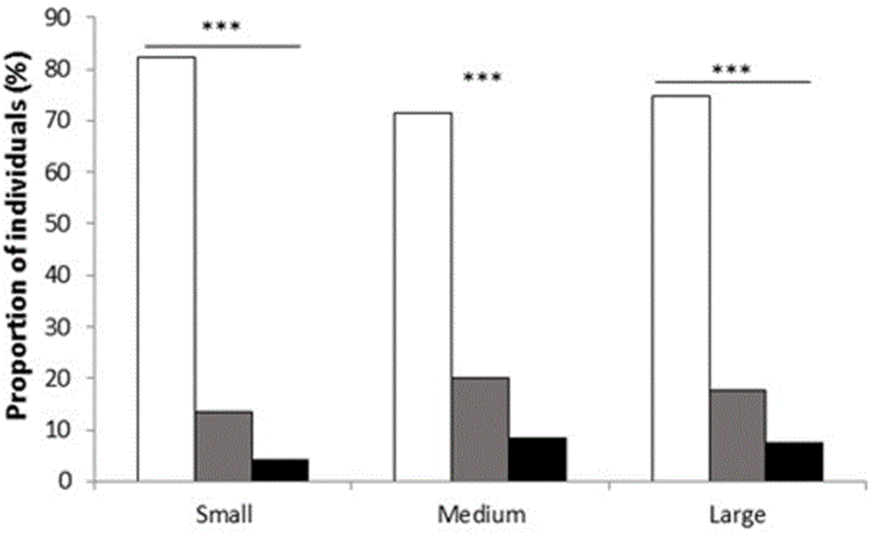

Fig. 6 Percentage of individuals conducting each behaviour for each size category. Motionless (white), moving (grey) and hunting (black). Results of the *G*-test: small fish (*G* = 236.9, *DF* = 2, *P*<0.0001), medium fish (*G* = 217.08, *DF* = 2, *P*<0.0001), and large fish (*G* = 179.2, *DF* = 2, *P*<0.0001)

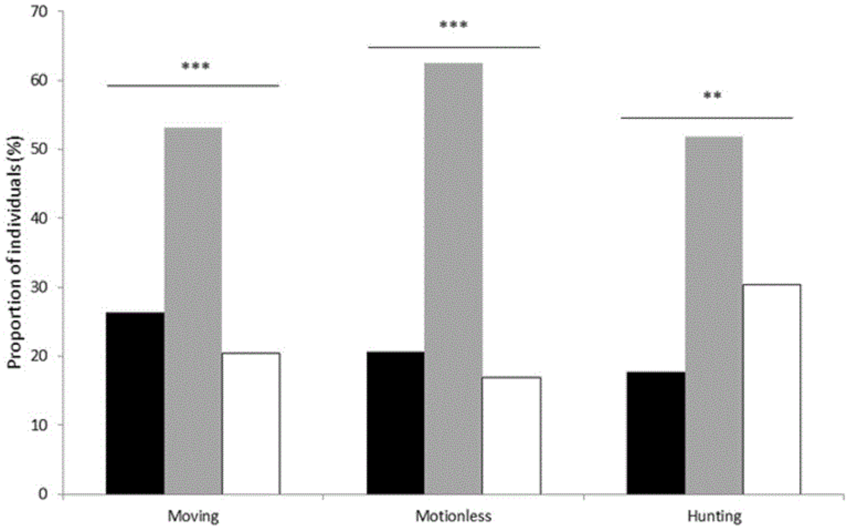

Fig. 7 Percentage of tone characteristics of lionfish, dark (black), medium (grey) and light (white) tones for each behaviour. Results of the *G*-test: moving (*G* = 48.67, *DF* = 2, *P* < 0.001), motionless (*G* = 100.7, *DF* = 2, *P* < 0.001), and hunting (*G* = 9.89, *DF* = 2, *P* = 0.007

Relationship between fish behaviours, biological traits and habitat characteristics

In our study, the large majority (85%; n = 675) of lionfish were observed in the wall reef, while only 4% (n = 33) were found in patchy reef and docks, 2% on sand and rocks, and less than 0.5% in mangroves and sea grass. We distinguish six clusters (Fig. 8A) from the SOM analysis (Fig. 8A, 8B, 8C, 8D), which allow us to relate the three behaviours identified in this study with postures, biological traits, and habitat/environment characteristics. Each behaviour can be associated with one or more clusters: "motionless" behaviour is associated with clusters A, B, C and D, “moving” and "hunting" behaviours with clusters E and F with two clearly separated groups reflecting two characteristic strategies that will be specified through SOM analysis (Fig. 8B, 8C, 8D). It appears that lionfish size is an important characteristic that separates fish into different clusters: larger fish are associated with clusters F and D; smaller lionfish are found principally in cluster B and in cluster F but in different SOM units than larger lionfish, and intermediate sized fish are regrouped in clusters A, C, E.

To clarify the complexity of SOM analysis, we will describe each cluster considering the associated behaviours, postures, biologic traits, habitats characteristics and environmental conditions. Cluster A regroups lionfish that are intermediate sized, motionless with a horizontal posture, and with dark or light tones. The fish in this cluster are present in dome structures on the reef, at a depth of between 21 and 30 meters, and during the morning. Cluster B regroups lionfish that are small, motionless, mainly in a horizontal posture, but also in inverted postures. These fish have intermediate tones. This is the only cluster that contrasts negatively with the reef habitat (white SOM units) and other habitats such as lagoons, docks, sand and rocks. In these habitats, the small lionfish are in inverted postures, observed in dome structures and mostly associated with rocks, dark support, and half-light in the morning. The SOM units associated with small fish, particularly for sand, lagoon and docks habitats are characterized by no current, low depth (< 10 m), and darkness (night and morning). Cluster C regroups exclusively intermediate size fish with intermediate tone, horizontal, sideways, head-up, inverted postures and motionless. Fish were encountered on the reef and in sea grass habitats. In reef habitats, fish were found at 21-30 meters deep, in dome structures with a wide variability of postures, while in sea grass habitat, fish were found at low depths (10 to 20 meters) and only in a horizontal posture. The cluster D regroups large motionless fish that only display horizontal postures. In this cluster, fish were found with different categories of tone, but associated with different habitats. The dark tone fish are associated with sand habitat while the intermediate and light tone ones are regrouped with reef habitats that also experience strong currents. This cluster also regroups SOM units with dark support associated with reef habitat, dome structures and intermediate tone fish. Finally, this cluster is associated with activity during the morning. Cluster E regroups exclusively intermediate size lionfish with intermediate tones, and the SOM units are clearly divided between moving behaviour in a horizontal posture, and hunting behaviour with a head-down posture, but all SOM units fit with the reef habitat. Moving behaviour is mostly associated with simple structures, and to a lesser extent with complex ones, with light substrate (clear support), low depth and during the morning. Hunting behaviour is associated with simple structures, light substrate, no current, low depth, during the afternoon, and under conditions of light. Cluster F regroups small light tone and large intermediate tone lionfish that are hunting or moving. All individuals that presented moving behaviour were in a horizontal posture while hunting behaviour fish displayed a head-down posture. However, some larger lionfish hunted with a head-up posture. In both cases, small and large fish, always hunted in complex structures and reef habitat, and to a lesser extent, small fish were observed in sand habitats. Moving behaviour was associated with simple structure in mangroves for small fish, and sand habitat for large lionfish. Small fish were also clearly associated with low depth (< 10 m), no current and dark conditions. The large lionfish were characterized by low depth when hunting. Large fish were active (hunting or moving) during the afternoon and under conditions of light, while small fish were hunting mostly during night and moving during the morning. All large fish were associated with light support (clear substrate) and simple structure when moving, and mostly with complex structure when hunting. All of these results are presented in Table 3.

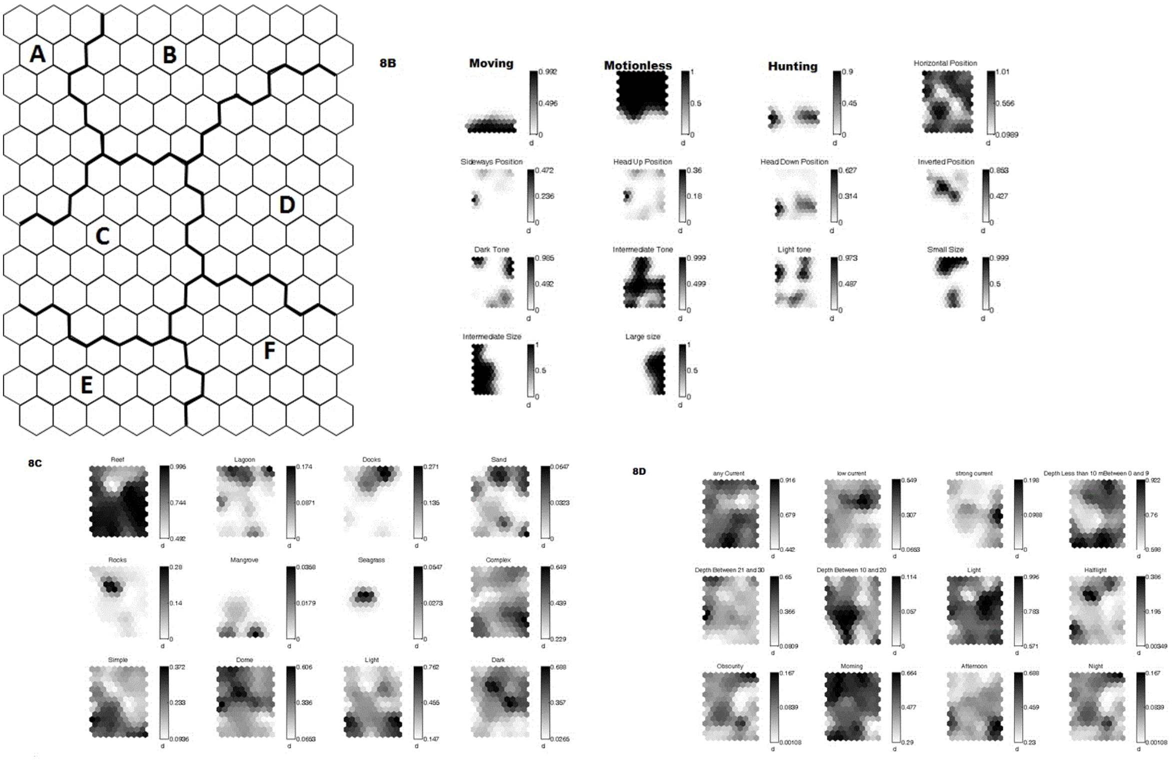

Fig. 8 Classification of all lionfish to establish a congruent relation between behaviours (see table 1 for description of behaviours and postures), biological traits (see material and methods for description), and habitat/environmental characteristics (see table 2 for description of the characteristics) using the Self-Organizing Map algorithm (SOM). Number of clusters construct by SOM analysis (a), SOM map for postures, biological traits and for lionfish behaviours (in bold) (b), SOM map for habitat characteristics (c), and SOM map for environmental characteristics (d)

Table 3. Synthesis of SOM results for all behaviour identified in this study (hunting, moving and motionless) considering the important factor of individual size (large, medium and small).

Size of lionfish	SOM results for fish traits, habitat and environmental characteristics
	HUNTING BEHAVIOUR
Large	Intermediate tones, head-down or head-up postures Reef habitat with complex structures, on light substrate at low depth Afternoon in light conditions

Intermediate	Intermediate tone and head-down posture
	Reef habitat with complex or simple structures, on light substrate at low depth
	Afternoon in light conditions and with any current
Small	Light tone, head-down or head-up postures
	Reef and sand habitats with complex structure on light substrate at low depth
	Night in dark conditions and with any current

MOVING BEHAVIOUR

Large	Intermediate tones, head-down or head-up postures
	Sand habitat with simple structure on light substrate
	Afternoon in light conditions
Intermediate	Intermediate tones, and horizontal posture
	Reef habitat with simple structure on light substrate at low depth
	Morning
Small	Light tone, and horizontal posture
	Mangrove habitat and simple structure on light substrate at low depth
	Morning in dark conditions and without current

MOTIONLESS BEHAVIOUR

Large	Intermediate tones, and head-down or head-up postures
	Reef habitat with complex structure on light substrate at low depth
	Afternoon in light conditions
Intermediate	Dark or light tones, and horizontal posture
	Reef habitat and dome structures at high depth
	Morning
	Or

	Intermediate tones, and horizontal or sideways or head-up or inverted postures
	Reef habitat with domes structures at high depth (for all positions)
	Sea-grass habitat at middle depth (only horizontal positions)
Small	Intermediate tone, and horizontal or inverted postures (only in dome structures)
	Lagoons, docks, sand, rock habitats on dark substrate at low depth
	Morning (sand and docks) or night (lagoons) in dark conditions and any current

Discussion

Our results show that in our area of study, lionfish are in general more active during the day, at low depths, and appear to spend most of their time resting. The lionfish were observed at the same frequencies alone or in a group. One of the most important findings from our observations concerns differences between habitat use according to lionfish activities and their size that may be considered as equivalent to their age (Edwards et al. 2014).

The three principal behavioural activities identified for lionfish are: motionless, moving and hunting. Our study confirms that lionfish hunt mainly in the head-down posture, as observed previously by Fishelson (1975) and Green et al. (2011). Older fish, also hunt with a head-up posture, and all size of fish may also use a horizontal posture. The head-up and horizontal postures are used to describe hunting lionfish for the first time. Hunting occurs principally at low depth areas, in reef habitat, generally in complex structures, and on light substrates. Large and intermediate fish hunt during the afternoon in the light, and small or younger lionfish during the night. The latter category is the only lionfish that hunts in other habitats, specifically areas of sand. These results suggest that the hunting strategy of lionfish is size-dependent and therefore, age-dependent, where small/young lionfish use different postures, hours of the day, and sometimes different habitats than older and larger fish.

Generally, lionfish rest, and very few individuals are observed hunting. The proportions of lionfish observed hunting or resting are similar to those for the diurnal fish *Ophioblennius atlanticus* Valenciennes, 1836 (Perciformes, Blenniidae) which spend 60% of their time resting, 16.5% for territorial defence, 15% swimming, and only 8.5% hunting (Nursall 1981). Smaller lionfish spend less time hunting (Layman et al. 2014), probably related to the higher proportion of crustaceans included in their diet at this stage of their development (Morris and Akins 2009; Layman et al. 2014). This, suggests that hunting behaviour in small fish is less conspicuous than for older fish, perhaps because younger fish learn hunting techniques and are unsuccessful piscivores, a strategy also found in the bluegill sunfish *Lepomis macrochirus* Rafinesque, 1810 (Perciformes, Centrarchidae) (Mittelbach 1981). This diet switch of lionfish from a diet based principally on crustaceans to one based on fish (Morris and Akins 2009; Valdez-Moreno et al. 2012), may explain the two different size/age-dependent strategies observed in our study. Similar size-dependent diet changes have been reported for other carnivorous reef fish (Lukoschek and McCormick 2001). Additionally, lionfish favour areas with low or no current, probably to facilitate the hunt with the aspiratory system and prey detection. Hunting in open areas, under twilight conditions (as observed for medium and large lionfish), probably involves vision. Lionfish have good visual capacity (Guthrie 1986). However, when hunting, small lionfish present a tendency to remain in the dark. So, under dark conditions, other senses may be used to detect prey, such as tactile capacity or the lateral line to detect crustaceans in the coral structure as demonstrated for other scorpaenids (Montgomery and Hamilton 1996). Another hypothesis to explain why younger lionfish hunt during the night, in the dark and sometimes in different habitats than larger fish, could be that they try to avoid being eaten by larger lionfish, as suggested by stomach contents (Valdez-Moreno et al. 2012), which show a high quantity of lionfish remains in our area of observation. The complexity of the habitat is also a good natural defence against predators' detections and attacks (Crowder and Cooper 1982; Grabowski 2004). Large lionfish can also use horizontal or head-up postures as strategies for the hunting and capture of fish included in their diet (Morris and Akins 2009; Valdez-Moreno et al. 2012) in clear and open areas. These areas present a greater risk to lionfish as they are much more visible to potential predators. The head-down posture makes lionfish more vulnerable to predators in these zones while the horizontal or head-up postures allow lionfish to detect possible threats. The success of the invasion of the lionfish in the Caribbean, and the limited impact of potential native predators (Hackerott et al. 2013; Valdivia et al. 2014) may be related with these evasion strategies. The size and natural defence of larger and older lionfish allow them to display their predatory behaviour in open areas, and are more detectable by possible lionfish´ predators during the day. However, the efficacy of the defence capacities of the lionfish is not well known (Morris and Whitfield 2009).

A specific use of habitat to carry out different behaviours, such as the covered shelters for resting, is common for nocturnal reef fish such as cardinalfish (Perciformes, Apogonidae) to avoid predation (Harmelin-Vivien 1975). The marine current is a determinant factor in the behaviour of other fish species, and it can be related to the choice of staying in one place to limit the energetic cost of displacement in high marine currents (Hobson and Chess 1978). Some studies (Anton et al. 2014; Valdivia et al. 2014) demonstrate that lionfish avoid areas with high swell to limit the loss of energy necessary to maintain their position. Furthermore, some authors (Anton et al. 2014; Valdivia et al. 2014) suggest that high currents decrease hunting success because lionfish hunt by squirting water at their prey in order to confuse them, and a strong sea current would affect this hunting strategy. In fact, no hunting behaviour of lionfish was reported in sites with high currents (Anton et al. 2014).

One important and interesting result is that around 50% of observed lionfish were associated with conspecifics. Little is known about the social structure of scorpaenids. Fishelson (1975) mentions that *Pterois miles* Bennett, 1828 is a solitary animal. McTee and Grubich (2014) found a greater association among conspecifics in *P. miles* compared to *Pterois radiata* Cuvier, 1829. This association suggests an aggregative behavioural tendency, due to attraction for the same shelter characteristics, particularly during rest behaviour, as observed by *Dendrochirus zebra* Cuvier, 1829 (Scorpaeniformes, Scorpaenidae) commonly know as the Zebra lionfish (Moyer and Zaiser 1981). This association could be provide a better defence against predators during movement, also hunting in groups could increase the probability of capturing prey (Rizzari and Lönnstedt 2014). Considering that *Pterois* spp. are low-speed predators (Albins and Lyons 2012), we propose that hunting in groups may increase their feeding success. In addition, it may be possible that by staying in groups during resting, lionfish may have more chance of detecting predators as frequently observed for various animals including fish (Hoare et al. 2004). Similarly, we regularly observed these fish observing congeners and adapting their behaviour according to others lionfish behaviour when trying to capture one individual of the group (personal observations).

Lionfish can be identified by the intensity of its tone from dark to light with a majority of observed fish presenting an intermediate tone. Our results show that the dark and intermediate tones of the fish are related with inactivity on a dark background or shelter, while the light tones are related to hunting activity on a pale background. Those differences could be adaptive, as observed for some poecliids in South America (Endler 1984). Do lionfish change their tone according to activities and habitat tonalities? Different mechanisms may be proposed to explain this process: 1) physical process by the presence of melanophores, xanthophores and iridophores (Hawkes 1974), 2) physiological process, such as colour changes in parrotfish related to the hormonal level (Cardwell and Liley 1991), or 3) behavioural processes as observed for octopus (Packard and Sanders 1971). Our results suggest that lionfish change colour according to activity and site. However, further studies are needed to understand the relationship between fish tone, activities and habitat tonality. Occasionally, we observed lionfish bleaching (a change from a dark to light colour), when captured by fishermen with a harpoon (personal observation).

Our study on a large number of individuals confirm that lionfish were found in a great diversity of habitats, not only on reefs, as previously shown by Fishelson (1975), and on where they are more abundant. We found them also under docks, by rocks, sand, patch reefs, and sometimes in mangroves and seagrass beds (Barbour et al. 2010; Biggs and Olden 2011; Claydon et al. 2011; Pimiento et al. 2013), as well as coastal estuaries (Jud et al. 2011). This confirms previous results (Claydon et al. 2011) that demonstrate that lionfish adapt themselves to a great range of habitats. Barbour et al. (2010) suggest that lionfish use mangrove as nurseries. Claydon et al. (2011) proposed that lionfish move from shallow habitats to deep reefs in Turks and Caicos; however, Pimiento et al. (2013) proved in the

Bahamas that in both habitats lionfish had a similar size and diet. In our study, lionfish display the three behaviours mostly on the reef, and use other types of habitats to move, or as a rest zone, but practically never to hunt. This observation suggests that in non-reef habitats lionfish are generally in transit, looking for new reefs or similar environment. Moreover, in the Caribbean it seems that habitats other than coral reef are mostly used by younger lionfish and cannot be considered as alternative habitats but as nurseries.

Our results showed that the immobility of lionfish is related mostly to horizontal posture, and this position is usually accompanied by deployment of the pectoral fins. We agree with Fishelson (1975), that this cryptic posture hinders recognition of the Lionfish as a predator, by potential prey. Lönnstedt and McCormick (2013) demonstrated, experimentally, that damselfish *Chromis viridis* Cuvier, 1830 (Perciformes, Pomacentridae) do not detect lionfish, when compared with other predators. This could suggest that a cryptic strategy may be used by lionfish against predators and explains why lionfish have few predators in the Caribbean (Maljković et al. 2008).

Our study provides evidence of the importance of understanding lionfish behaviour and the use of its habitat to allow the development of better management strategies for this invasive species. For example, differences in habitat use between younger and older lionfish may be linked with different strategies for their management, such as capture methods or developing traps. In our area of study, this information could allow lionfish to be caught at the right moment and in the right place. Furthermore these results help explain the success of the lionfish invasion, such as an ability to use different habitats according to their age, a capability of adapting themselves to the environment in relation to foraging activity, and escaping from potential predators including cannibalism. In addition, because commonly observed in groups and not only hunting but during resting in shelters, we may expect they are also less vulnerable to predators. This group strategy may also explain the low predation that those fish suffer from potential local predators and their success as invasive species.

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Compliance with ethical standards

Conflict of interest

The authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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CAPÍTULO 3

What are the characteristics of lionfish and other fishes that influence their association in diurnal refuges?

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Abstract

In Caribbean reefs, the lion fish *Pterois volitans* is an invasive species that causes severe negative ecological effects, especially as this crepuscular predator consumes very diverse prey. Lionfish are not active during the day and stay in their refuges, sharing these spaces with various other fishes. The aim of this study is to determine which fishes are associated with the lionfish in their shelters, and what characteristics both the invasive and native species may influence and explain such coexistence between a predator and its potential prey. Through diving and snorkelling, we visited 141 lionfish refuges, mostly caves, where we observed 204 lionfish and 494 other fish from 16 native species. We recorded species and abundance, as well as lionfish size and abundance. Half of the lionfish were observed in groups and the majority were large-sized. The association with most fish species seems fortuitous, but three species, *Gramma loreto*, *Chromis cyanea*, and *Canthigaster rostrata*, were frequently observed in association with lionfish. Numerous fish juveniles, most likely *Scarus coeruleus,* were also observed together with the invasive predator. The more commonly associated fishes, particularly, *G. loreto* are mostly associated with large-sized lionfish that were found in groups. The associated fishes are also generally found in groups. *Gramma loreto* is a potential cleaner of the lionfish; the reasons for the association between these fish species and the invasive lionfish may be more complex than a simple predator-prey relationship and are discussed based on their biological traits and previously reported lionfish trophic ecology and predation behaviour.

Key words: *Pterois volitans*, invasive species, behaviour, *Gramma loreto*, predation

Introduction

Invasive species are considered the second most important cause of species endangerment and extinction (Lowe et al. 2000). The invasion of the Indo-Pacific red lionfish, *Pterois volitans* (Linnaeus, 1758) (Scorpaeniformes, Scorpaenidae) into Caribbean and Atlantic reefs can be considered one of the most damaging recent marine invasions (Hixon et al. 2016). Early studies suggest that the ecological impact of this top predator could have devastating effects in the invaded zones, due to their opportunistic and generalist feeding habits that allow high rates of predation (Meister et al 2005; Morris & Akins 2009; Hixon et al. 2016).

Hunting lionfish may herd and corner prey with their pectoral fins (Allen & Eschmeyer 1973; Fishelson 1975), or may squirt a jet of water to confuse prey before capturing them (Albins & Lyons 2012). In the Bahamas, lionfish mainly predate teleost reef fishes, invertebrates such as crustaceans (mostly shrimps), and to a lesser extent molluscs (Morris & Akins 2009). Foraging activity is mainly crepuscular (activity primarily in the transition periods around sunrise and sunset, and inactive the rest of the time) (Green et al. 2011; Green & Côté 2014). Generally, large lionfish eat fish, whereas small lionfish forage on crustaceans (Morris & Akins 2009). Lionfish feed principally on crevice-dwelling species from families Gobiidae, Labridae, Grammatidae, and Apogonidae (Morris & Akins 2009). In the Mexican Caribbean, the lionfish hunts during the night and rests during the day, generally in caves on the reef (pers. obs.). Nocturnal predation by lionfish (*P. miles* (Bennett, 1828)) was also observed by Fishelson (1975) in its natural native range in the Red Sea. In Belize, Selwyn et al. (2013) observed that the presence of lionfish affects fish prey density according to fish species, suggesting that lionfish selectively attack available prey. Furthermore, lionfish diet may vary according to habitat type, seasons, and size classes (Dahl & Patterson 2014).

Fishes have developed different mechanisms to avoid predation. Fish juvenile use chemical signals to detect potential predators (Atema et al. 2002; Mitchel et al. 2011). Karplus & Algom (1981) showed the importance of visual cues to detect predators, such as the size of mouth and the distance between eyes. Marsh-Hunkin et al. (2013) showed that both visual and chemical signals are important to detect the native Nassau grouper; Perciformes, Serranidae) and invader predators (lionfish) by two Caribbean coral reef fish (*Coryphopterus glaucofraenum* Gill, 1863 and *Gnatholepis thompsoni* Jordan, 1904; Perciformes, Gobiidae.

Lönnstedt & McCormick (2013) propose that the high success of lionfish is due to its cryptic nature. Indeed, those authors demonstrated that the damselfish, *Chromis viridis*

(Cuvier, 1830) (Perciformes, Pomacentridae) is not able to detect the visual signals of zebra lionfish (*Dendrochirus zebra* (Cuvier, 1829)), and respond only to their scent. Green & Côté (2014) described the most important prey characteristics (body size, body shape, position in the water column, aggregation behaviour) that determine the vulnerability level of fishes to lionfish predation. These authors showed that fishes that are small, shallow-bodied, solitary, resting on or just above the reef, or nocturnally active are the most vulnerable, whereas fishes with a parasite-cleaning behaviour are less vulnerable. Furthermore, they mentioned that fishes living in crevices, or under ledges, are not vulnerable to lionfish.

In the invaded area, lionfish are distributed on the reef, artificial structures, in mangroves and over seagrasses (Claydon et al. 2011). Jud & Layman (2012), in Florida, reported that lionfish are territorial and show site-fidelity. Anton et al. (2014) and Valdivia et al. (2014) mentioned that lionfish prefer complex sites without wave energy. On the reefs of the Mexican Caribbean, lionfish are frequently observed in groups (María del Carmen García-Rivas 2014, unpublished manuscript). During daytime, lionfish rest motionless in caves (refuges), where various other species of fishes (adults and juveniles) also occur, living close to their potential predator (María del Carmen García-Rivas 2014, personal observation). The presence of potential prey close to such predators is unusual, because prey are normally able to evaluate potential predator risks and avoid danger by looking for “enemy free space” in niches without predators (Jeffries & Lawton 1984).

Considering the available information, we expected that the number and size of lionfish could be a determining factor for the presence of other organisms. Also, we expected that particular characteristics of some fishes make them less susceptible to lionfish predation and thus favour their association. Consequently, our study is focused on the following questions: 1) which fishes and other organisms are present with motionless lionfish in their daytime refuges? 2) do the number and size of lionfish present in diurnal refuges influence the presence of other fish? and 3) do associated fishes have characteristics that explain why they are not repelled by the presence of lionfish?

Material and methods

Data collection

We conducted lionfish observations from 2013 to 2014 off the Quintana Roo coast, Mexican Caribbean (Fig. 1). Three sites were monitored: Mahahual (18°42'N, 87°42'W), Banco

Chinchorro Biosphere Reserve (18°44'N, 87°19'W), and Xcalak Reef National Park (18°21'N, 87°48'W). Data were obtained through direct observations of individual lionfish by SCUBA diving, and using a GoPro Hero III™ camera. We surveyed the reef at intervals and always between 7:00 h and 19:00 h, at depths from 1 to 30 m.

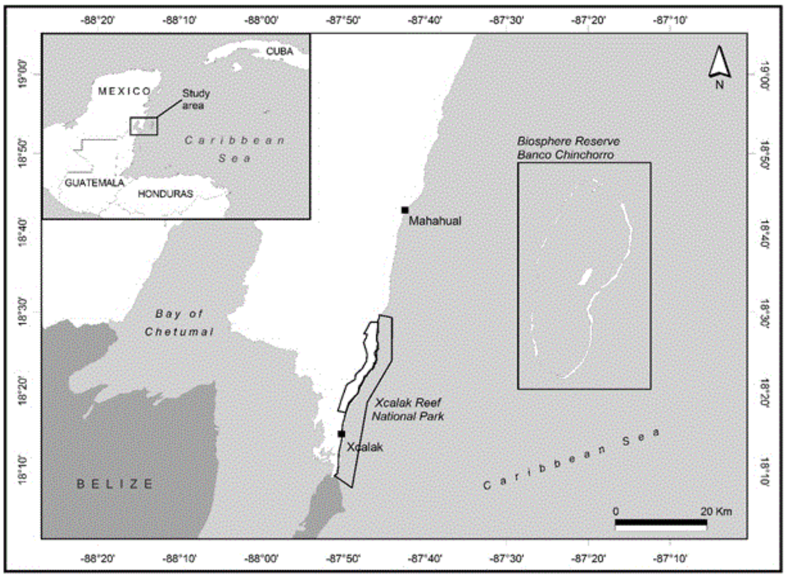

Figure 1. Areas of lionfish records used for this study: Mahahual, Banco Chinchorro Biosphere Reserve and the Reef of Xcalak National Park, in the southern Mexican Caribbean.

Only lionfish that remained motionless in their refuges were considered for this study. The refuges are caves in the reef structure with a roof and two or three walls. This standardisation of the refuge selection allowed us to minimise an effect of refuge characteristics on the presence of organism. For each cave in which lionfish were observed, we counted the number of *Pterois volitans* present and estimated their size as follows: small (< 10 cm in length), medium (from 10 to 15 cm in length), or large (> 15 cm in length). In a 0.5-m-radius area around the lionfish, we also counted and identified (to species level) the associated fish during the dive, or used the video recordings. Some adult individuals and juveniles, that could not be identified but were considered for the analyses, were labelled as 'unidentified' and 'juvenile', respectively. We also noted interactions between fishes, such as predation and cleaning.

In addition, in Xcalak Reef National Park stationary we carried out visual censuses following methods described by Bohnsack & Bannerot (1986). Here, we selected areas with and without lionfish to compare prey fish densities in the presence or absence of *P. volitans*.

Statistical analysis

The following information was recorded: 1) the proportion of lionfish found alone, in groups of two individuals, in groups of three individuals, and in groups of four or more individuals; 2) for each associated species of fish found with lionfish in the caves, we determined the number of caves where they were observed, the percentage of sites where we observed the species, the total number of individuals observed, and the mean number of individuals found per cave.

A *G*-test was used to test for significance in differences to compare: 1) the number of lionfish observed by size class, 2) the association of lionfish following their size, 3) the number of sites with lionfish which did or did not have associated organisms, and 4) the number of individuals (alone, two or three, ≥ four) of one particular associated species when present with lionfish in the caves.

We used a non-parametric Mann-Whitney *U*-test (recommended when data are not normally distributed) to compare the number of lionfish per site with and without associated organisms according to their size (small, medium, large), and we applied the Bonferroni correction to those comparisons. An χ^2- test was performed to compare the proportion of caves with and without associated organisms according to the number of lionfish present in the caves (one, two, three, and ≥ 4 lionfish), we also used the Bonferroni correction to those comparisons. The *U*-test was also used to compare prey fish density between censuses with vs. without lionfish. For all these tests, significance was assessed at $p<0.05$ with lionfish.

Multidimensional scaling analysis (MDS) was used to explore relationships among the size of the individual lionfish (small, medium, large), the number of lionfish present in a refuge (alone, two lionfish, ≥ three lionfish), and the presence of associated species. All analyses were processed with STATISTICA 7.0 or R (R Core Team 2015).

Results

During our observations we never observed lionfish predation toward another fish. On the other hand, we observed one case of cleaning behaviour of *Gramma loreto* Poey, 1868 on the left flank of a lionfish.

We observed a total of 204 lionfish in 141 similar diurnal refuges (caves): 47.5% (*n* = 97) were alone, 32.4% (*n* = 66 on 33 sites) were in groups of two individuals, 8.8% (*n* = 18 on 6 sites) were in groups of three individuals, and 11.3% (*n* = 23 on 5 sites) were in groups of four to six individuals. We observed significantly more ($G = 69$, DF = 2, $P < 0.001$) large lionfish (*n* = 113) than medium and small (*n* = 70 and *n* = 21 respectively) lionfish. Small and medium-sized lionfish were not associated with large ones (small: $G = 15$, DF = 1, $P < 0.001$; medium: $G = 32$, DF = 1, $P < 0.001$). In contrast, small and medium-sized lionfish showed a significant association ($G = 3.9$, DF = 1, $P = 0.04$): 72% of small lionfish were found with medium sized lionfish. Half out of the 141 sites where lionfish were observed ($n = 76$, 54%) were also inhabited by other species ($G = 0.85$, DF = 1, $P = 0.4$), principally fishes ($n = 494$), and a few shrimps ($n = 2$) at only one site.

Regarding the effect of lionfish size on the number of lionfish present with or without associated fishes (Fig. 2), for small and medium lionfish there were no significant trends, while for large lionfish we observed significantly more lionfish individuals when other fishes were present ($U = 246$, $P = 0.01$).

The analysis of the influence of the number of lionfish individuals per site (caves) on the presence or absence of associated fishes (Fig. 3) showed that the presence of just one lionfish in the caves has no influence on the presence or absence of other fish, while when two lionfish were present in the caves we observed significantly more caves with than without associated fish ($\chi^2 = 8.77$, DF = 1, $P = 0.003$). Few refuges with three or more lionfish were observed and were not be included in the analysis.

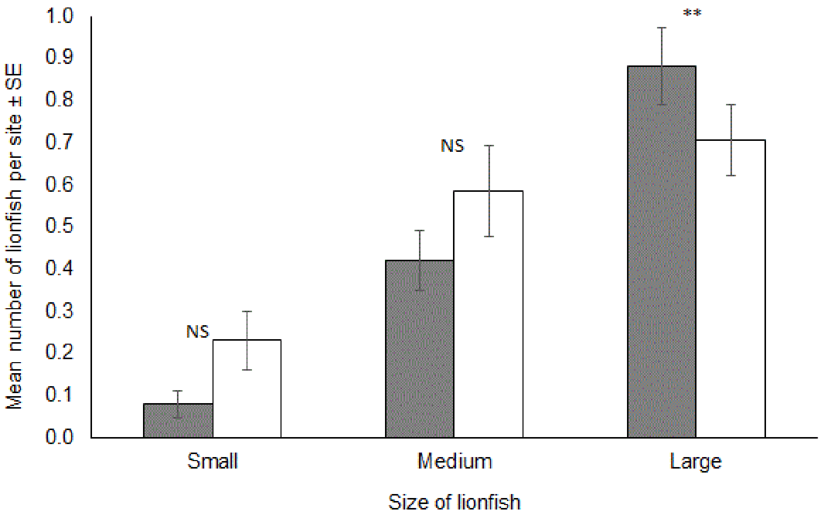

Figure 2. Mean number and standard error of lionfish per diurnal refuge according to their sizes with associated organisms (grey) or without presence of organisms (white). Mann-Whitney *U*-test, NS for not significant, ** $P < 0.01$.

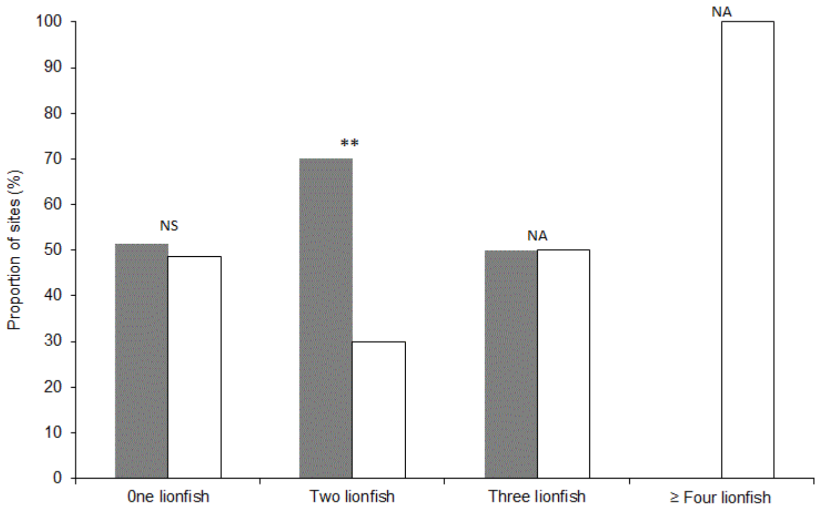

Figure 3. Proportion of sites with lionfish with associated organisms (grey) and without associated organisms (white) for solitary lion fish for lionfish found in groups of two, three or four or more lionfish. Chi-Square test: ** $P < 0.01$, NS for not significant, NA for not applicable.

24 % of all refuges occupied by lionfish were also occupied by *Gramma loreto* (Perciformes, Grammatidae), and 11% by *Canthigaster rostrata* (Bloch, 1786) (Tetraodontiformes, Tetraodontidae) or *Chromis cyanea* (Poey, 1860) (Perciformes, Pomacentridae). Fish juveniles and other fish species were not commonly observed with lionfish (Table I). The presence of lionfish did not negatively affect the presence of other fishes. In the presence of lionfish, the density of *G. loreto* was 0.545 (individuals per stationary census), vs. a density 0.347 fish per census without lionfish, a non-significant difference ($U = 337$). Comparing the data with and without lionfish for several other species, we never observed a negative effect of the presence of lionfish on other fishes: e.g. *C. rostrata* (2.34 with vs. 1.49 without, $U = 362$, ns), *Acanthurus coeruleus* Bloch & Schneider, 1801 (0.418 with vs. 0.778 without, $U = 231$, ns), or *Thalassoma bifasciatum* (Bloch, 17891) (1.297 with vs. 2.159 without, $U = 191$, $p = 0.06$, ns).

We observed between 1 and 13 *G. loreto* individuals, with a mean of 2.5 lionfish per site (Fig. 4 and Table I). *Gramma loreto* was the most frequently found species associated with lionfish, and was present significantly more often in groups than alone (Fig. 4). *Chromis cyanea* was present in refuges with lionfish in abundances of 1 to 11 individuals, clearly associated in groups and rarely alone (Fig. 4). Although *C. rostrata* was present in a high proportion of refuges with lionfish (21%, Table I), it is mainly found alone or in small groups (Fig. 4). *Scarus coeruleus* (Edwards, 1771) (Perciformes, Scaridae) and *Diodon hystrix* Linnaeus, 1758 (Tetraodontiformes, Diodontidae) were present at a low number of sites inhabited by lionfish (7% and 1% respectively; Table I) and significantly more were found in large rather than small groups or alone (Fig. 4). All other fishes were found at a very low number of sites, alone or in small groups (Table I and Fig. 4).

Table I. Information of fish and shrimp species associated with lionfish in 76 diurnal refuges in southern Quintana Roo reefs, Mexican Caribbean. Only refuges in which at least one organism was associated with lionfish were considered. n_S: number of sites where species was found, %: percentage of sites containing the species, n_F: number of species individuals observed, mean (± SE): mean number of fish from species observed per site. Furthermore, we added information from available literature concerning predation and recruitment; a: from Valdez-Moreno et al. (2012), b: Morris & Atkins (2009), c: Green et al. (2011), d: Selwyn et al. (2013), -: not reported as prey, +: low predation, ++: commonly predated, R+: recruitment positively affected, R-: recruitment negatively affected, Rn: Recruitment not affected by lionfish, ?: no information available.

	This study				Information from literature			
					Predation			Recruitment
Fish species	n_S	%	n_F	Mean (± SE)	a	b	c	d
Gramma loreto Poey, 1868	34	45	86	2.52 (± 0.4)	+	++	-	Rn
Chromis cyanea (Poey, 1860)	16	21	59	3.68 (± 0.6)	-	+	-	R-
Canthigaster rostrata (Bloch, 1786)	16	21	25	1.56 (± 0.2)	-	-	+	?
Scarus coeruleus (Edwards, 1771)	5	7	34	6.8 (± 3.4)	-	-	-	?
Thalassoma bifasciatum (Bloch, 1791)	4	5	11	2.8 (± 1.0)	++	++	+	R+
Stegastes adustus (Troschel, 1865)	2	3	7	3.5	-	-	-	Rn
Apogon phenax Böhlke & Randall, 1968	2	3	4	2	-	-	-	?
Diodon hystrix Linnaeus, 1758	1	1	25	25	-	-	-	?
Halichoeres bivittatus (Bloch, 1791)	1	1	3	3	-	+	+	R-
Haemulon flavolineatum	1	1	2	2	+	-	+	?

(Desmarest, 1823)								
Halichoeres garnoti (Valenciennes, 1839)	1	1	1	1	++	++	-	R+
Fish Larva	6	8	55	9.1 (± 3.1)	?	?	?	?
Shrimp species								
Cinetorhynchus rigens Gordon, 1936	1*	1	2	2	-	+	?	?

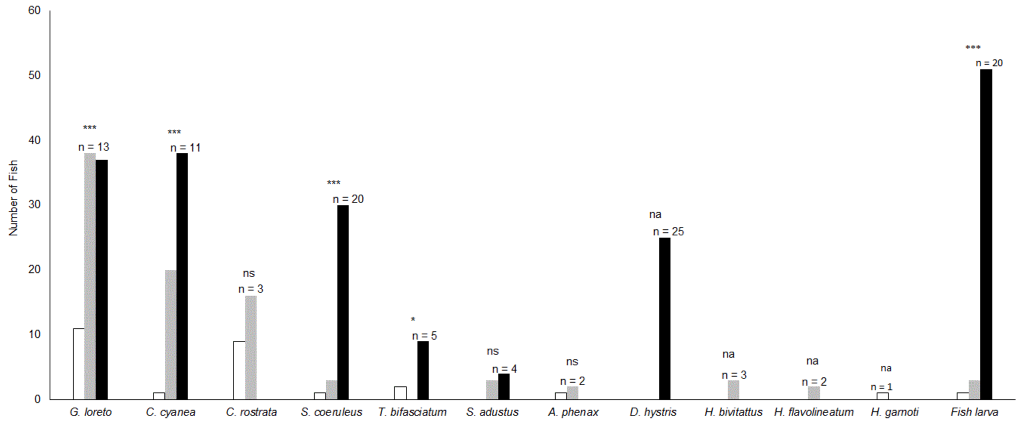

Figure 4. Total number of solitary (white), small groups (two or three individuals, grey) or large groups (four and more individuals, black) of different fish species associated with lionfish in their refuges. *G*-tests: ns for not significant, na for not applicable, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. The numbers on the top of black bars represent the maximum number of fish observed in a refuge with lionfish.

The first dimension of the MDS analysis (Fig. 5) characterised the number of lionfish present and the size of the lionfish, while the second dimension separated the small lionfish (negative side) from the large ones. The three more abundant and frequently associated fishes, *G. loreto, C. cyanea*, and *S. coeruleus*, were mainly found with groups of lionfish (two or three); *C. cyanea* and *S. coeruleus* were both associated with large lionfish, whereas *G. loreto* did not show a clear preference for a particular lionfish size. The other abundant associated fish, *C. rostrata*, was clearly associated with medium-sized, solitary lionfish.

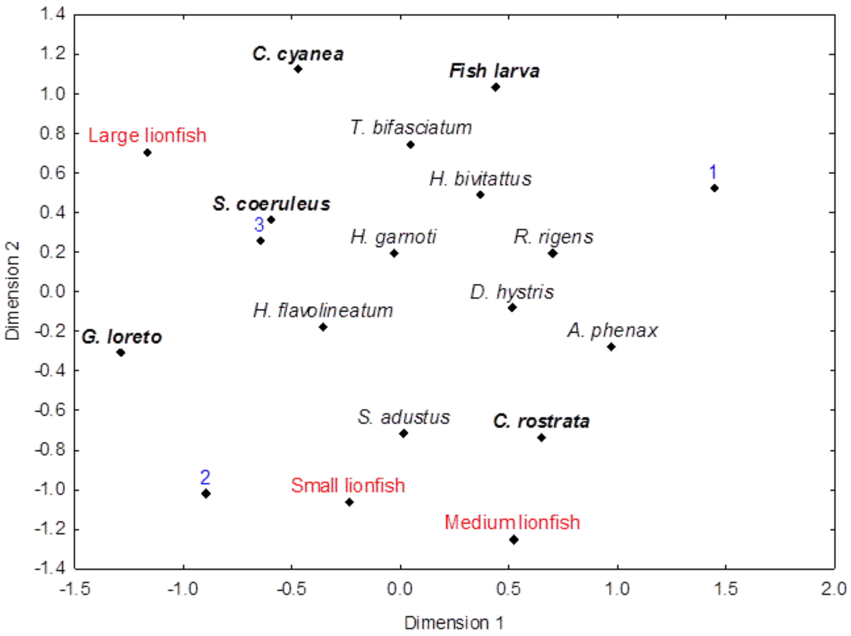

Figure 5. Multidimensional scaling analysis included lionfish being solitary (1), grouped by two (2) and three (3) individuals, lionfish size (large, medium, and small), and associated organisms (species, see Table I for complete names). The most frequently observed fishes are in bold.

Discussion

Our study shows that the presence of lionfish does not negatively or positively affect the presence or density of other fishes, if we consider the five species that we more commonly observed sharing the same refuge with this potential predator. (The Royal Gramma, *Gramma loreto,* was the most abundant, and the most frequently encountered fish in association with lionfish in their diurnal refuges. This particular species was mostly associated with groups of lionfish. This association may seem strange, considering that *G. loreto* is considered to be strongly predated by lionfish in the Bahamas and Cuba (Morris & Akins 2009; Ingemann & Webster 2015; Cobián et al. 2016; Ingemann 2016). However, *G. loreto* has rarely been found in the stomachs of lionfish on the Mexican Caribbean reefs, where Valdez-Moreno et al. (2012) found only three *G. loreto* individuals in the stomach of 157 lionfish. In accordance with our results, recent research in the Bahamas showed that lionfish predates several fish species, but never *G. loreto*, (Green et al. 2011). Moreover, in Belize (bordering our study area), *G. loreto* recruitment is not affected by the invasive lionfish (Selwyn et al. 2013).

Gramma loreto is known to be a fish cleaner that removes parasites, mucus, fungi, and diseased tissue from their client (Wicksten 1995). The large frequency of coexistence of this species with lionfish in our study may be due to cleaning behaviour. Did lionfish become a new client for this cleaner fish in the Mexican Caribbean? During our observations, we did observe cleaning behaviour of *G. loreto* on lionfish. Sikkel et al. (2014) and Loerch et al. (2015) showed that lionfish have a low susceptibility to generalist ectoparasites in the Caribbean, but the mechanisms of this resistance to infestation are unknown. In addition, Sellers et al. (2015) showed that ectoparasite infestation on lionfish is lower at higher latitudes and increased from Florida to Panama. In the Mexican Caribbean, where we carried out this study, these authors reported only a single case of parasitism by a gnathiid isopod. Interestingly, Böhlke & Randall (1963) mentioned that gnathiid isopod ectoparasites occur in the stomach of *G. loreto*. This information, combined with our results (high number of *G. loreto* associated with lionfish), and field observations, could suggest that *G. loreto* is an active cleaner of lionfish, which could also help explain the low ectoparasitism level observed on *Pterois volitans*.

Gramma loreto was principally observed in groups. Green & Côté (2014) suggest that cleaner fish, occurring in groups and in refuges during the day, display characteristics that reduce the possibility of being predated by lionfish. The Royal Gramma is present mainly with groups of large lionfish. This association is not random, but depends on lionfish characteristics. It would be interesting to investigate if both species obtain some advantages when associated during the day in reef caves.

The other commonly observed fish in association with lionfish, and more specifically associated with groups of large *P. volitans*, was the Blue Chromis, *Chromis cyanea*. The recruitment of this species is negatively affected by *P. volitans* (Selwyn et al. 2013), but it has not been observed in stomachs of lionfish in our study area (Valdez-Moreno et al. 2012), and only a few individuals were found to be preyed upon by lionfish in the Bahamas (Morris & Akins 2009). According to Marsh-Hunkin et al. (2013), Blue Chromis persists on the reef despite lionfish predation. In fact, this species, as other fishes associated with the lionfish, may be able to recognise and escape from potential predators, and also survive lionfish predation (Karplus et al. 1982; Marsh-Hunkin et al. 2013). In our study, *C. cyanea* were observed in diurnal refuges, at places and at times that do not fit with *P. volitans* foraging activity; furthermore, they were generally observed in groups, so the possibility of predation by lionfish is low (Green & Côté 2014).

Scarus coeruleus is another fish frequently observed with lionfish, and tends to be present with groups of large *P. volitans*. As with the chromis, the possibility that *S. coeruleus* was predated upon by lionfish in the refuges is low. Furthermore, this fish has not been mentioned as prey or being affected in other ways by lionfish (see references in Table I). The most likely hypothesis is that *S. coeruleus* shares the same habitat as the lionfish because they are commonly observed together on coral reefs (Dorenbosch et al. 2004). However, the juveniles of this species may be preyed upon by *P. volitans*.

The Caribbean sharp-nose puffer, *Canthigaster rostrata*, is also present in association with lionfish in our study sites, but independent of any specific lionfish characteristic (group, size). Predation by lionfish on this species was suggested by Morris & Akins (2009), who found one individual in the stomach of a *P. volitans* specimen in the Bahamas. Green et al. (2011) also observed it being preyed upon by lionfish in the Bahamas. However, no *C. rostrata* individuals were found in the stomachs of lionfish from our study area (Valdez-Moreno et al. 2012). This spongivorous fish (Loh & Pawlik 2009) inflates its body as a defence strategy against predators, and is not frequently preyed on by other species of fish (Gochfeld & Olson 2009). It is interesting that this fish is the only one of the four species most commonly associated with the lionfish that is clearly not associated with groups and larger lionfish.

Diodon hystrix has never been mentioned as prey for the lionfish in the Mexican Caribbean (Valdez-Moreno et al. 2012) nor in Bahamas (Morris & Akins 2009). The porcupine fish is known for its behavioural strategy of inflating its body as well as for tetrodotoxin a potent, potentially fattal neurotoxin that protects it from predators (Bast el al. 1983). This fish appears to be moderately associated with solitary lionfish, certainly because they share the same habitat, caves within the reef, during the day (Darling et al. 2011; Green et al. 2011).

Only a few individuals of the Bluehead Wrasse, *Thalassoma bifasciatum* (Perciformes, Labridae), were observed associated with lionfish. The Bluehead Wrasse is a common prey of the lionfish in the Caribbean and the Bahamas (Morris & Akins 2009; Valdez-Moreno et al. 2012; Cobián et al. 2016). However, *T. bifasciatum* has shown a positive change in recruitment since the lionfish invasion (Selwyn et al. 2013), despite being preyed upon. Some individuals of *Stegastes adustus* (Troschel, 1865) (Perciformes, Pomacentridae) were observed in association with the lionfish; this species has not suffered from the lionfish invasion, according to Selwyn et al (2013). However, *Stegastes* species, with the exception of *S. adustus*, are commonly observed being preyed on by *P. volitans* (Morris & Akins 2009; Valdez-Moreno et al. 2012) especially one of the smallest damselfishes, *S. partitus* (Poey, 1868) (Cobián et al. 2016).

Although we observed a few individuals associated with lionfish, the Mimic Cardinalfish, *Apogon phenax* Böhlke & Randall, 1968 (Perciformes, Apogonidae)*,* is not often preyed upon by it (Morris & Akins 2009; Valdez-Moreno et al. 2012). The wrasses, *Halichoeres bivittatus* (Bloch, 1791) and *H. garnoti* (Valenciennes, 1839) (Perciformes, Labridae), are not frequently associated with lionfish but are regularly preyed upon by them (Morris & Akins 2009; Valdez-Moreno et al. 2012; Cobián et al. 2016), but it is not certain whether or not the lionfish invasion has affected its recruitment (Selwyn et al. 2013). Shrimps may be considered as a common prey of the lionfish (Prakash et al. 2012). In the Caribbean the shrimp *Cinetorhynchus rigens* (Gordon, 1936) (Decapoda, Rhynchocinetidae) is commonly preyed upon by the lionfish (Morris & Akins 2009; Valdez-Moreno et al. 2012), but only few individuals were observed in diurnal refuges with *P. volitans*.

The presence of lionfish does not appear to repel other species of fish, as half of the diurnal refuges were occupied by other organisms; fish even tend to stay close to the predator. The fishes observed in association with lionfish differ in relative abundance and diversity from those observed in lionfish stomachs in the same area (Valdez-Moreno et al. 2012). It appears that the fishes found in lionfish stomachs are more diverse than those in the refuges; however, not all fishes could be identified in our study, and more than half the species found in stomachs could not be identified (Valdez-Moreno et al. 2012), making the comparison inaccurate. Some fishes seem to be present in higher abundance associated with the lionfish in diurnal refuges than found as part of their diet, including *G. loreto* (Valdez-Moreno et al. 2012). In contrast, very few shrimps were observed in caves with lionfish, in comparison with the number of individuals present in stomach contents (Valdez-Moreno et al. 2012). It is very likely that shrimps had a low occurrence in caves occupied by lionfish and other fish; since shrimps and crustaceans usually inhabits smaller refuges (Caddy 2014).

Differential microhabitat use by lionfish may explain these dissimilarities. Lionfish hunt actively in microhabitats other than caves and at different times, and use caves exclusively for resting; they hunt during the night in open and sandy areas on the coral reef or directly on the coral structure, but never in the caves, or crevices, where they rest during the day (Green & Côté 2014). Furthermore, differences in lionfish predation on *G. loreto* may be due to variation in geographical and temporal fish distribution. As frequently observed, prey tend to avoid predators in time and space, while predators tend to reach their prey in their new space and timing (Fischhoff et al. 2007). In this context, Morris & Akins (2009) mentioned that lionfish are diurnal predators in the Bahamas, while other studies describe them as nocturnal or crepuscular predators (Green et al. 2011; Green & Côté 2014). Another hypothesis is that the differences observed in terms of *G. loreto* predation by lionfish, may reflect the availability of various other preferred prey. This can favour a switch for predators from one kind of prey to another (prey-switching), learning where and how to catch a new prey, as commonly observed for generalist predators (see examples in Hénaut et al. 1999, 2000). In this context, lionfish may switch between prey and predation strategies according to prey availability, or prey may demonstrate behavioural changes when faced with this predator.

Why is it that in caves during the day, fish are observed with a potential predator? The simplest explanation is because those diurnal refuges have characteristics that attract different species of fishes. However, it is interesting to observe that when large lionfish are in groups, they are associated with more fishes than when they are alone. Particularly, groups of lionfish are found with the three most commonly associated species, *G. loreto, C. cyanea*, *S. coeruleus*. In a first approximation, we would expect that the more lionfish in the caves, the less associated organisms, particularly fishes are present, because they may be eaten when nocturnal predation occurs, since as fishes display a great capacity to learn and avoid predators (Mitchell et al. 2011). Another hypothesis is that fishes are attracted to the lionfish as they provide protection for fishes in their resting microhabitat by deterring other potential predators. Lionfish have practically no predators in the Caribbean, with only one isolated observation of a grouper eating a small (61 mm) lionfish (Maljković et al. 2008). However, groupers are overexploited through fishing, and it appears that they do not have the capacity to control lionfish populations (Mumby et al. 2011). The possibility that lionfish repel other predators may explain why *G. loreto, C. cyanea*, and *S. coeruleus* are associated with them, especially when lionfish are in groups of large individuals. Another alternative explanation is that naïve fishes do not recognise lionfish as a threat (e.g. Anton et al. 2016)

The relationship between invasive lionfish and the community of native fishes on Caribbean coral reefs may be much more complex than a simple and destructive relationship of an invasive predator preying on naïve native fauna. Our study suggests that the presence of lionfish may offer new perspectives for native fauna, such as new associations with different native fishes. Those associations could have new functions, e.g. lionfish being clients of cleaners, or offering protection against other predators. The majority of studies on invasive species tend to demonstrate the negative impact of those species upon native ones in their new ecosystem (Rodríguez 2006). Of course, the negative impact of alien arrival in a new ecosystem cannot be minimised; however, the invasive effect in its negative perspective could be moderated, even more if invasive species are simply correlated and may hide other impacts, particularly the consequences of human activities (Ewel & Putz 2004; Gurevitch & Padilla 2004; Didham et al. 2005). Our perception of biological invasions may have to be revised particularly in transformed or altered ecosystems (Tassin & Kull 2015), or seek a longer-term perspective of the arrival of non-native organisms (Willis & Birks 2006). In this context, several studies demonstrate that invasive species may offer new interactions and also associations for native species; this is particularly true for introduced predators (Rodriguez 2006). Since lionfish eradication seems impossible (Barbour et al. 2011), the new associations observed between lionfish and native fishes suggest that lionfish will progressively become participants in Caribbean biodiversity.

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CAPÍTULO 4

More predators and not so effective spines for the invasive lionfish in the Caribbean

SOMETIDO A

The Science of Nature

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Abstract

Lionfish are invasive predators that have colonized large areas of the Caribbean Sea. They have very few natural predators in their new environment and their highly venomous spines provide them with excellent protection against any native predators. Our research generates a list of 25 species that have been observed eating lionfish. The venomous spines of the lionfish do not appear to act as a deterrent to these species. Several species of fish, sharks and a cormorant have been observed actively searching for lionfish and subsequently consuming them entirely. We conclude that in the Caribbean, lionfish currently have many more potential predators than those considered at the beginning of the invasion, and furthermore, their venomous spines do not prevent predation by native species. These observations alter the paradigm that in the Caribbean, the lionfish has only a few predators, principally due to the protective function of their spines.

Key words Shark, venomous spines, management, coral reefs, behavior.

Introduction

The lionfish *Pterois volitans* L. 1758 (Scorpaeniformes, Scorpaenidae) is an invasive species of high voracity (Côté and Maljković 2010) and is one of the main threats to Atlantic reefs. It reduces the abundance of native species and increases competition for food and habitat (Morris and Atkins 2009; Barbour et al. 2010; Layman and Allgeier 2012). In the Bahamas, lionfish have resulted in a 79% reduction in fish recruitment (Albins and Hixon 2008) and a decrease of 65% of the total biomass of 42 prey species (Green et al. 2012). Their bodies are covered with poisonous spines that may kill potential native fish' predators (Albins and Hixon 2008). In their natural habitat, the cornet fish, *Fistularia commersoni*, has been identified as a natural predator of *Pterois miles* (Bernadsky and Goulet 1991). Maljkovic' et al. (2008) found a small red lionfish in the stomach of a tiger grouper (*Mycteroperca tigris*) and others in the stomachs of Nassau groupers (*Epinephelus striatus*), also mentioning that fishermen had observed groupers hunting lionfish in the Bahamas. Jud et al. (2011) reported a green moray eel, *Gymnothorax funebris*, consuming a wounded lionfish in the Loxahatchee River, USA. Mumby et al. (2011) suggest that lionfish numbers are controlled by groupers, in contrast to Hackerott et al. (2013) who found no relationship between the densities of groupers and lionfish on 71 reefs invaded by the fish. In addition, studies of stomach contents have confirmed cannibalism in lionfish (Valdez-Moreno et al. 2011). Concerned by the rapid expansion of this invasive fish, different countries have actively encouraged extraction through fishing tournaments or hunting by recreational divers (Akins 2013). Surprisingly, even if scientific literature considers lionfish predation is very limited and because the poisonous spine of this fish, our observations and public information suggests that lionfish as much more potential predators than considered by specialists. The aim of this study is to find out and report using own observations and public sources of information, a larger list of species that can hunt and eat the venomous lionfish.

Materials and methods

We carried out direct observations on organisms that predate on lionfish in the Mexican Caribbean (Banco Chinchorro, Playa del Carmen, Xcalak, Contoy Island, Cozumel Island), Roatan (Honduras), and in the Bahamas. In addition, we also searched for videos (Youtube®) and photos on the internet in relation to organisms that had been reported eating lionfish. The species observed eating freshly captured or free-living lionfish were identified and recorded, as was the location of each video/photo. Furthermore, in Banco Chinchorro, we had the opportunity to observe the behavior of nurse shark when accompanying divers during lionfish capture, and we report it.

We describe the behavior of the lionfish, their predators and focus on nurse shark observations. All the species observed eating lionfish are presented in Table 1, including geographical data and the source of the information.

Results and discussion

We identified 25 species that feed on lionfish (Table 1). All the observations were made throughout the Caribbean where the lionfish is an invasive species (Fig. 1). Fish were the most commonly observed taxon eating fresh dead or dying lionfish, with 14 species, including three groupers, three snappers, two triggerfish, and two moray eels (Fig. 2). We also found seven species of sharks that consumed lionfish (Table 1). The spiny lobster was the only invertebrate species observed eating a fresh dead lionfish. Other species observed eating lionfish included three vertebrates (Fig. 3), one turtle, one crocodile, and one cormorant. Specific species observations occurred in different localities: nurse sharks were observed eating lionfish in the Mexican Caribbean and in Nicaragua while the ocean triggerfish was seen feeding on them in Florida and in the Mexican Caribbean. In Mexico, Florida and Honduras the lionfish was predated on by the green moray while barracuda were observed eating lionfish in Mexican waters, Belize and Saint Martin (Table 1). However, the fact that organisms preying on healthy wild lionfish was rarely observed, must be considered when interpreting the results; the consumption of individuals that are freshly killed or dying is not comparable with predation on healthy wild lionfish. Organisms such as lobster or triggerfish are certainly not lionfish predators. However, organisms such as sharks appear to be capable of eating live lionfish. Crocodiles that inhabit mangroves, such as the opportunist American crocodile presents in Banco Chinchorro (Charruau et al. 2010), could potentially predate on lionfish observed in mangrove and sea grass habitats. The cormorant was also observed actively foraging for a lionfish, shallowing it and then returning to the water to fish for a second one (Fig. 3). This species of bird appears to be an active predator of lionfish.

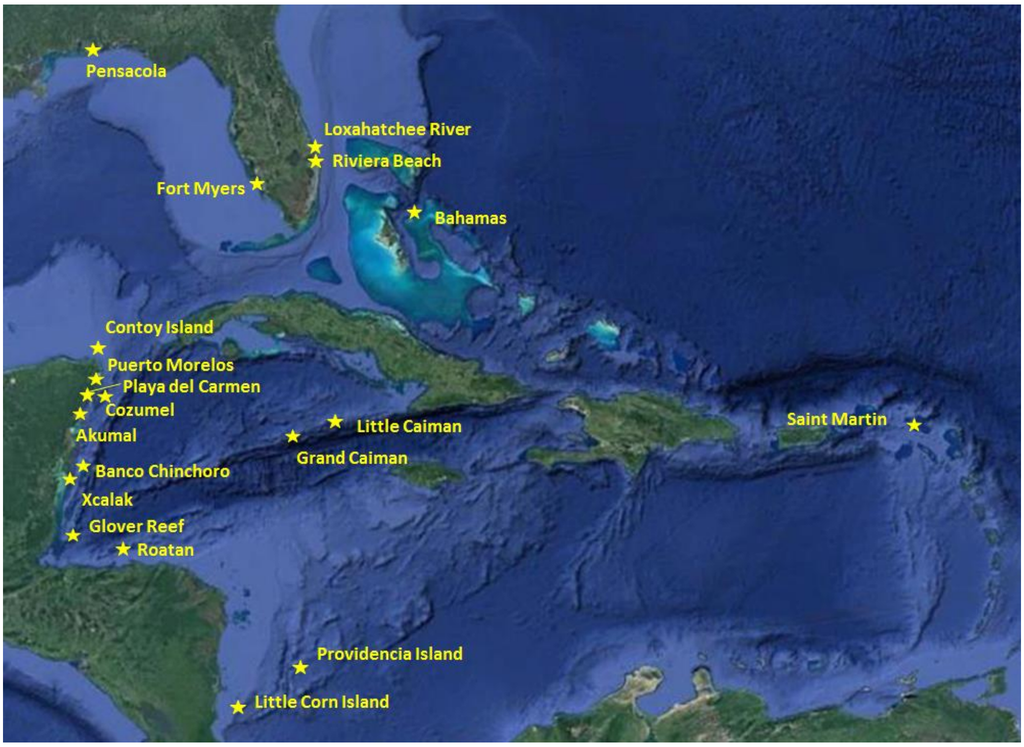

Fig. 1. Locations where consumer and/or predator's species of lionfish have been observed in the Caribbean 1

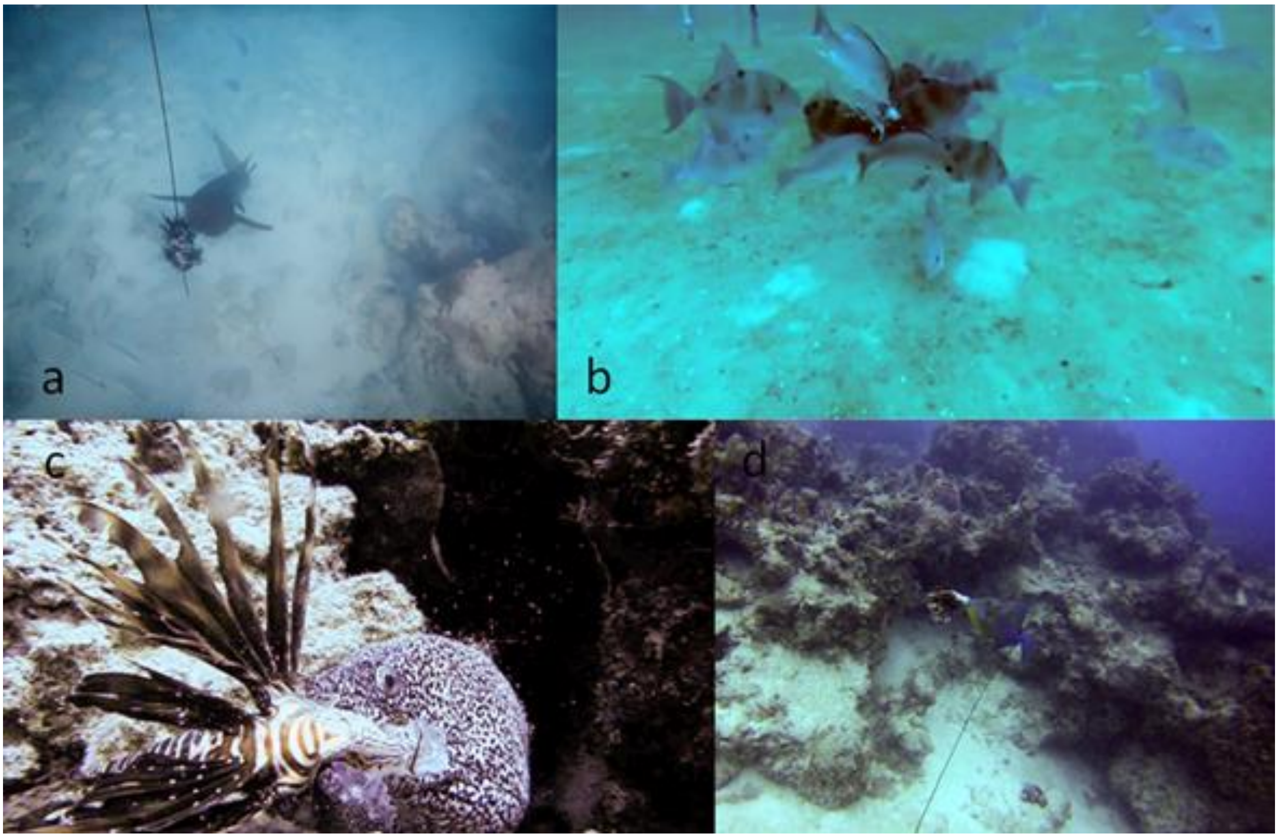

Fig. 2. Sharks and other fish eating lionfish. (a) nurse shark (*G. cirratum*) (photo I. Aguirre), (b) snapper (*Lutjanus sp*.) observed in Pensacola, USA (photo Alex Fogg), (c) spotted morays (*G. moringa*) observed in Playa del Carmen, Mexico (photo Jorge Lorií), (d) queen triggerfish (*B. vetula*) observed in Banco Chinchorro, Mexico (photo Maria del Carmen García-Rivas).

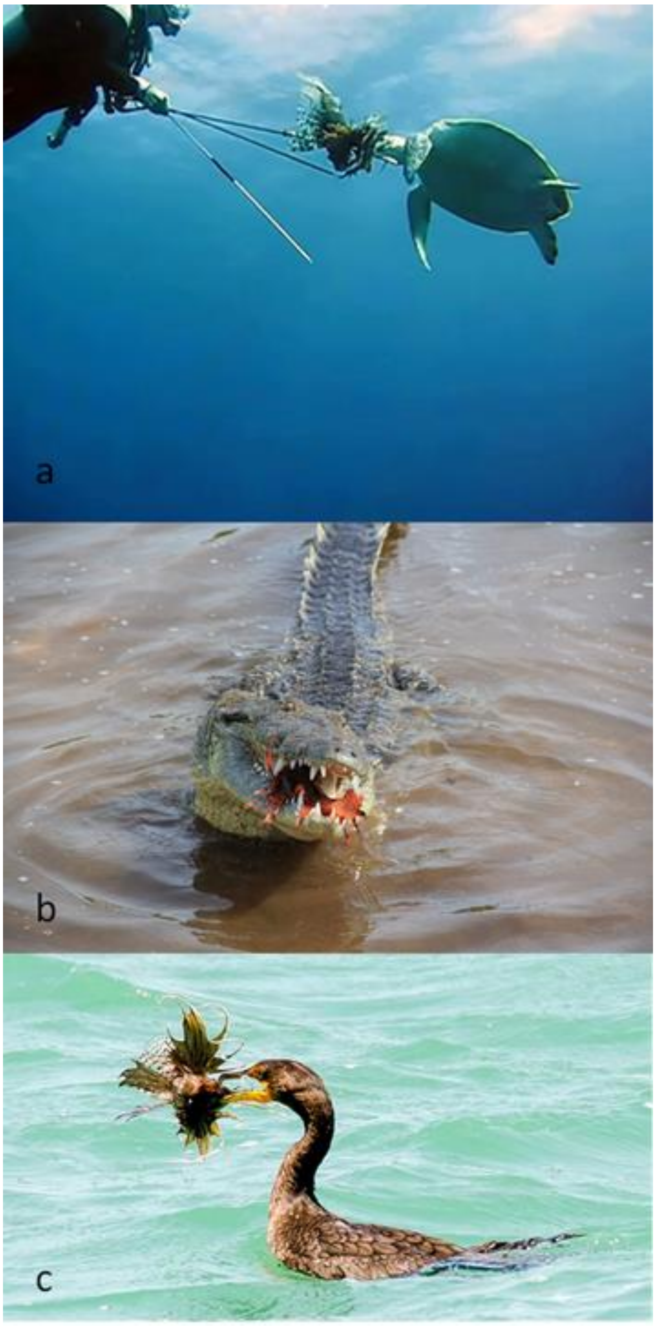

Fig. 3. Vertebrates that are consumers of lionfish. (a) green turtle (*Chelonia mydas*) (photo S. Regher), (b) American crocodile (*Crocodylus acutus*) (photo Yann Hénaut), (c) Double-crest cormorant (*Phalacrocorax auritus*) (photo Karen DeHays).

Table 1. Inventory of species known to eat lionfish. In this table, we regroup information obtained through our own observations, information found in youtube® and internet, and information from the literature (see references). We provide the common name, the scientific name and family, the localities and country when available.

Common name	Species (family)	Localities	References
Spiny Lobster	*Panulirus argus* (Palinuridae)	Not mentioned	Brown (2011)
Nurse shark	*Ginglymostoma cirratum* (Ginglymostomatidae)	Banco Chinchorro and Contoy Island (Mexico); Little Corn Island (Nicaragua)	This study; Hunkler (2012)
Reef Shark	*Carcharhinus perezi (*Carcharinidae)	Bahamas	This study
Lemon Shark	*Negaprion brevirostris* (Carcharhinidae)	Bahamas	This study
Reef Shark	*Carcharhinus perezi* (Carcharhinidae)	Bahamas	Clarke (2012)
Silky Shark	*Carcharhinus falciformis* (Carcharhinidae)	Roatan (Honduras)	Power (2015)
Blacktip Shark	*Carcharhinus limbatus* (Carcharhinidae)	Providencia (Colombia)	Unknown (2015)
Bull Shark	*Carcharhinus leucas* (Carcharhinidae)	Playa del Carmen (Mexico); Roatan (Honduras)	This study
Queen Triggerfish	*Balistes vetula* (Balistidae)	Banco Chinchorro (Mexico)	This study

Ocean Triggerfish	*Canthidermis sufflamen (*Balistidae)	Banco Chinchorro, Cozumel Island, and Xcalak (Mexico); Pensacola, Florida (USA)	This study; Fogg (2013)
Hogfish	*Lachnolaimus maximus* (Labridae)	Banco Chinchorro (Mexico)	This study
Saucereye Porgy	*Calamus calamus* (Sparidae)	Banco Chinchorro (Mexico)	This study
Barracuda	*Sphyraena barracuda* (Sphyraenidae)	Glovers Reef (Belize); Saint Martin Island	Millet (2013); Butler (2014)
Toad fish	*Sanopus barbatus* and *S. splendidus* (Batrachoididae)	Roatan (Honduras); Cozumel Island (Mexico)	Unknown (2014)
Dog Snapper	*Lutjanus jocu* (Lutjanidae)	Roatan (Honduras)	Westy (2015)
Snapper	*Lutjanus* griseus (Lutjanidae)	Pensacola, Florida (USA)	Fogg (2013)
Mutton snapper	*Lutjanus analis* (Lutjanidae)	Grand Cayman	Davidson (2010)
Goliath grouper	*Epinephelus itajara* (Serranidae)	Preston Bay (Little Cayman)	Hart (2015)
Tiger grouper	*Mycteroperca tigris* (Serranidae)	Bahamas	Maljković et al. (2008)
Nassau grouper	*Epinephelus striatus* (Serranidae)	Bahamas; Bloody Bay Wall (Little Caiman)	Kim (2015); Clarke (2012); Maljković et al. (2008)

Spotted moray	*Gymnothorax moringa* (Muraenidae)	Riviera Beach, Florida (USA)	Wang (2010)
Green moray	*Gymnothorax funebris* (Muraenidae)	Roatan (Honduras); Loxahatchee River, Florida (USA); Cozumel Island (Mexico)	This study Westy (2015) Jud et al. (2011)
Green turtle	*Chelonia mydas* (Cheloniidae)	Akumal and Xcalak (Mexico)	Unknown (2013)
Crocodile	*Cocodrylus acutus* (Crocodylidae)	Banco Chinchorro (Mexico)	This study
Double-crest Cormorant	*Phalacrocorax auritus* (Phalacrocoracidae)	Fort Myers Beach, Florida (USA)	DeHays (2012)

This apparently large spectrum of potential predators is certainly more limited, because without human intervention it would be difficult for various species to spot and catch the lionfish (Lönnstedt and McCormick 2013). However, video footage of several organisms show that once the lionfish has been detected, there are no signs of hesitation in approaching and eating it, in the same way as for a familiar prey. Furthermore, the manipulation and ingestion of freshly caught dead or almost dead lionfish occurs without any precautionary behavior, despite their still venomous spines (Unknown 2013). On several occasions, we observed nurse sharks actively searching for lionfish. The lionfish tried to avoid the sharks, demonstrating that they had learned that this species was a predator.

Sharks, groupers, other large fish, toadfish, green turtle, crocodiles, and cormorants are clearly predators or potential predators of lionfish. Previous reports have identified only a few species predating on lionfish, namely two groupers (Maljković and Van Leeuwen 2008) and one moray (Jud et al. 2011). It appears that lionfish have many more predators or potential predators than previously described in the literature.

It is commonly accepted that because of their spines, lionfish are unlikely to have many predators in the Caribbean. Our results also contrasted strongly with this general assumption, as many species of sharks and several fish, for example the toadfish, are able to swallow a whole (dead or dying) lionfish (Fig. 4). Previous observations have shown that both morays and groupers have no problem manipulating dead lionfish, while our study provides evidence that turtles can also eat lionfish without taking any specific precautions. Crocodiles and cormorants are both able to eat an entire lionfish despite their venomous spines. By consuming injured or freshly killed lionfish, predators may eventually learn how to capture living individuals without being affected by the spines, as demonstrated in the videos of snappers preying on a lionfish (Hart 2015), and a spoted snapper (Unknown 2011).

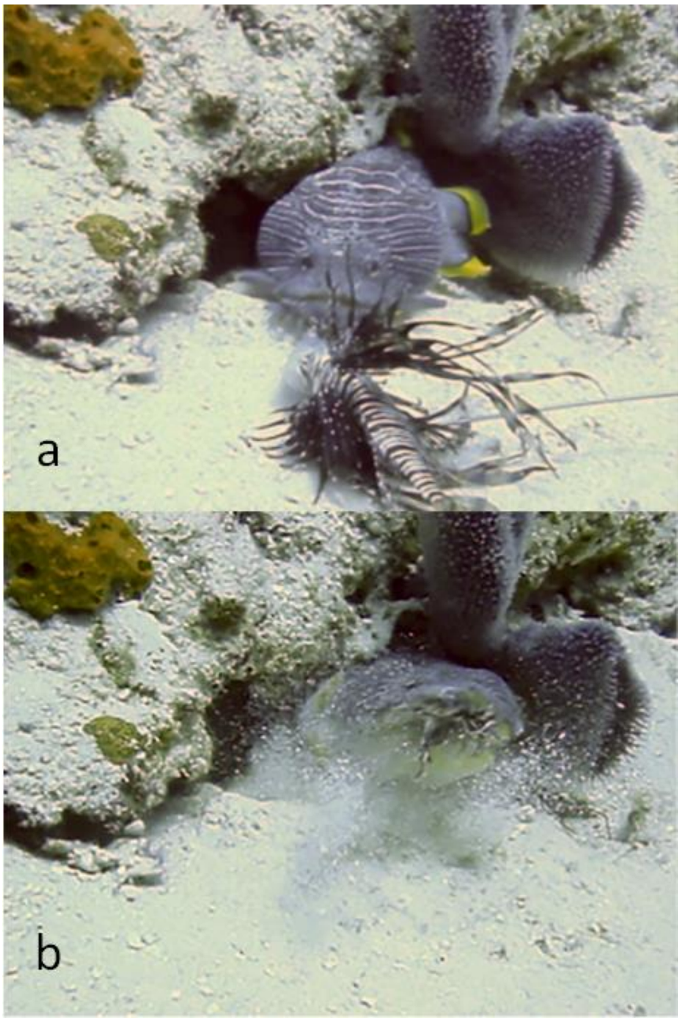

Fig. 4. Toad fish, *Sanopus splendidus* (Batrachoididae), eating a lionfish. (a) front of the fresh captured lionfish, and (b) gobbling the entire lionfish (photo Ray Hunley).

In Banco Chinchorro, we commonly observed the nurse sharks insistently following scuba divers; on one occasion a nurse shark took the string used to carry the lionfish with the captured specimens from one diver. In the same place, we observed two nurse sharks followed the scuba divers that were using a harpoon, and whenever they captured a lionfish, the sharks would take the fish from the string. We observed sharks searching for lionfish in their caves on the reef. One remarkable observation occurred when divers were looking for lionfishes in their diurnal refuges, primarily caves; the sharks swam next to the scuba divers during the hunt, got ahead of the divers, and then rummaged the reef cavities; they tried to suck out lionfish twice. However, the lionfish showed clear evasive and swift behavior, hiding from the nurse sharks in reef cavities. The evasive behavior of lionfish in Banco Chinchorro was to swim slowly away from the potential predator or scuba divers and if possible, hiding inside caves on the reef. The nurse sharks were even observed followed the scuba divers even up to the surface. Our observations lead to various presumptions: the lionfish recognize nurse sharks as predators in Banco Chinchorro, and this must have been a learned behavior. Consequently, nurse sharks are possibly natural predators of the lionfish. Nurse sharks inhabiting the Banco Chinchorro Biosphere Reserve may help divers to catch lionfish. In other localities where nurse sharks do not prey on lionfish, they may be trained to become predator of this invasive fish.

Our results show that lionfish have many more potential predators than previously thought. In addition, the venomous spines of the lionfish do not seem to be a barrier for potential predators, although this has been considered as an explanation for the success of the invasion (Albins and Hixon 2008). According to the food web structure model of Arias-González et al. (2011), the reef is more susceptible to the damage caused by the lionfish when sharks and other carnivores are eliminated from the fish community. Therefore, given that, groupers are overfished, they are unable to predate and control lionfish (Mumby et al. 2011). We conclude that potential predators may have learned to recognize lionfish as prey. Consequently, we recommend maintaining and extending the protection of all species that are susceptible in the Caribbean region, in order to increase the possibilities of controlling the lionfish population.

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CAPÍTULO 5

DISCUSIÓN

Uno de los objetivos de esta investigación fue describir la conducta del pez león en relación con el uso del hábitat. En una muestra de 793 individuos de pez león en vida libre, se identificaron tres comportamientos principales: cacería, descanso y desplazamiento, así como ocho posturas. En este estudio no se registró comportamiento agonístico o territorial a diferencia de la territorialidad mostrada con despliegues agonísticos a congéneres y conspecíficos en su distribución natural (Fishelson, 1975). La territorialidad o defensa de recursos manifiesta competencia por recursos (alimenticios, refugios, o reproductivos); el hecho de no presentar este comportamiento demuestra la amplia disponibilidad de recursos en la zona de estudio, condición que facilita la dispersión de especies invasoras.

Tampoco se registró comportamiento evasivo, de huida ante depredadores, ni de apareamiento. La reproducción de *P. volitans* es en total obscuridad y de larga duración (Fishelson, 1975) por lo que se recomienda incrementar el esfuerzo de observación nocturna.

Entre las características de los ecosistemas que los hacen susceptibles a ser invadidos se encuentra la ausencia de depredadores para la especie invasora, así como de especies nativas morfológica o ecológicamente similares a la invasora, es decir, posibles competidores (Williams y Meffe 2005). En este sentido, la ausencia de depredadores del pez león es uno de los factores que se ha mencionado como importante en el éxito de su dispersión (Morris, 2009; Morris y Akins 2009; Mumby et al. 2011, Hackerott et al. 2013; Valdivia et. al. 2014). En las áreas estudiadas en el presente trabajo, sus posibles depredadores como tiburones o peces carnívoros grandes, han disminuido por sobrepesca (Arias-González et al. 2011). En la literatura sólo se habían registrado restos de peces león en estómagos de serránidos (Maljković et al. 2008) y morena, (*Gymnothorax funebris* Jud et al. 2011; *G. moringa*: Muñoz, 2017). En el presente estudio (Capítulo 4) se contabilizaron 24 consumidores y/o potenciales depredadores de peces león muertos o heridos capturados por buzos, en donde además de tiburones, meros y morenas, se observan otros vertebrados como peces sapo, peces ballesta, cormoranes, tortugas y cocodrilos; el cormorán cazó activamente consumiendo dos peces león vivos, así mismo el tiburón gata en Contoy. Estos registros demuestran que organismos nativos pueden aprender a comer pez león, y que las espinas que habían sido consideradas como un factor limitante en la depredación (Halstead et al. 1955; Morris 2009), no son tan eficaces. Esos resultados cambian la visión inicial del pez león como una especie invasiva inmune a depredadores hacia una especie vulnerable con muchos consumidores y depredadores potenciales. Esa ausencia inicial de registros de depredadores puede ser explicada por la ausencia de evidencia o registros documentados, así como por el hecho de que los depredadores deben aprender a reconocer y cazar una nueva presa tal como sucedió con individuos de *Orius majusculus* (un insecto hemíptero) en condiciones experimentales donde se demostró que individuos que estaban expuestos con su presa, depredaban más eficientemente que aquellos que no habían tenido contacto

(Hénaut et al. 2000), lo mismo que la araña de la seda de oro *Nephila clavipes* en vida libre (Hénaut et al. 2014).

El porcentaje de peces león observados cazando en el Caribe mexicano (7%) parece bajo en comparación con las Bahamas y Filipinas (14% y 10% respectivamente) (Cure et al. *2*012) en donde se hizo seguimiento de individuos. Esa diferencia puede relacionarse con la disponibilidad de alimento en cada sitio: Banco Chinchorro tiene la mayor densidad de peces de las familias Acanthuridae, Scaridae y Serranidae en el Arrecife Mesoamericano (García-Salgado et al. 2008), de modo que la proporción baja de individuos observados cazando activamente, probablemente reflejan la facilidad para encontrar presas en ecosistemas sanos.

Los resultados del Capítulo 2 mostraron que el uso del hábitat y la conducta del pez león varían según la talla, además el comportamiento de cacería fue observado con mayor frecuencia en individuos medianos y grandes, y en menor grado en pequeños, hecho que puede relacionarse con un consumo de presas diferenciado de acuerdo con la talla de los invasores. La dieta del pez león varía según la talla (Morris y Akins, 2009; Muñoz et al. 2011; Valdez-Moreno et al. 2012; Côté et al. 2013; Dahl y Patterson, 2014); los peces león chicos consumen preferentemente crustáceos, mientras que las tallas mayores presentan mayor frecuencia de peces en su dieta (Morris y Akins 2009; Layman et al. 2014, Zaldívar 2015). Otros peces arrecifales carnívoros también cambian su dieta al crecer (Lukoschek y McCormick, 2001). La baja frecuencia observada de peces pequeños cazando, tal vez se deba a que la captura de crustáceos es menos conspicua, mientras que la cacería de peces es una conducta evidente, especialmente por las variaciones que se han descrito de acecho y acorralamiento, y desconcierto de presas mediante chorros de agua (Morris y Akins, 2009; Albins y Lyons, 2012). En este trabajo se registraron dos nuevas posturas de cacería del pez león, además de la de cabeza abajo, descrita anteriormente (Fishelson, 1975; Green et al. 2011): la postura cabeza arriba observada en peces grandes, y la caza de manera horizontal presente en todas las tallas. Esta variedad de posturas para cazar puede facilitar la búsqueda y detección de presas en diferentes situaciones y tipos de hábitat. Igualmente, la postura horizontal se relaciona con el desplazamiento, y la de cabeza abajo para peces pequeños localizados en muelles, rocas o arena. Estos resultados en la diversidad de posturas y hábitats para cazar pueden facilitar su alimentación generalista considerada como un factor de éxito en la invasión, la cual se puede relacionar con la teoría de que la "oportunidad de nicho" facilita las invasiones (Shea y Chesson, 2002). La "oportunidad del nicho" depende de la disponibilidad de alimento, enemigos naturales, condiciones ambientales y la interacción entre los diferentes factores, en ambientes perturbados se acentúa (Niemelä y Mattson, 1996). En el caso de los arrecifes del Caribe el abatimiento de los peces carnívoros por su sobrepesca puede ser un factor definitivo del establecimiento del pez león al dejar un "nicho vacío".

Nuestros resultados mostraron que peces león medianos y grandes cazaron preferentemente en horas de luz y en espacios abiertos sobre corales, con postura horizontal y boca abajo, hecho que puede relacionarse con su baja susceptibilidad a ser depredados discutida por diferentes autores (Fishelson, 1975; Maljković et al. 2008; Morris 2009; Arias-González et al. 2011; Leung et al. 2011; Mumby et al. 2011; Hackerott el al. 2013; Valdivia et al. 2014). Se identificó que los peces león pequeños mostraron el comportamiento de cacería con mayor frecuencia en la noche que en el día, tal vez para evitar la depredación, siendo que en esta etapa pueden ser vulnerables ante sus propios congéneres (Fishelson, 1975; Valdez-Moreno et al. 2012). En las horas de luz, la cacería fue más frecuente durante el crepúsculo, tal como se ha reportado anteriormente (Fishelson, 1975; Green et al. 2011; Cure et al. 2012) en *P. miles* y *P. radiata* (McTee y Gubrich, 2014), lo cual conlleva las ventajas de poder alimentarse de especies diurnas y nocturnas, así como ser menos detectado por las propias presas y depredadores. También, es durante el día que se desplazan con mayor frecuencia los individuos grandes, lo cual se asocia al cambio de sitios de alimentación a sitios de descanso: en las cavernas o refugios pocas veces estaban cazando. Los desplazamientos registrados fueron a velocidades bajas y por tanto de bajo costo energético, por lo que se considera que su energía puede enfocarse en crecer y reproducirse (ver Capítulo 2). En su área nativa los peces león adultos se dispersan y van de aguas someras a profundas, en donde los machos buscan activamente a las hembras (Fishelson 1975, 1997) ya que en el presente estudio no se registró la dirección de los movimientos ni se observaron conductas reproductivas, se recomienda dirigir estudios enfocados a ello. Por otra parte, en las islas Turcas y Caicos, los peces león adultos se distribuyen en zonas profundas y los jóvenes en manglares y pastos (Claydon et al. 2012).

En los tres tipos de sustrato (simple, complejo y caverna) se presentaron los tres comportamientos (cacería, descanso y desplazamiento), hecho que demuestra su flexibilidad conductual y que en cualquier tipo de hábitat puede desarrollar las actividades básicas lo que favorece a la invasión.

Adicionalmente, encontramos a los peces león cazando en sitios con poca corriente o sin oleaje, conforme a lo reportado anteriormente (Anton et al. 2014; Valdivia et al. 2014) y con los trabajos de Cure y colaboradores (2014), quienes relacionan este comportamiento con el ahorro de energía y una cacería efectiva; además, los peces en general cuando se encuentran en zonas de corrientes y oleaje que provocan movimientos en el pez tienden a mantener su postura natural para no perder la eficiencia de la línea lateral (Webb et al. 2010). En relación con el color del pez león y su comportamiento, se registró una mayor frecuencia de peces de color obscuro que descansaban en cuevas y oquedades, y de peces de color claro que cazaban, lo cual sugiere que tal vez pueden adaptar su color a la actividad o al color del entorno, tal como lo hacen muchos organismos crípticos marinos (Brockmann, 1973). El cambio de color en peces león se ha observado también al ser capturados con arpón: palidecen de manera inmediata (obs. pers.). Sin embargo, para entender la relación entre las diferentes tonalidades de color del pez león, sus actividades, y su uso del hábitat se requiere mayor investigación.

Al igual que en su zona nativa (Cure et al. 2014), el pez león en nuestra zona de estudio se encontró agrupado en la mitad de los casos. Esta tendencia confirma que no son individuos territoriales, sino que se toleran entre sí y que pueden seleccionar los mismos refugios para descansar; además, al agregarse pueden protegerse de depredadores (Rizzari y Lönnstedt, 2014). En este trabajo, observamos que los peces león descansan en oquedades y cuevas del arrecife, sitios en donde se encuentran otros organismos, en su mayoría teleósteos. Sin embargo, no se encontró diferencia significativa en el número de individuos de siete especies en sitios con o sin pez león.

Las especies más observadas fueron: *Gramma loreto, Chromis cyanea, Canthigaster rostrata, Diodon hystrix*, *Thalassoma bifasciatum*, *Halichoeres bivittatus*, *Stegastes adustus, Apogon phenax*, y el camarón *Rhynchocinetes rigens,* en su mayoría, presas del pez león en el Atlántico (Albins y Hixon, 2008; Green et al,. 2012). No obstante, en el área de estudio, no todas estas especies se han reportado como presas del pez león (Valdez-Moreno et al. 2012), tal vez porque se requiere mayor esfuerzo de muestreo, o bien porque el pez león selecciona activamente a sus presas (Kindinger y Anderson, 2016), o porque algunos peces tengan menos posibilidad de ser depredados, según el tamaño, forma del cuerpo, posición en el agua y comportamiento gregario de los peces (Green y Côté 2014). Esta coexistencia en sitios de reposo refleja que el depredador no repele a sus presas potenciales, hecho que coincide con los estudios experimentales de Anton y colaboradores (2016) en el Atlántico, quienes demostraron que ocho especies nativas no reconocen al pez león como depredador, entre ellas dos especies y un género que encontramos asociadas al pez león en nuestro estudio (*H. bivitattus, Th. bifasciatum* y *Stegastes* sp.) e incluso algunas como *G. loreto* son más numerosas en sitios donde hay peces león y en mayor número con peces grandes y agrupados, posiblemente por búsqueda de protección ante otros depredadores. Además *G. loreto*, se conoce por ser una especie limpiadora y remover parásitos, mucus, hongos, y diferentes enfermedades a sus "clientes" (Wicksten, 1995). En una ocasión durante este estudio se observó un *G. loreto* limpiando a un pez león en Xcalak (obs. pers.) y se encontró como ectoparásito de un pez león a un isópodo gnátido,el cual es presa de *G. loreto* (Böhlke y Randall, 1963), por lo que estas observaciones, aunque anecdóticas, pueden reforzar la posible relación de limpiador-cliente entre *G. loreto* y *P. volitans*. No obstante la susceptibilidad a ectoparásitos en el pez león parece ser baja (Sikkel et al.

2014; Loerch et al. 2015), la piel del pez león muestra actividad antibacterial (Stevens et al. 2016), además de que la infestación de ectoparásitos en peces león se incrementa hacia el sur, desde Florida a Panamá (Sellers et al. 2015). Se recomienda realizar más observaciones en este sentido. Las especies invasoras ofrecen nuevas interacciones para las especies nativas, especialmente en el caso de los depredadores introducidos (Rodríguez, 2006).

Nuestro estudio sugiere que el pez león puede interactuar con diferentes peces nativos en nuevas funciones, por ejemplo, como cliente de limpiadores, o bien ofreciendo protección contra otros depredadores. La mayoría de los estudios sobre especies invasoras tienden a demostrar el impacto negativo de esas especies sobre las nativas en su nuevo ecosistema (Rodríguez, 2006). Por supuesto, el daño en los ecosistemas por la llegada de un invasor no puede ser minimizado; sin embargo, el efecto negativo invasivo se puede moderar si al analizar los impactos se considera que la invasión se facilitó por ocupar ecosistemas perturbados por actividades humanas; comúnmente los daños antropogénicos son más importantes que los ocasionados por la especie invasiva (Ewel y Putz, 2004; Gurevitch y Padilla, 2004; Didham et al. 2005). Es importante cambiar nuestra percepción de las invasiones biológicas, particularmente en ecosistemas transformados o alterados (Lugo, 1992; Tassin y Kull, 2015), y buscar la restauración de los ecosistemas centrando acciones en la recuperación de especies nativas y la mitigación de las alteraciones humanas, lo cual nos lleva a soluciones a más largo plazo más allá de simplemente controlar la llegada de organismos no nativos. (Willis y Birks, 2006).

Mediante estudios paleontológicos se ha logrado identificar que los cambios en las estructuras arrecifales ocasionados por la presencia humana han sido los más severos en los últimos 220 000 años. Los arrecifes del Caribe se conformaban principalmente por especies de crecimiento ramificado con predominio de *Acropora palmata y A. cervicornis,* (Pandolfi, y Jackson, 2006) ;sin embargo, estas especies fueron seriamente dañadas por distintos factores humanos en especial la sobrepesca que ocasionó un cambio en las cadenas tróficas (Hughes, 1994) así como eventos de blanqueamiento y la casi total desaparición del erizo diadema *Diadema antillarum* (Pandolfi et al, 2003).

En el Sistema Arrecifal Mesoamericano se identificaron como principales amenazas la destrucción del hábitat costero, el aumento de la sedimentación, el manejo inadecuado de aguas negras por el incremento de la población humana y los desarrollos turísticos (Arrivillaga y Garcia-Salgado, 2004). En Quintana Roo, en los últimos 30 años antes de la llegada del pez león ya se había perdido el 50% del arrecife y manglar; particularmente, en el sur del Estado, ya se habían documentado impactos antropogénicos sobre la ictiofauna del arrecife previo a la llegada del invasor (Morales-Aranda, et al. 2012) por lo que, si bien se ha identificado en el peor escenario al pez león, como el posible factor de extinción de especies de peces del arrecife (Albins y Hixons, 2013), no se puede ignorar el contexto de los impactos humanos anteriores.

Analizando el manejo de la especie invasora en la zona de estudio, desde su primer registro se realizaron diversos torneos y programas de captura y consumo. Conforme a los resultados del presente estudio se recomienda continuar con las capturas dirigiendo los esfuerzos a las horas crepusculares y búsqueda en las oquedades y cavernas, evitar zonas de oleaje y corriente, así como dejar a los peces león muertos en el arrecife o bien dárselos a las especies mencionadas en la lista de consumidores para fomentar a que posibles depredadores lo consuman.

Además de las capturas, por medio de los programas es primordial dirigir esfuerzos a recuperar las poblaciones de peces carnívoros y posibles depredadores; en ese sentido, la Reserva de la Biósfera Banco Chinchorro cuenta con tres zonas núcleo (CONANP, 2000), y un refugio pesquero (Diario Oficial de la Federación, 2013), mientras Xcalak contiene tres subzonas de refugio y una de protección en donde no se permite la pesca (CONANP, 2004). Sin embargo, la pesca furtiva es una de las principales amenazas, por lo que se recomienda que la Comisión Nacional de Pesca aumente su vigilancia, así como que ordene y mejore las regulaciones en la extracción y comercialización de la escama. Hhasta ahora la única especie en veda es el mero criollo *E. striatus*; sin embargo, su periodo no abarca los periodos de reproducción de las diferentes especies distribuidas en la zona.

A cinco años de la presencia del pez león su impacto sobre la producción de langosta espinosa, *Panulirus argus,* en Banco Chinchorro no ha sido evidente (Sosa-Cordero et al. 2014). Tampoco sobre la ictiofauna el efecto ha sido claro, ya que las áreas de mayor densidad de peces león coinciden con las áreas donde causó mayor impacto el huracán Dean en 2007 (Priego 2014) y no se pueden distinguir los dos efectos, tal vez el buen estado de conservación del arrecife de Banco Chinchorro le permite ser más resiliente a los impactos del pez león. Debido a que la erradicación del pez león parece imposible (Morris, 2009), la coexistencia entre el pez león y organismos nativos sugiere que esta especie invasiva será progresivamente parte y actor de la biodiversidad caribeña. Sin embargo, es necesario tener un ecosistema sano para que se pueda lograr una coexistencia que no afecte de manera dramática a la biodiversidad.

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CAPÍTULO 6

CONCLUSIONES

1. En las localidades estudiadas se clasificaron las conductas del pez león, *P. volitans* en tres categorías o conductas principales: cacería, descanso y desplazamiento, con ocho posturas.
2. En estas localidades, esta especie invierte el 7% de su tiempo en cacería, siendo la menor inversión de tiempo reportada hasta ahora en su ámbito de origen y el área invadida.
3. El pez león puede realizar todos los comportamientos en cualquier microhábitat y bajo cualquier condición ambiental, lo cual refleja una plasticidad conductual que favorece su éxito como invasor.
4. De manera fina las estrategias de vida dependen de la talla, los peces medianos y grandes cazan preferentemente en el día y en espacios abiertos, mientras que los juveniles prefieren alimentarse en la noche, hecho que se puede relacionar con una mayor susceptibilidad de depredación de las tallas menores
5. No mostró comportamientos agonísticos ni de huida, lo cual demuestra que no es territorial, además tienen tendencia a agruparse, hecho que puede relacionarse con la ventaja ante depredadores.
6. Además de una coloración críptica, espinas venenosas, y forma corporal inusual, se propone que la flexibilidad del comportamiento y ocupación de hábitat del pez león son dos características más para disuadir a los depredadores potenciales.

7. Los peces león y sus presas potenciales coexisten en los diferentes tipos de microhábitat, lo cual demuestra que no hay una evasión activa, el invasor puede inducir nuevas asociaciones ante especies nativas por ejemplo como cliente para limpiadores o como protección ante depredadores de otras especies que su presencia repele.
8. Se aumenta la lista de posibles depredadores del pez león de tres a 17 y de 24 consumidores, además refleja que las espinas no son tan eficaces para repeler depredadores.
9. El estudio permite generar información que mejora la búsqueda y control de la especie enfocando la captura a oquedades y sitios complejos de poca corriente, así como dirigir esfuerzos a mejorar el estado de conservación de peces carnívoros locales que promuevan una presión de selección más efectiva que nuestros esfuerzos por disminuir su población. Además, los posibles depredadores naturales pueden alcanzar todo el ámbito hogareño del pez león, mientras que las capturas por buzos están limitadas por la profundidad.
10. El control de la especie invasiva no debe minimizar la situación de los arrecifes en el Caribe mexicano; se debe reconocer que los arrecifes están impactados por actividades humanas y que el control del pez león es una medida de mitigación del daño mínima, comparada con las requeridas para disminuir las afectaciones de las actividades humanas que han afectado la biodiversidad de los arrecifes.

CAPÍTULO 7

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