1. Introduction

The lionfish (*Pterois volitans / Pterois miles* complex) is considered an invasive alien species (IAS), because it is found in territories outside its native area and can become a threat to biodiversity in the invaded area, in addition to cause damage to the environment and economic losses (Bax et al., 2003; Mendoza-Alfaro et al., 2011). IAS can cause substantial changes in recipient ecosystems (Blackburn et al., 2014) and are among the main risks associated with the extinction of various organisms (Bellard et al., 2016). For these reasons, its study, management and control should be considered a priority.

Native to the Indo-Pacific, lionfish is established successfully in the western Atlantic Ocean and the Caribbean Sea as an invader (Morris and Akins, 2009; Schofield, 2010). The first record in the invaded area dates from 1985, in Florida, United States of America (USA) (Morris and Akins, 2009). During the following years, was detected its presence on the coasts of several countries (Schofield, 2010). The first report of lionfish in Cuba was made in 2007; subsequently, observations of lionfish were reported in numerous localities of the country (Chevalier-Monteagudo et al., 2008). In 2010 sightings and capture reports already indicated its presence on the USA southeast coast, most of the Caribbean, the Gulf of Mexico and some areas of South America (Schofield, 2010).

This IAS has numerous characteristics that guarantee its success in the invaded area, among them is the general diet that includes various native fishes and invertebrates (Muñoz et al., 2011; Dahl and Patterson III, 2014; Pantoja et al., 2017). Interaction with their preys and competitors in non-native habitats is one of the main concerns arising after the invasion.

Although this species has successfully invaded estuaries, seagrass beds and mangroves, coral reefs constitute one of the most affected ecosystems (Morris and Akins, 2009, Kulbicki et al., 2012). Coral reefs are subject to numerous stressful factors (Fabricius, 2005; Baker et al., 2008; Bruno et al., 2019) and could suffer an accelerated deterioration with this invader pressure. For instance, lionfish could harm reef health by affecting native fishes and invertebrates through direct predation (Green and Côte, 2010; Cobián-Rojas et al., 2018b) and competition for food (Morris and Akins, 2009; Albins, 2013). In addition to possible ecological damage, it could also cause serious economic losses in the invaded area, by affecting fishing and tourism (Morris and Whitfield, 2009; Morris and Green, 2013).

Comentado [MOU1]: the quote of the descriptor would be good

Con formato: Fuente: Sin Cursiva

Comentado [MOU2]: It cannot become a threat; it is already a real threat

The rapid lionfish spread and its potential impact on the invaded ecosystems have made necessary to carry out new studies that expand the current knowledge about this fish. Therefore, it has been extensively studied in the Atlantic and the Caribbean, even surpassing in quantity and topics addressed, the research developed in its natural range. This fact has conducted to have higher knowledge of the biology and ecology of lionfish than of many native species in the invaded area. The revision and analysis of researches focused on lionfish from a broader vision, has become a necessity. Valuable reviews have been made that address several topics such as invasion, impacts, control, reproduction, life history, phylogeography and genetics (Côté et al., 2013; Rittermann, 2016; Côté and Smith, 2018; Díaz-Ferguson and Hunter, 2019). However, in these reviews the information about lionfish in Cuba is absent or very scarce, despite the importance of the study of lionfish in this country and the existence of numerous Cuban researchers related to the subject. Knowledge of lionfish in Cuba is essential for the comprehensive management of these IAS in the Western Atlantic and the Caribbean Sea, since its geographical location makes it a key country within the invaded area. For instance, Cuba may be the largest exporter of lionfish larvae with high levels of connectivity to all the other precincts (Johnston and Purkis, 2015). The present review aims to analyze the most relevant characteristics of the biology and ecology of lionfish as IAS, with emphasis in Cuba. It provides, for the first time, a comprehensive analysis of lionfish information and results from Cuba, which is adequately contrasted with previous studies of other invaded areas, particularly, from the Greater Caribbean. The information contained in this review may be of great use to researchers in the field of lionfish biology and ecology in the invaded area, and provides greater visibility into the history, characteristics, and impact of this invader in the largest of the Antilles.

2. Search Methodology

This review is not focused on analyzing all the lionfish scientific knowledge, rather is focused on the comprehensive analysis of the most important aspects of lionfish and the main gaps in the species current knowledge and management. Therefore, this contribution was prepared during five years of exhaustive search of published articles related to the biology and ecology of lionfish, and other aspects of interest that may contribute to its natural history knowledge and management. Google scholar was used with the search terms “lionfish invasion”, “lionfish impact”, “control of lionfish population”, “lionfish biology and ecology", "lionfish diet", "lionfish uses", and other specific terms for the different subjects. Alternative keywords were also used, e.g., "*Pterois volitans*", "*Pterois*", and combined with terms relative to geographic locations: "Caribbean", "invaded areas", "native area". Although researches on lionfish in its native distribution range were also reviewed, most priority was given to articles on lionfish as an invader in the Western Atlantic and the Caribbean Sea. Particular importance was given to the Cuban studies, which also include M.Sc. and Ph.D. thesis. Some articles not directly dealing with lionfish were included, since they provide useful information for the review. Articles in English and Spanish language were taken into account, published from 1985 (first report of lionfish in the invaded region) until 2022; with the exception of a key article from 1959 focused on the lionfish venom as the main defense mechanism in these species.

More than 150 articles were consulted, of which 136 contributed to the article main text. In addition, the native distribution of *Pterois volitans* and *Pterois miles* was added as supplemental material, wich is based on the information available in FishBase [AquaMaps: Kaschner et al. (2019)]. The chronology of lionfish invasion in the Atlantic Ocean and the Caribbean Sea was summarized using the maps provided by the USGS web site (https://www.usgs.gov/media/images/1985-2018-lionfish-invasion). Additionally, with information of 18 diet studies from different invaded regions, a graph representsthe most common fish families and all the crustaceans, mollusks and algae/seagrass identified on lionfish and the number of studies in which they were observed. The graph was created using the R language (R Core Team 2020) and the ggplot2 package (Wickham, 2016).

A total of 91 research articles were used to summarize the lionfish current knowledgethrough a figure (map) and a table. These 91 articles were classified into nine themes: Abundance, Toxicology, Control, Diet, Genetic / Phylogenetic, Impact, Invasion, Reproduction / Development, Behavior. Using this later information and the geographic coordinates of each study location, the map with the distribution of studies by subject was produced. The program QGIS, version 3.4.5-Madeira, was used for all the maps creation.

3. Original geographic distribution and invasion

Natural geographical zone of distribution and geographic zone of invasion

Con formato: Normal, Interlineado: sencillo

Eliminado: ¶

Lionfish are native to the tropical waters of the western Pacific Ocean and the eastern Indian Ocean. The natural distribution of *P. volitans* includes the Indian and Pacific oceans, and covers a very large area; while *P. miles* is native to the Red Sea, the Persian Gulf and the Indian Ocean, with the exception of Western Australia (Fig. 1) (Schultz, 1986).

Lionfish have spread rapidly across a wide geographic region, mainly from the USA southeastern coast to the Brazilian coast. Since the early 1990 its presence has been reported in the western Atlantic, however, as of 2010, a significant dispersal of this invader was observed in the region (Fig. 2).

The first sighting of lionfish in the western Atlantic occurred in Florida in 1985 (Morris and Akins, 2009). Other observations were recorded subsequently in 1992, due to the accidental release of six individuals from a home aquarium in Biscayne Bay, Florida (Courtenay, 1995 cited by Morris and Akins, 2009). During the following years, sporadic appearances of the species occurred along the USA coasts (Whitfield et al., 2002; Schofield, 2009).

Lionfish were reported in the Bermuda Islands in 2000 (Whitfield et al., 2002), in the Bahamas in 2004, in the Turks and Caicos Islands in 2006, in Colombia, the Cayman Islands, Jamaica, Puerto Rico, Haiti, Belize and the Dominican Republic in 2008 (Guerrero and Franco, 2008; Schofield, 2009). In 2009 it was registered in Mexico, Panama, Honduras, Costa Rica (Schofield, 2009) and Nicaragua (Schofield, 2010); and in 2014 in Brazil (Ferreira et al., 2015).

Chevalier-Monteagudo et al. (2008) made the first report of lionfish in Cuba in 2007, from the capture of two specimens of *P. volitans*, in Los Caimanes keys southern coast, Villa Clara. In June 2007, another specimen was captured on the southeast coast of the Baconao Aquarium in Santiago de Cuba. Subsequently, observations of *P. volitans* / *P. miles* were reported in numerous localities of the country (Chevalier-Monteagudo et al., 2008). It is estimated an initial settlement on the northern coast between late 2006 and early 2007, and from 2009, when they colonized the southern coast from east to west (Chevalier-Monteagudo et al., 2014). Lionfish populations were stabilized in 2011 in the northern coast, while in the south, densities began to stabilize later (Chevalier-Monteagudo et al., 2014). In 2010, the lionfish was considered as an IAS established throughout the Cuban archipelago.

Comentado [MOU3]: In reality, at least 100 organisms are required for the invasion to be successful, so the theory of the intentional release of 6 organisms is not very conclusive.

Comentado [MOU4]: The first record in Mexico was on an island (Cozumel), later it was recorded in the continental coastal zone.

Comentado [MOU5]: What is meant by stabilize? rather they were established during the year they mention; The establishment and other processes of succession and evolution could be assessed later and during this period if one could already speak of stabilization of the populations...

3.1. Density in its distribution areas

Along its natural distribution areas, ca. 0.25-0.26 ind./100 m^2 (ind.: lionfish) average densities have been recorded, with a range from 0 to 1.11 ind./100 m^2 (Darling et al., 2011; Kulbicki et al., 2012) (Table 1). On the contrary, in the Atlantic Ocean its density tends to be notably higher, e.g., densities higher than 1 ind./100 m^2 in the Mesoamerican Reef, in Cuba (Jardines de la Reina) (Hackerott et al. 2013), and in the Bahamas (Green and Côté, 2008; Darling et al., 2011) (Table 1). In artificial reefs in the Gulf of Mexico the densities recorded are even higher, e.g. 14.7 ind./100 m^2 (Dahl and Patterson III, 2014) and 32.98 ind./100 m^2 (Dahl et al., 2019).

Comentado [MOU6]: the densities presented in several countries are not very precise. In the Mexican Caribbean, these have been from 5-10 and up to 60 ind individuals per hectare.

In Cuba, reported lionfish densities are relatively high (2.1 ind./100 m^2) (Chevalier-Monteagudo, 2017), compared to these documented in the Indo-Pacific (Darling et al., 2011; Kulbicki et al., 2012) and in other locations in the western Atlantic (1.1 ind./100 m^2; 0.1 - 3.9 ind./100 m^2) (Table 1). Even higher density values have been reported in the Guanahacabibes National Park (GNP) and in the tourist coast of Holguín (Cobián-Rojas et al., 2016; Reynaldo et al., 2018). In GNP it is considered one of the most abundant species on coral reefs and densities above 5.0 ind./100 m^2 have been recorded (Cobián-Rojas et al., 2016; 2018a), while in the tourist coast of Holguín have been recorded lionfish densities of 12.42 ind./100 m^2 (Reynaldo et al., 2018). One of the main concerns related to the lionfish invasion in Cuba is the ability of their populations to grow rapidly in number. On the coast of Holguín in just one year, there was a notable increase in the density of this invader (1.01 ind./100 m^2 in 2013, 7.5 ind./100 m^2 in 2014) (Vega et al., 2015; Reynaldo et al., 2018), a fact that shows the need to strengthen control strategies.

Eliminado: 2016; 2018

4. Factors that have allowed its successful establishment

The speed and success of the lionfish expansion in the Atlantic Ocean and the Caribbean Sea indicate that it has been favored by its biological and ecological traits, as revealed by several researches. For instance, it has characteristics that are predictors of the ability of non-native fishes to invade territories outside its natural range (Morris and Whitfield, 2009; Côté and Smith, 2018): extensive native distribution range (Schultz 1986), wide diet (Morris and Akins, 2009; Cure *et al.*, 2012), ability to tolerate long periods of fasting [up to 10 weeks of fasting] (Fishelson, 1997), traits that allow to consume large and elusive prey [stomach with the ability to expand 30-32 times, large diameter of its mouth, high suction capacity, large protrusion of the premaxilla] (Fishelson, 1997; Rojas-Vélez et al., 2019), and preys that not recognize it as a predator (Albins and Lyons, 2012; Berchtold and Côté, 2020) and lack of defenses against lionfish (Santamaría et al., 2008). In addition, lionfish have: high physical tolerance (Fishelson, 1997; Burford et al., 2019), effective defense mechanisms [spines loaded with poison] (Saunders and Taylor, 1959; Cohen and Olek, 1989; Whitfield et al., 2006), absence of effective biotic resistance mechanism in the invaded area (Hackerott et al., 2013; Valdivia et al., 2014; Cobián-Rojas et al., 2018b), resistance to ectoparasites (Côté and Smith, 2018), rapid growth [growth rate (K) equivalent to 0.42 for an entire population sampled in Little Cayman, with estimates of 0.38 for males, and 0.57 for females (Edwards et al., 2014), although values higher than these have been found by other authors (see Côté and Smith, 2018)]; early sexual maturity (Bustos-Montes et al., 2020), long breeding season [all year] (Morris and Whitfield, 2009; Morris et al., 2011a; Gardner et al., 2015), high fecundity [1800 - 41 945 eggs per laying] (Gardner et al., 2015), larval period with an adequate duration to achieve a wide dispersal [20 - 35 days] (Ahrenholz and Morris, 2010), ability to travel long distances [1.38 km] and even crossing large areas of sand considered barriers to the movement of most reef fishes (Tamburello and Côté, 2014), relatively large body size [45 cm in total length, with sexual dimorphism where the male reaches the largest sizes and presents slower growth] (Whitfield et al., 2006; Morris and Whitfield, 2009; Darling et al., 2011; Edwards et al., 2014) and relatively high longevity [ca. 10 years] (Froese and Pauly, 2019). Importantly, a recent research based on a sample of 64 lionfish from the northwestern of Havana (Cuba), provides new knowledge regarding aspects of the reproductive biology of lionfish that allow its successful establishment (Cruz-López et al., 2020). In addition to record sexual dimorphism in lionfish [higher length and weight in males than in females], these authors recorded high number of gametes in the gonads, semicystic spermatogenesis and reproductive activity during all year. All these are clear advantage for lionfish as species, but particularly as invasive .

Comentado [MOU7]: as an alien and invasive species

Regarding parasitism, lionfish have been shown less quantity and diversity of parasites than other Atlantic fishes found in similar environments (Côté and Smith, 2018). The characterization of the parasitic fauna of the lionfish in Cuba showed that the composition of parasitic species by taxonomic group is poor; the infection parameters have very low values and differ markedly from those reported in native hosts that live in the same sites as the lionfish analyzed (Chevalier-Monteagudo et al., 2013). These authors suggest that native parasitic communities have not yet established and consolidate their life cycles in this new host. All the discussed characteristics allow understanding how has been possible the lionfish establishment and dispersion so successfully and rapidly in the Caribbean and the western Atlantic.

5. Habitats invaded by lionfish

Lionfish have occupy a wide range of habitats, including estuaries, seagrass beds, coral reefs, hard and rocky bottoms, channels, and mangroves. It has been observed taking refuge in association with biotic and abiotic structures present in these habitats, e.g. rocks, coral heads, artificial structures such as concrete blocks, retaining walls and posts, and softer structures such as sponges, walls of blowouts in seagrass beds and in mangrove roots (Barbour et al., 2011; Claydon et al., 2012; Pimiento et al., 2013). The depth range reported for this invader is 2 - 55 m (Froese and Pauly, 2019); however, it has been repeatedly described in mesophotic reefs more than 60 m deep, in the native and invaded areas (Andradi-Brown et al., 2017; Luiz et al., 2021). There are records of its presence at more than 245 m depth in Curaçao (247 m), Honduras (250 m), Bahamas (300 m), and Bermuda (304 m) (Andradi-Brown, 2019 and reference therein).

In Cuba, the presence of lionfish has been observed in shallow coral reefs (Chevalier-Monteagudo, 2017; Cobián-Rojas et al., 2018a, b) and mesophotic reefs at a maximum depth of 188 m (Reed et al., 2018; Cobián-Rojas et al., 2021). Additionally, this invader has been recorded in mangroves (Pina-Amargós et al., 2012; Guardia et al., 2017; Rodríguez-Viera et al., 2018), seagrass beds (del Río et al., 2022), submerged artificial structures and muddy bottoms with stones (Chevalier-Monteagudo et al., 2013), and it is also usually abundant in artificial shelters used in the lobster fishery (Rodríguez-Viera et al., 2018). In Holguín, higher densities of lionfish have been recorded in the fore reefs (0.3 ind./100 m^2) compared to other habitats such as seagrass beds (0.1 ind./100 m^2) (Vega et al., 2015). Regarding the lionfish size among different habitats, a comparative study between mangrove and coral reefs in Cayos de San Felipe National Park, estimated lower lionfish sizes in mangroves (average size: 126 mm) to those estimated in coral reefs (241-258 mm) (Guardia et al., 2017). In a recent study carried out in the Punta Francés National Park (PFNP), lionfish caught in seagrass beds had smaller sizes (average length: 212 mm) than those captured in coral reefs

Eliminado: occupied

Eliminado: conquered

Comentado [MOU8]: also, in docks for small boats and in soft corals

Comentado [MOU9]: 0 to 55 m

Comentado [MOU10]: in the bahamas with a submarine, lionfish have been recorded at a depth of 300 m
In Puerto Morelos, Mexico we have collected organisms at 60 meters

Eliminado:

(average length: 252 mm) (del Río et al., 2022). This trend has been observed also in Holguín, where larger individuals have been recorded in coral reef patch and fore reef than those observed in the artificial refuges, seegrass beds and estuaries (Vega et al., 2015).

6. Predatory behavior and diet

The predatory strategy of the lionfish is practically unique among the predatory fishes from the western Atlantic and the Caribbean. When the lionfish chooses his target, it corners the prey against a rock or confined space using its large pectoral fins, moving close enough with its fins extended, and attacks quickly (Côté and Maljkovic, 2010; Albins and Hixon, 2011). In addition, it can expel rapid jets of water that cause a disorder in the lateral line system of the prey fishes, and it creates a small current that disorients, causing the prey movement towards the lonfish mouth (Cure et al., 2012). Apparently, lionfish prefer to grab their prey by the head, which allows them to avoid accidents with the spines and limits the possibilities of escape (Albins and Lyons, 2012). Generally, they swallow the whole prey (Morris and Green, 2013).

In the Indo-Pacific, lionfish generally feed during dawn and dusk (Cure et al., 2012). However, a study carried out in the Bahamas showed greater predatory activity in the morning, mainly between 07:00 am and 11:00 am, with a significant decrease during the afternoon (Morris and Akins, 2009). In contrast, subsequent research conducted in the Bahamas and Cayman Islands shows twilight feeding behavior (Green et al., 2011; Cure et al., 2012). In Cuba, a higher consumption of preys has been observed in the morning, especially in the hours of 8:00 am-10:00 am even until 12:00 m (Chevalier-Monteagudo et al., 2013). However, studies aimed at evaluating the nocturnal diet of lionfish in Cuba have shown a higher proportion of full stomachs, a more diverse diet, and a greater predominance of fishes compared to the daytime diet (Chevalier-Monteagudo, pers. comm., ANC, 1st street No. 6002, Playa, Havana, Cuba).

Numerous studies show that the lionfish is a generalist predator capable of varying the composition of its diet depending on the most available preys in the region where it lives (Arredondo-Chávez et al., 2016; Peake et al., 2018; Sancho et al., 2018). However, some studies have shown that lionfish can also exhibit preferences for certain preys, (Ritger et al., 2020; Santamaria et al., 2020). After conducting numerous samplings aimed at studying lionfish diet in Cuban locations, a great diversity of food entities was recorded (Chevalier-

Comentado [MOU11]: generalist carnivore

Monteagudo et al., 2013). In addition, it was observed a strong correlation between the number of entities found in the lionfish diet and the densities in the wild, wich includes several fish families and species. This trend suggests that lionfish did not present preferences for specific preys in these localities, but rather feed on the most available preys.

6.1. Diet components

Lionfish have a primarily piscivorous diet, supplemented with crustaceans and other invertebrates such as echinoderms and mollusks (Green et al., 2011; Chevalier, 2017, Dahl et al. 2017). In the invaded area they have a broader diet (Albins and Hixon, 2008; Dahl and Patterson III, 2014; Pantoja et al., 2017). For instance, numerous fish families have been recorded in the stomach contents of lionfish (Fig. 3). Among the best represented families are: Pomacentridae, Acanthuridae, Blennidae, Labridae, Serranidae, Gobiidae, Grammatidae, Apogonidae, Atherinidae, Mullidae, Monacanthidae, Scaridae, Haemulidae and Carangidae (Morris and Akins, 2009; McCleery, 2011; Sandel, 2011; Muñoz et al., 2011; Valdez-Moreno et al., 2012; Arredondo-Chávez et al., 2016; Hackerot et al., 2017). However, crustaceans may become more important than fishes in the lionfish diet (Dahl and Patterson III, 2014; Villaseñor-Derbez and Herrera-Pérez, 2014). The proportional importance of crustaceans in the diet is inversely related to the size of this predator. Larger lionfish tend to increase fish consumption and decrease crustacean consumption, in addition to preferring larger prey; this ontogenetic change has been observed in numerous studies (Morris and Akins, 2009; Muñoz et al., 2011; Arredondo-Chávez et al., 2016; Peake et al., 2018; Sancho et al., 2018).

In Cuba, several studies have been developed aimed at knowing the main components of the lionfish diet (García, 2015; Vega et al., 2015; Pantoja, 2016; Cobián-Rojas et al., 2016; Pantoja et al., 2017; Chevalier-Monteagudo, 2017; del Río et al., 2022). These have analyzed the stomach content of lionfish from different Cuban locations. The identified food entities are included in three main groups: fishes, crustaceans and mollusks, in that order of abundance. The most important fish families for the diet have been Pomacentridae, Gobiidae, Scaridae, Holocentridae, Mullidae, Labridae and Acanthuridae. In the case of crustaceans, the orders Decapoda, Mysida, Stomatopoda and Isopoda, the infraorder Brachyura and

Comentado [MOU12]: there is a nutritional differentiation based on the state of maturity; adults have a slightly different diet than juveniles or smaller organisms.
In the lionfish invasion zone, there is enough food available, so they wait for their preferred prey before consuming any.

Arredondo-Chávez et al., 2016

Comentado [MOU13]: first molluscs and then echinoderms

Eliminado:

Eliminado:

Comentado [MOU14]: especially in youth stages, not so in adults shrimps (infraorders Stenopodidea and Caridea, and the superfamily Penaeoidea) have predominated.

7. Potential impact of lionfish in the invaded area

Comentado [MOU15]: the impacts are no longer potential, they are already a reality throughout the invasion zone and they are occurring now...

One of the great concerns that have arisen after the lionfish invasion is its effect on other native organisms, since its arrival breaks the existing balance in the invaded ecosystem. Once the invasion has occurred, there is a new predator, a new competitor and perhaps a new prey, which tends to reach high densities and has characteristics that guarantee its success as an invader (Fig. 4).

7.1. Impact by predation

Numerous studies have shown that the lionfish is capable of producing great effects on coral reef communities through the direct predation of native fishes and invertebrates (Albins and Hixon, 2008; Morris and Akins, 2009; Valdez-Moreno et al., 2012; Cobián-Rojas et al., 2018b). Some alarming results show that there is the possibility that it could even cause the extinction of endemic native species of limited distribution (Côté and Smith, 2018). As generalist predator, lionfish include numerous fishes and invertebrate's species from the western Atlantic and the Caribbean (Morris and Akins, 2009; Dahl et al., 2017), and is capable of consuming preys on reefs at a rate higher than that which native populations can assimilate (Green and Côte, 2010). However, Peake et al. (2018) suggest that the fact that lionfish is an opportunistic generalist predator considerably reduces the risk of causing prey extirpation, since it consumes the most abundant and available preys. The deterioration of coral reefs due to the presence of lionfish would also affect other organisms that depend on these ecosystems, so the consequences could be very serious. One of the greatest information gaps is its synergistic effect with additional stressing factors already existing in coral reefs [e.g., eutrophication, sedimentation, increase in water temperature, coral bleaching, overfishing] (Loya and Kramarsky-Winter, 2003; Fabricius, 2005; Eakin et al., 2019; Jackson et al. 2014). These interactions can enhance the deterioration of these ecosystems.

Comentado [MOU16]: at least local extinctions

Eliminado: invertebrates

Comentado [MOU17]: consumes the prey it wants, if they are not available at moment A, it waits for moment B to consume it and this, which occurs in the natural environment, contradicts what was mentioned by Peake et al, 2018

Comentado [MOU18]: and the effect of the massive arrival of sargassum to the greater Caribbean

By altering food webs, lionfish could unleash cascading repercussions that affect the entire ecosystem. The possibility of lionfish decimating populations of important herbivores, i.e. parrotfish (Scaridae) and surgeonfish (Acanthuridae), has been raised, as these have been identified as part of their diet in numerous studies (Fig. 3) (Albins and Hixon, 2008; Morris and Akins, 2009; Cure et al., 2012; Arredondo -Chávez et al., 2016; Chevalier, 2017; Pantoja et al., 2017). By feeding on herbivorous fishes, the control that these key groups carry out over macroalgae is compromised, an essential process for maintaining the coral reefs health (Fig. 4) (Morris, 2013; Steneck et al., 2014; Kindinger and Albins, 2017). It has been shown that some herbivores such as parrotfish may not recognize the lionfish as a predator, which considerably increases the predation risk (Berchtold and Côté, 2020), or may change their behavior (e.g., decreased general grazing intensity) and produce an increase of algal cover on coral reefs (Eaton et al., 2016; Kindinger and Albins, 2017).

Lionfish also can feed on juvenile snapper and grouper (Fig. 4) (Morris and Akins, 2009; Villaseñor-Derbez and Herrera-Pérez, 2014; Dahl et al., 2017), important groups that include potential lionfish predators (Maljkovic and Van Leeuwen, 2008). Additionally, lionfish feed on cleaning fishes (e.g. *Thalassoma bifasciatum*) which can alter the structure and function of communities on invaded reefs (Fig. 4) (Tuttle, 2017).

Given the threat posed by *P. volitans* / *P. miles* to invaded ecosystems, it became a necessity to carry out local studies that provide observations of its impact on the community structure and the abundance of fishes and other organisms present in their diet. Some experiments have shown that lionfish can considerably reduce the fish recruitment and fish forage, as well as the abundance and richness of native fishes that constitute its prey, an effect that is greater when native predators are also present (Albins and Hixon, 2008; Green et al., 2012; Albins, 2013; 2015; Samhouri and Stier, 2021). The possibility that these experimental effects can be extrapolated to the entire reef has been contemplated (Morris and Green, 2013). However, should be taken into account that the lionfish effects on native prey in small-scale experiments do not necessarily reflect the results in nature (Hackerot et al., 2017).

Hackerot et al. (2017) conducted a study on a larger geographic scale and found no evidence that lionfish appreciably affected the density, richness, or composition of prey fishes. In contrast to these results, a study aimed at examining the impact of lionfish invasion on a wide regional and temporal scale, suggested that experimental studies to small-scale reef patches in the Bahamas could provide good indications of the impact of the invasion in a wider region (Ballew et al., 2016). Another study on a regional scale showed that species at risk of extinction, those of fishing interest and those threatened by overfishing, contribute little to the diet of lionfish in the western Atlantic (Peake et al., 2018).

Eliminado:

Comentado [MOU19]:

The lionfish diet studies in different Cuban locations allowed detecting which are the most affected fishes and invertebrates by direct predation, in addition to providing information about their effects on them (e.g. García, 2015; Pantoja, 2016; Pantoja et al., 2017). The analysis of the main ecological relationships of lionfish in Havana reefs showed that lionfish effect is limited to the lionfish most abundant fish prey families and species (García, 2015). *P. volitans* doesn't affect the population variables of the usual lionfish fish preys neither the ecological variables of the ecosystem, after studying several Cuban locations (Chevalier-Monteagudo, 2017). The new associations detected between native fishes and this invader show the possibility that lionfish is progressively becoming in an additional component of the Caribbean's biodiversity (Chevalier-Monteagudo, 2017). Concordantly, no changes were detected in most of the diversity and equity indices of the fish communities in GNP, when comparing several years before the lionfish invasion and years after the invasion (Cobián-Rojas et al., 2018a). These authors discussed that variations in richness, diversity, and equity appear to be more related to reef structure and the effects of fishing than to lionfish abundance. However, in other study conducted in GNP, it was detected that the abundance and size of preys decreased as the abundance of lionfish increased (Cobián-Rojas et al., 2018b). Analysis of the density, size, biomass and diet of lionfish in the GNP suggests that their impact on preys may increase when the invader reaches larger sizes and its populations grow (Cobián-Rojas et al., 2016). Additional studies are required to assess the impact of lionfish as a predator after several years of invasion on a larger geographic scale and in different ecosystems invaded in Cuba and in other areas of the region.

Comentado [MOU20]: I think it is a very eventful conclusion

7.2. Impact by competition

Lionfish can also harm other organisms through competition for food or shelter (Fig. 4) (Morris and Whitfield, 2009; Morris and Green, 2013; Dahl et al., 2017). This invader occupies the same habitats, and consumes the same preys as many native fish species and macroinvertebrates (Morris and Green, 2013; Arredondo-Chávez et al., 2016; Peake et al., 2018). A possible competition for food has been evidenced between lionfish and native fish such as *Cephalopholis cruentata, Cephalopholis fulva*, squirrelfishes (Holocentridae), *Epinephelus guttatus* and *Lutjanus apodus*, due to the overlap between their isotopic niches (Curtis et al., 2017; Eddy et al., 2020; Murillo-Pérez et al., 2021). Although some researches have not detected that lionfish affect the density and species richness of its competitors

(Chevalier-Monteagudo et al., 2013; Elise et al., 2014; Chevalier-Monteagudo, 2017), the effect that may have over them, in conditions of low availability of resources, constitutes an important concern. Competition with lionfish could affect the behavior, distribution, growth, survival, and even population size of competitors (Morris and Green, 2013).

Some studies suggest that lionfish could surpass native predators in the competition for food resources and decrease the abundance of the species that constitute their prey (Albins and Hixon, 2008; Morris and Akins, 2009; Albins, 2013). This fact could be explained taking into account that this invader tends to grow faster (Albins, 2013; Bustos-Montes et al., 2020) and can consume prey at a higher rate than some of these predators (Albins, 2013; Marshak et al., 2018). Additionally, its morphological characteristics offer mechanical advantages for the consumption of a wide variety of benthic and cryptic animals (Rojas-Vélez et al., 2019).

In terms of competition for space, lionfish have a similar habitat preference to *Panulirus argus* and *Diadema antillarum*, so it could compete with these native invertebrates for refuges, if their availability is limited. The invader cause an increase in the activity (time spent: active vs resting) of *P. argus* that could cause a decrease in growth rates and an increase in the risk of predation (Hunt et al., 2020). Besides it has been observed that fishes predated by lionfish use shelters similar to those of this invader, which could lead to competition for this resource. However, it has been shown that lionfish share daytime shelters with some of these fishes (e.g., *Gramma loreto, Canthigaster rostrata, Chromis cyanea*) and the possibility that they act as a client of cleaners or as a protector against other predators is raised (García -Rivas et al., 2017).

Cuban researches have been also focused on evaluating the impact of lionfish over its possible competitors. A study performed in eight localities within six Cuban provinces, compared the densities of lionfish with those of grouper species that have similar ecological niches to that of the invasive fish (e.g., *Cephalopholis cruentata, Cephalopholis fulva* and *Epinephelus guttatus*) (Chevalier -Monteagudo et al., 2013). It was observed that lionfish densities tend to be similar or higher than those of their possible competitors and the possibility that the invasive fish could displace some of these native groupers from their ecological niche, and prevent the recovery of their populations. However, no significant correlations were observed between lionfish and the fish families that constitute their potential predators and competitors, in terms of abundance, biomass and mean size

(Chevalier-Monteagudo et al., 2013). In a later study, Pantoja et al. (2017) detected a low overlap among the diets of lionfish and those of the Haemulidae, Serranidae and Holocentridae families in GNP. It was shown that, although lionfish are essentially piscivorous like snappers (Lutjanidae) and groupers (Serranidae), its diet content differs in the proportion of fishes, crustaceans and mollusks. Therefore, these authors suggest that lionfish probably do not constitute a threat to native fishes of similar trophic level in the competition for food resources. Additionally, Chevalier-Monteagudo (2017) did not detect that *P. volitans* populations altered the population variables of their main competitors in this same location.

7.3. Socio-economic impact

In addition to threatening the ecological functioning and biodiversity of reefs, lionfish represent an economic risk (Morris and Whitfield, 2009; Arredondo-Chávez et al., 2016). Among the most vulnerable sectors are fishing and tourism, which are of great importance to many countries in the Caribbean and the Atlantic Ocean (Morris and Green, 2013). The fisheries sector is affected by the inclusion of juvenile stages of commercially valuable species (e.g., *Epinephelus striatus; Ocyurus chrysurus; Rhomboplites aurorubens; Haemulon aurolineatum; Lutjanus campechanus; Pristipomoides aquilonaris* and *Pagrus pagrus*) in the diet of lionfish (Morris and Whitfield, 2009; Morris and Akins, 2009; Ballew et al., 2016; Dahl et al., 2017; Peake et al., 2018). Additionally, the presence of crab and shrimp species important for fisheries (e.g. *Menippe mercenaria* and *Farfantepenaeus duorarum*) has been detected in their diet (Sancho et al., 2018). The predatory activity of lionfish on such species of commercial interest could reduce their catches, hinder efforts aimed at the recovery of fishing populations and slow down initiatives aimed at the management and conservation of these groups (Morris and Akins, 2009; Morris and Green, 2013).

The ecological impact of lionfish can potentially cause a reduction in tourist interest in the most affected areas, due to the decrease in the attractiveness of the reefs. In Cuba the lionfish has been registered in areas of interest for tourism, e.g. Holguín's tourist coastline (Vega et al., 2015; Reynaldo et al., 2018), the GNP (Cobián-Rojas et al., 2016; 2018a, b), the PFNP (del Río et al., 2022), Jardines de la Reina National Park (Pina-Amargós et al., 2012; 2021). In such cases, should be noted that all these represent recreational diving sites, an activity that depends considerably on the attractiveness of the fauna and the ecosystem as a whole. Therefore, the need for adequate control of this invader in these areas is evident, to avoid damaging the ecosystems vital for tourism and thereby affecting the economy. The concern generated in this regard has prompted studies aimed at evaluating the impact of lionfish and the establishment of effective control strategies in some of these affected areas (Labastida et al., 2015; Cobián-Rojas et al., 2016; Pantoja et al., 2017; Cobián-Rojas et al., 2018 a, b; del Río et al., 2022).

8. Control of lionfish populations

Since the beginning of the invasion, the potential impact of this IAS has aroused the interest of researchers in detecting possible natural drivers of their populations. In the Caribbean, lionfish have been found in the stomachs of large groupers (Maljkovic and Van Leeuwen, 2008; Mumby et al., 2011; Côté and Smith, 2018), which highlights the possibility that groupers can act as a biological controller of this IAS. In a recent study of Dahl and Patterson (2020), lionfish were tracked using an acoustic system on artificial reefs, and strong evidence regarding lionfish predation was obtained pointed to sharks or large groupers as predators, since several species have been observed in the area.

Mumby et al. (2011) detected evidence of the probable predation of lionfish by groupers. However, the overfishing of groupers (Whitfield et al., 2006) and predation during their juvenile stages by lionfish (Morris and Akins, 2009; Villaseñor-Derbez and Herrera-Pérez, 2014), hinder their effective participation as natural control in the Caribbean. In subsequent studies carried out in Cuba, Bahamas, Belize, Mexico and Colombia no evidence of predation by potential predators (i.e., groupers and snappers), has been observed (Valdivia et al., 2014; Cobián-Rojas et al., 2018b; Rojas-Vélez et al., 2019). Additionally, in a recent study, the stomach contents of more than 200 groupers of five species were analyzed, and the presence of lionfish was not observed among their prey (Smith and Côté, 2021). Such results suggest that the invasion of lionfish cannot be controlled by its potential predators, even when the latter can show a relatively high biomass, e.g., average biomasses of 7.6 g m^{-2} in Caribbean reefs (Valdivia et al., 2014) and 20.0 g m^{-2} in Exuma reefs (Bahamas) (Mumby et al., 2011).

In the absence of effective natural control over lionfish in the Caribbean and western Atlantic, the development of management plans targeting these species has become a necessity. Lionfish extractions are of great importance as a control strategy, since it has been observed that they can decrease their density, and therefore, the potential impact over native prey fishes and overthe most vulnerable components of the ecosystem (Frazer et al., 2012; Côté et al., 2014; Samhouri and Stier, 2021). In addition to density, lionfish sizes have decreased in response to this strategy in various regions within the invaded area, e.g., Bonaire, USA, Bahamas, Cayman Islands, Cuba and Mexico (Frazer et al., 2012; Akins, 2013; Cobián-Rojas et al., 2018a, b). The success of removals could be significantly increased if coordinated removal programs are carried out in connected areas (Díaz-Ferguson and Hunter, 2019).

Cuba is a key exporter of lionfish larvae, so it should be a prime target for lionfish control efforts, and therefore a primary location to implement a comprehensive lionfish culling program (Johnston and Purkis, 2015). Periodic lionfish captures have been carried out in Cuban MPAs, as is the case of the GNP and the PFNP. In a recent study in the PFNP, the average size of lionfish tended to decrease over time, evidencing the effectiveness of systematic extractions performed in the area (del Río et al., 2022). For instance, after the largest extraction of lionfish during that study (226 individuals, average length: 259.52 mm), a notable decrease was observed in the average lengths of the specimens (210.63 mm), which is attributed precisely to the effect of these catches (del Río et al., 2022). In GNP the International Lionfish Fishing Tournament is held annually, unique of this kind in Cuba. To date, five tournaments have been held, which are focused on controlling lionfish through mass catches by divers from local communities, national and foreign professional divers; at the time that is promoted the species consumption by local communities. In the framework of these events, 660 lionfish individuals have been caught in the modality of free diving and autonomous diving, with the participation of 103 fishermen (Cobián-Rojas, pers. comm., GNP, Pinar del Río, Cuba). The catches show a tendency towards the decline of the species in a period of five years in GNP. However, these massive captures have been made in a small sector of this area (less than 10% of the total area), and although they are also captured in the framework of other activities such as scientific expeditions and guided dives carried out by the International Diving Center María la Gorda, it is considered that the control of this invader is insufficient in the GNP. Far from diminishing the importance of the tournaments, this is an example of systematic control of invasive species and contributes directly to the conservation of the coral reefs in GNP and the region. Importantly, in other Cuban areas (non-marine protected areas), lionfish populations have decreased likely as result of submarine fisheries (Chevalier-Monteagudo et al., 2013).

9. Uses of lionfish

Although the lionfish is seen as a negative component in invaded ecosystems, even for human being, it can provide some benefits. They can be used as food, as biomonitoring species of contamination, in aquariums, handycrafts and for obtaining drugs. Besides it can represent an additional tourist attraction during recreational diving, although this is debatable (Whitfield et al., 2002; Sri Balasubashini et al., 2006 a, b; Chel-Guerrero et al., 2020; Van den Hurk et al., 2020).

The use of lionfish as food constitutes an alternative that could contribute to reducing its density in the western Atlantic and the Caribbean. In Cuba, lionfish is recognized as an edible species and is consumed daily in coastal communities (Chevalier-Monteagudo et al., 2013). Educating people about the environmental problems that this invader can cause and its possible use as food, can favor a possible market for lionfish meat (Simnitt et al., 2020; Blakeway et al., 2021). If demand is sufficient, lionfish populations could be reduced to levels that allow the restoration of native ecosystems. For these reasons, evaluating the benefits of its consumption should be a priority in new researches.

In this regard, has been evidenced that proteins and peptides obtained from lionfish muscle has a high quality, due to their amino acid composition (Chel-Guerrero et al., 2020). Additionally, it provides a potential source of antioxidants and chelators, with higher values than those obtained in other species of high demand in human consumption (e.g. *Salmo salar, Onchorhynchus kisutch, Theragra chalco-gramma, Rhopilema esculentum*) (Nakajima et al., 2009; Zhuang et al., 2010; Girgih et al., 2013; Guo, 2015; Chel-Guerrero et al., 2020). The possible accumulation of contaminants in the lionfish musculature is a concern when promoting their use as food. However, a recent study analyzed the presence of 16 rare earth elements and traces of 23 elements in the muscles of a lionfish from Cuba (Squadrone et al., 2020). The results obtained show that lionfish meat is safe and valuable as a source of protein and minerals for the local population.

Substances with possible pharmacological use can be obtained from lionfish. The venom contained in their spines produces reversible changes in the blood and vital organs of mice, and contains many bioactive substances that bind with high affinity to physiological targets

Eliminado: non marine

Comentado [MOU21]: lionfish meat and even the skin, has a high level of protein and fatty acids, so its consumption is highly recommended and with it, control populations Castro-González et al,. 2019 http://lajar.ucv.cl/index.php/rlajar/article/view/vol47-issue5-fulltext-13/1112 and could be used for therapeutic purposes (Sri Balasubashini et al., 2006b). Besides it has been shown to have antitumoral, hepatoprotective and antimetastatic effects in mice with Ehrlich's ascites carcinoma (Sri Balasubashini et al., 2006a), which suggests the possibility of its use in the development of drugs for the cancer treatment. Additionally, proteins and peptides obtained from lionfish muscle with an iron chelating activity greater than 50%, can be used for the treatment of diseases characterized by a high accumulation of iron (e.g., thalassemia major, sickle cell anemia, myelodysplastic syndromes or different subtypes of congenital anemias) (Villegas, 2006; Chel-Guerrero et al., 2020).

Recently, the use of lionfish has also been proposed in the biomonitoring of oil spills in coral reef ecosystems (Van den Hurk et al., 2020). Its use for these purposes has the advantage that, being an invasive species, there are no restrictions on its capture.

The proper management of lionfish as a generator of such benefits may be possible, and importantly, it could represent a profitable and efficient tool in the control of their populations in the western Atlantic and the Caribbean. New studies are required to provide the necessary knowledge to ensure maximum use of this invasive fish. These elements reflect that, in contrast to its multiple potentially negative effects, the lionfish could be considered a species that generates notable ecological and socioeconomic benefits.

Comentado [MOU22]: It is a highly debatable comment, every invasive species tends more to bring negative effects than favorable ones.

10. Final considerations

Considering other reviews articles, which have been focused on the analysis of scientific publications per topic and year, we provide a current view over the well-known lionfish as a marine successful invasor. Importantly, we put in this context the information regarding lionfish in Cuban waters, enriching the background knowledge, giving a novel and relevant information.

Summarizing, the lionfish invasion in the Atlantic Ocean and the Caribbean Sea constitutes a major concern for the scientific community and marine protected area managers, since its colonization capacity and the speed with which it has spread, make it a potential threat for the integrity of invaded ecosystems. This concern has been reflected on the wide range of scientific publications, focused on diverse topics of lionfish in the invaded area, which is notable when compared with those from its native distribution (Fig. 5; Table S1). Lionfish is a new predator with the potential to affect negatively populations of native organisms, by direct predation or by competition for trophic resources. This invader has numerous morphological and behavioral characteristics that ensure its success in a wide variety of habitats. Since the beginning of the invasion, several studies have been carried out that allow the evaluation of its impact in different regions within the invaded area. However, contradictory results have been obtained, which generate the current controversy: is lionfish so dangerous, or do the affected ecosystems return to a new state of equilibrium even with the presence of this invader? It is therefore necessary to carry out new studies to expand current knowledge about the abundance and distribution of lionfish in invaded ecosystems, its impact on them, the composition of their diet and the state of the main affected species. New research should cover broader time scales, enabling a more complete analysis of its impact on native species and ecosystems. The knowledge generated will increase the efficiency of the control and management plans in the invaded areas. These plans should include the development of environmental education programs aimed at the entire population, mainly those living in coastal communities, as well as actions that promote fishing and the consumption of lionfish. New investigations directed to the use of this species, expand the possibilities of management and the implementation of its potential benefits.

Comentado [MOU23]: Since it is not now news and the species in fashion, now the massive arrival of sargassum in the Caribbean is in the spotlight, the funds for lionfish studies are less, scarce or do not exist and this makes it difficult to generate current information and that of proposals to respond to the huge problem that remains

Acknowledgments

Thanks to Davier Ojeda for their technical assistance in drawing the diagram, and also to Alejandro Camejo for reviewing the English of the manuscript.

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Con formato: Inglés (americano)

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COMMENTS IN TITLES OF FIGURES AND TABLES

Figure 1. Natural range of the lionfish species *Pterois violitans* and *P. miles*

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on figure 2, there are maps and data published at least until the year 2020, it is suggested to update this figure

In the diagram of figure 4, sharks, rays and barracudas are missing from the diagram

table 1 organize geographically for the invasion zone and to make its analysis more explicit

Con formato: Fuente: Sin Cursiva