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Low Pufferfish and Lionfish Predation in Their Native and Invaded Ranges Suggests Human Control Mechanisms May Be Necessary to Control Their Mediterranean Abundances

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The silver-cheeked toadfish (*Lagocephalus sceleratus*, from the pufferfish family Tetraodontidae) and the Pacific red lionfish (*Pterois miles*, family Scorpaenidae) have recently invaded the Mediterranean Sea. *Lagocephalus sceleratus* has spread throughout this entire sea with the highest concentrations in the eastern basin, while more recently, *Pterois miles* has spread from the Eastern to the Central Mediterranean Sea. Their effects on local biodiversity and fisheries are cause for management concern. Here, a comprehensive review of predators of these two species from their native Indo-Pacific and invaded Mediterranean and Western Atlantic ranges is presented. Predators of Tetraodontidae in general were reviewed for their native Indo-Pacific and Western Atlantic ranges, as no records were found specifically for *L. sceleratus* in its native range. Tetraodontidae predators in their native ranges included mantis shrimp (Stomatopoda), lizardfish (*Synodus* spp.), tiger shark (*Galeocerdo cuvier*), lemon shark (*Negaprion brevirostris*), sea snakes (*Enhydrina* spp.), catfish (*Arius* spp.),

cobia (*Rachycentron canadum*), skipjack tuna (*Katsuwonus pelamis*), and common octopus (*Octopus vulgaris*). The only reported predator of adult *L. sceleratus* in the Mediterranean was loggerhead turtle (*Caretta caretta*), whereas juvenile *L. sceleratus* were preyed by common dolphinfish (*Coryphaena hippurus*) and garfish (*Belone belone*). Conspecific cannibalism of *L. sceleratus* juveniles was also confirmed in the Mediterranean. Pufferfish predators in the Western Atlantic included common octopus, frogfish (Antennariidae), and several marine birds. Predators of all lionfish species in their native Indo-Pacific range included humpback scorpionfish (*Scorpaenopsis* spp.), bobbit worms (*Eunice aphroditois*), moray eels (Muraenidae), and bluespotted cornetfish (*Fistularia commersonii*). Lionfish predators in the Mediterranean included dusky grouper (*Epinephelus marginatus*), white grouper (*Epinephelus aeneus*), common octopus, and *L. sceleratus*, whereas in the Western Atlantic included the spotted moray (*Gymnothorax moringa*), multiple grouper species (tiger *Mycteroperca tigris*, Nassau *Epinephelus striatus*, black *Mycteroperca bonaci*, red *Epinephelus morio*, and gag *Mycteroperca microlepis*; Epinephelidae), northern red snapper (*Lutjanus campechanus*), greater amberjack (*Seriola dumerilli*), and nurse shark (*Ginglymostoma cirratum*). The sparse data found on natural predation for these species suggest that population control via predation may be limited. Their population control may require proactive, targeted human removals, as is currently practiced with lionfish in the Western Atlantic.

Keywords: cannibalism, invasive alien species, marine protected areas, predator-prey, trophic ecology, *Lagocephalus*, *Pterois*

INTRODUCTION

To date, approximately 500 of the 800 non-native or alien species detected in the Mediterranean arrived through the Suez Canal (Galil et al., 2016, 2018; Zenetos et al., 2017; Zenetos and Galanidi, 2020). The rate of introductions has further increased within the last decade, likely due to the 2015 recent widening of the Suez Canal, as well as detection and documentation by citizen scientists (Samaha et al., 2016). Invasive alien species are a global threat affecting biodiversity, tourism, recreational activities, the economy, and human health (Bax et al., 2003; Bailey et al., 2020), and, following habitat destruction, is the strongest global driver of native species extinctions (Bellard et al., 2016). Marine biological invasions are of particular concern in the Mediterranean Sea, where there are over 17,000 native species of which 20–30% are endemic (Coll et al., 2010). Despite this high biodiversity, ecosystem health is impaired by cumulative stressors (Micheli et al., 2013). The Mediterranean Sea is one of the most affected regions from overfishing, which has drastically reduced top predator populations and driven substantial changes to food web dynamics (Prato et al., 2013; Boudouresque et al., 2017). These stressors are expected to be further exacerbated by climate change and biological invasions (Bianchi and Morri, 2003; Azzurro et al., 2019). The influx of non-native species is most severe in the Eastern Mediterranean Sea (Ulman et al., 2019) where “Lessepsian migrants” (Por, 1978) enter in the Mediterranean via the Suez Canal since its creation in 1869. During 2000–2005, an average of one new Lessepsian migrant arrived per month (Streftaris et al., 2005). Native community diversity and structure appear to be dramatically altered from these introductions

(D’Amen and Azzurro, 2020). For example, around the island of Rhodes (Greece), 11 out of 88 fish species recorded were found to be non-native species (Kalogirou et al., 2010). Lessepsian migrants make up 85% of total teleost abundance in southeastern Turkey in 2015 (Mavruk et al., 2017), and are likely the cause of a native mollusk population collapse in Israel (Albano et al., 2021).

Knowledge of a system’s predators for an invasive species can help understand the potential direct and indirect impacts of the new species in the food web and evaluate the potential resiliency of the native community to this disturbance (Grüss et al., 2017; Chagaris et al., 2020). Such knowledge should be kept current and consider contemporary co-evolutionary and ecological processes of the ecosystem (Lee, 2002; Lambrinos, 2004). This is particularly germane for the Eastern Mediterranean as its species assemblages are undergoing rapid changes driven by warming waters, Lessepsian migrants, species tropicalization, and fishing pressure (Gücü et al., 2021). Ultimately, the application of this understanding can be used to inform management priorities for monitoring, control, and mitigation efforts.

The silver-cheeked toadfish *Lagocephalus sceleratus* (Gmelin, 1789, of the Tetraodontidae four-toothed family of pufferfishes) and the common lionfish *Pterois miles* (Bennett, 1828, of the Pteroinae subfamily of Scorpaenidae) are two piscivorous Lessepsian invaders of high concern. *Lagocephalus sceleratus* was first recorded in the Mediterranean in Turkish waters of the Aegean Sea in 2003 (Figure 1A; Akyol et al., 2005), followed by Israel in 2004 (Golani and Levy, 2005), and next in Rhodes and Crete in Greece (Corsini et al., 2006; Kasapidis et al., 2007). Within a few years, *L. sceleratus* were abundant throughout Aegean and Levantine coasts (Katsanevakis et al., 2020c). Their

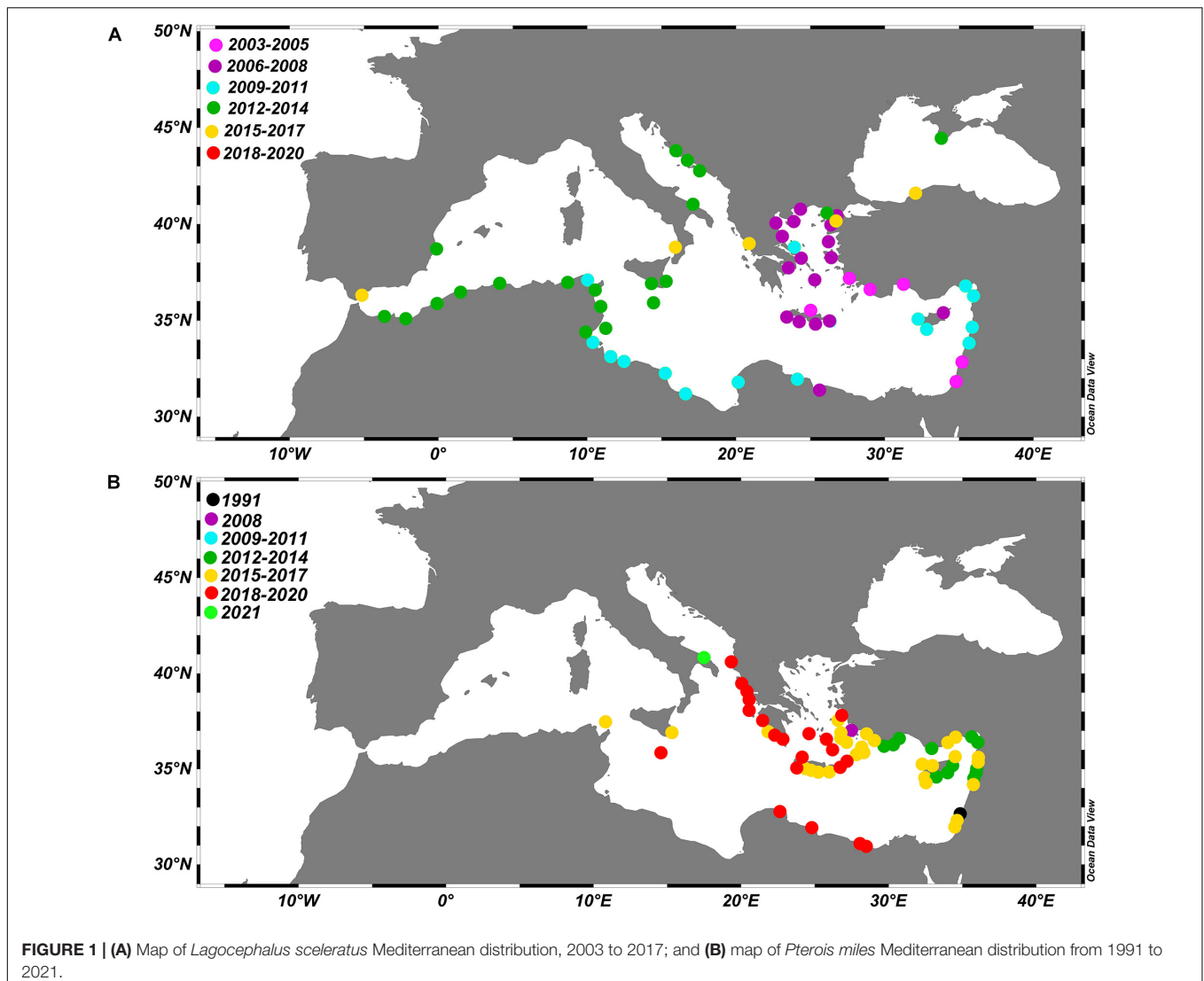


FIGURE 1 | (A) Map of *Lagocephalus sceleratus* Mediterranean distribution, 2003 to 2017; and **(B)** map of *Pterois miles* Mediterranean distribution from 1991 to 2021.

range expanded throughout the Mediterranean Sea during the following decade and are now found from the Strait of Gibraltar to the Black Sea (Akyol and Ünal, 2017; Azzurro et al., 2020; Gücü et al., 2021). Prior to 2010, *L. sceleratus* were only found at depths above 80 m, but they have been progressively expanding their depth range and, in April 2021, were recorded at their deepest depth of 220 m (Sabrah et al., 2006; Aydın, 2011; Ulman et al., in review). *Lagocephalus sceleratus* occupy a wide variety of benthic habitats, including sand, mud, rock, and seagrass meadows (Kalogirou et al., 2010, 2012; Kalogirou, 2013).

The *P. miles* invasion was first recorded in the Mediterranean in 1991 off Israel (Figure 1B), although was not reported again for another 20 years from Lebanon (Golani and Sonin, 1992; Bariche et al., 2013). Evidence of an expanding population were first reported from Cyprus in 2014. Their population then rapidly expanded through the entire Eastern Mediterranean to the central basin in Italy, Malta, and Tunisia (Kleitou et al., 2016; Dimitriadis et al., 2020).

Lionfish in general prefer rocky substrata but *P. miles* has been found to inhabit similar habitats as *L. sceleratus* in the Mediterranean, including mud (Özbek et al., 2017) and seagrass meadows (Savva et al., 2020). *Pterois miles* has been found at 140 m depth in the Mediterranean Sea (Katsanevakis et al., 2020b; Poursanidis et al., 2020). Aggregations of over 30–35 individuals per 10 m² have been observed off Lebanon and Cyprus (Kleitou et al., 2021). Recently, separate reports from Turkey and Greece have recorded areas with densities as high as 30–40 *P. miles* individuals per 10 m² (Dimitriadis et al., 2020; Ulman et al., 2020; Kleitou et al., 2021).

Both species are highly invasive due to their potential for health impacts to humans and ecological effects in invaded communities. The *L. sceleratus* pufferfish is highly toxic due to high concentrations of tetrodotoxin (TTX) in their tissues, an extremely potent neurotoxin (Katikou et al., 2009; Kosker et al., 2016), and it is the second-highest toxic pufferfish in the Mediterranean after the yellow-spotted puffer (*Torquigener flavimaculosus*) (Kosker et al., 2018). Tetrodotoxin can be fatal

to humans through paralysis even at very small doses of 1–2 mg (Madejska et al., 2019). From TTX research in *L. sceleratus*, the season, sex and tissue were found to have high variability with gonads having the highest rates, followed by liver, intestines, skin and muscle; and, in general, all-female tissues were found to be toxic throughout the year aside from female muscle in winter (Kosker et al., 2016). Consumption of *L. sceleratus* has caused dozens of human fatalities in the Mediterranean region, which is an underestimation given that many tetrodotoxin related fatalities are not officially recorded (Ben Souissi et al., 2014). *Lagocephalus sceleratus* also compete with native species and have negatively affected cephalopod populations and fisheries via predation (Kalogirou, 2013). Furthermore, they disrupt fishing operations by damaging fishing nets, severing longline and handline hooks, and depredation of catches. Costs due to damaged fishing gear per fisher have increased from 183 USD to 370 USD from 2011 to 2016 along the Turkish Levantine coast (Ünal et al., 2015; Ünal and Bodur, Ünal and Bodur; Gücü et al., 2021).

Pterois miles populations appear to be already impacting native species in the Mediterranean Sea. Their diet off Rhodes (Greece) was mainly composed of fish (78%) from the Gobiidae, Tripterygiidae, Sparidae, and Labridae families (in descending order, respectively, Zannaki et al., 2019). Similarly, off Cyprus, their diet was found to be exclusively composed of native macrofaunal species, including several commercially important species (Savva et al., 2020). The expected ecological effects from lionfish may be severe, given the widespread impacts of invasive lionfish to native fish communities and ecosystem processes in the Western Atlantic (Dahl et al., 2016; Hixon et al., 2016; Côté and Smith, 2018). Lionfish also pose risks to humans as the venom in their 18 spines can cause cardiovascular, neuromuscular, and cytolytic effects, ranging from mild reactions, including swelling, to extreme pain and paralysis in upper and lower extremities (Vetrano et al., 2002; Kiriake et al., 2013). Unlike *L. sceleratus*, no human fatalities have been reported from lionfish.

Here, a comprehensive review of predators for pufferfish and lionfish is undertaken for their native and invaded ranges, however, in the Mediterranean, predators are reviewed only for the highly invasive *L. sceleratus* and *P. miles*. Following this review, we discuss whether natural predation may offer biological control over these invasive species and then present recommendations for their Mediterranean region management.

MATERIALS AND METHODS

We compiled datasets to document predation records on: (1) pufferfish family (Tetraodontidae) and lionfish genus (*Pterois*) in their Indo-Pacific native ranges; (2) *Lagocephalus sceleratus* and *P. miles* in their Mediterranean Sea invaded ranges; and (3) Tetraodontidae and *Pterois* spp. in their Western Atlantic invaded ranges. Predation records for this review were collected from the scientific literature and unpublished sources. Unpublished sources included conference and government reports (i.e., “gray” literature), current research, author

communications with fishers, and citizen reported records. These citizen records included photos and videos found online through social sharing platforms, specifically from YouTube, Facebook and Twitter. These photo and video records were validated when deemed necessary via personal communications from the authors with the citizen that recorded the predation event to ensure consumption did occur. For Twitter and Youtube, the following search terms were used: puffer, pufferfish, lionfish, pufferfish (or lionfish) eaten by, pufferfish (or lionfish) attacked by, eats pufferfish (or lionfish), attack(s) pufferfish or lionfish. For Youtube, after one record was found, other suggested similar videos were monitored for content.

RESULTS

Predation Records on Pufferfish and Lionfish in Their Indo-Pacific Native Ranges

No predation records were found specifically for *L. sceleratus* in its native range but predation records on the pufferfish

TABLE 1 | Predatory records on Tetraodontidae and *Pterois* spp. in their Indo-Pacific native ranges.

Common name	Scientific name	Date/Source
(A) Tetraodontidae predation		
Mantis shrimp	<i>Stomatopoda</i>	Lurot, 2015; https://cutt.ly/DkqVDbY
Lizardfish	<i>Synodus</i> sp.	Santhanam, 2017
Tiger shark	<i>Galeocerdo cuvier</i>	Santhanam, 2017
Moray eel	Muraenidae	Brazolov; https://cutt.ly/wkecmbC
Lemon shark	<i>Negaprion brevirostris</i>	Arthur, 2017; https://cutt.ly/ekrFP4b
Common octopus	<i>Octopus vulgaris</i>	Taylor and Miller; https://cutt.ly/gkqBpEK
Sepik beaked sea snake	<i>Enhydrina zweifeli</i>	Santhanam, 2017
Asian beaked sea snake	<i>Enhydrina schistosa</i>	Santhanam, 2017
(B) Lagocephalus inermis predation		
Cobia	<i>Rachycentron canadum</i>	Mohamed et al., 2013; Saha et al., 2019
Catfish	<i>Arius</i> sp.	Mohamed et al., 2013; Saha et al., 2019
Skipjack tuna	<i>Katsuwonus pelamis</i>	Mohamed et al., 2013; Saha et al., 2019
(C) Pteroinae predation		
Bluespotted cornetfish	<i>Fistularia commersonii</i>	Bernadsky and Goulet, 1991
Humpback scorpionfish	<i>Scorpaenopsis</i> spp.	Hochleithner 2008; https://cutt.ly/hly83Qf
Bobbit worm	<i>Eunice aphroditois</i>	Pistolesi, 2013; https://cutt.ly/Bly3XGM
Yellow edged moray	<i>Gymnothorax flavimarginatus</i>	Bos et al., 2017
Giant moray	<i>Gymnothorax javanicus</i>	Bos et al., 2017

family Tetraodontidae included the following (**Table 1**): Mantis shrimp (Stomatopoda), lizardfish (*Synodus* sp.), tiger shark (*Galeocerdo cuvier*), lemon shark (*Negaprion brevirostris*), sea snakes (*Enhydrina* sp.), catfish (*Arius* sp.), cobia (*Rachycentron canadum*), skipjack tuna (*Katsuwonus pelamis*), and common octopus (*Octopus vulgaris*).

In their Indo-Pacific native ranges, records of predation on lionfish species included bluespotted cornetfish (*Fistularia commersonii*), bobbit worms (*Eunice aphroditois*), humpback scorpionfish (*Scorpaenopsis* spp.) and moray eels (*Gymnothorax* sp.) (**Table 1**).

Predation Records on Pufferfish and Lionfish in Their Invaded Ranges

Mediterranean Records

A photograph of *C. caretta* biting an adult *L. sceleratus* was taken from Antalya, Turkey in 2019 (**Table 2A** and **Figure 2A**). This predation was later confirmed by video from the Mediterranean coast of Egypt in August 2020 (**Table 2A**). After discovery of the video, the filmmaker was contacted via email and sent photos of the existing pufferfish species in the region, and he identified *L. sceleratus* as the prey item he was filming. In support of this, the other pufferfish species do not reach the same large size as *L. sceleratus*, and from these two checks, the record was validated. We found strong evidence of *L. sceleratus* cannibalism in the Mediterranean with 16 total records of *L. sceleratus* juveniles found in adults, with six juveniles found inside one specimen from Tunisia. A dozen other Tetraodontidae species (namely the highly toxic *T. flavimaculosus*, Ulman, unpubl. data) were also found in adult *L. sceleratus* stomachs in Turkey and Tunisia (**Tables 2A,B**). Juveniles of *L. sceleratus* in the Mediterranean Sea appear to have a wider range of predators than adults. Our search indicated juveniles are preyed upon by common dolphinfish (*Coryphaena hippurus*), garfish (*Belone belone*), and larger *L. sceleratus* (**Table 2B** and **Figures 2B–I**).

Interestingly, we found four records of adult *L. sceleratus* preying on lionfish in Turkey and Cyprus (**Table 2C** and **Figure 3**). Multiple records of lionfish predation in the Eastern Mediterranean Sea were also reported for dusky grouper (*Epinephelus marginatus*) in Turkey, Greece, and Lebanon, as well as one predation record by white grouper (*Epinephelus aeneus*) in Cyprus (**Table 2C** and **Figure 3**). There is also one new record of a common octopus consuming a live lionfish (Crocetta et al., 2021).

Western Atlantic Records

As *L. sceleratus* are not present in the Western Atlantic, the Tetraodontidae predation records included octopus and frogfish (Antennaridae) and several marine birds: Yellow-footed gull (*Larus livens*), blue heron (*Ardea herodias*), tri-colored heron (*Egretta tricolor*), and osprey (*Pandion haliaetus*) (**Table 3**).

In the Western Atlantic, recorded predators of *P. volitans* and *P. miles* species included multiple species of groupers (tiger *Mycteroperca tigris*, Nassau *Epinephelus striatus*, black *Mycteroperca bonaci*, red *Epinephelus morio*, and gag *Mycteroperca microlepis*; Epinephelinae), greater amberjack (*Seriola dumerilli*), moray eels (*Gymnothorax* spp.), nurse shark

(*Ginglymostoma cirratum*), lemon shark (*Negaprion brevirostris*), and northern red snapper (*Lutjanus campechanus*) (**Table 3**). Cannibalism was also reported and confirmed in the Northern Gulf of Mexico (NGoM) populations with density-dependent rates (Dahl et al., 2017, 2018). Most predation records were from stomach content analyses, thus it cannot be determined whether predation took place on live or dead lionfish, except from live field observations made from SCUBA dives and studies employing tagging. Two (out of 20) lionfish installed with acoustic telemetry tags on the NGoM artificial reefs were consumed by fast-moving predators such as sharks (Dahl and Patterson, 2020). Tethering experiments on Caribbean coral reefs also show that native predators can consume live lionfish tethered to lead weights (Diller et al., 2014), although it is unknown whether these fish escaped or to what extent the tethering affected the predator-prey interactions.

DISCUSSION

This study compiled new and existing records on the predators of two highly invasive species in the Mediterranean Sea from their native and invaded ranges. For *L. sceleratus* adults in the Mediterranean, recorded predators included only loggerhead turtles and cannibalism, whereas for the less toxic juveniles, predation records included the white grouper, garfish and dolphinfish. Recorded predators of *P. miles* in the Mediterranean included *L. sceleratus*, white grouper, dusky grouper, and common octopus. Overall, we found relatively few predation records for these two species, suggesting that population control might only be possible via removal by human or natural control via disease/parasites unless we enhance and protect native predator populations (Kleitou et al., 2020). Here, the possible biological and ecological reasons for these low accounts of predation are discussed together with their implications for Mediterranean marine managers.

Both Tetraodontids and Scorpaenids have strong chemical and physical defense mechanisms that appear to deter predators. Predation on toxic Tetraodontidae species is limited to predators with TTX-resistant sodium channels in their nervous systems, capable of tolerating the uptake of the poison. It would be interesting to test if the loggerhead turtle also has these TTX-resistant sodium channels present, given that it was the only found predator thus far of an adult *L. sceleratus*. TTX resistant channels are present in other species such as the greater blue-ringed octopus (*Hapalochlaena lunulata*) and marine flatworms (Polycladida), as well as other Tetraodontidae (Saito et al., 1984, 1985), all containing TTX themselves. Scorpaenids similarly use venomous spines as a defense mechanism, and this venom contains acetylcholine and a neurotoxin affecting neuromuscular transmission (Cohen and Olek, 1989). Additionally, both species can enlarge their body size. Pufferfish can inflate with water to become 2–3 times their normal size. This inflation was fatal to a would-be predator by preventing a lemon shark from getting water to its gills (**Table 2A**)¹. *Pterois* species also extend their

¹<https://cutt.ly/ekrFP4b>

TABLE 2 | Predatory records on *Lagocephalus sceleratus* and *Pterois miles* in their Mediterranean invaded ranges; photo credits after Figure reference.

Predator	Date	Location	Evidence type	Figure #, References, or note
(A) Predatory records of adult <i>L. sceleratus</i> in the Mediterranean				
<i>Caretta caretta</i>	11/2019	Antalya, Turkey	Photo	2A. <i>L. sceleratus</i> in mouth. Mayor of Antalya
<i>Caretta caretta</i>	08/2020	Simla, Egypt	Video	https://cutt.ly/ljSV5YH ; Saad Al sharahani
<i>L. sceleratus</i> (500 x)	2019-2020	Datça, Turkey	Pers. comm.	Used <i>L. sceleratus</i> as bait to fish <i>L. sceleratus</i> with hook and line, S. Taşkıran
(B) Predatory records on juvenile <i>L. sceleratus</i> in the Mediterranean				
<i>Epinephelus aeneus</i>	04/2018	Xylofagou, Cyprus	Photo	Figure 2B. Stelios Yiangou
<i>Coryphaena hippurus</i>	07/2019	Limassol, Cyprus	Photo	Figures 2C,D,E. D. Papadopoulos, Kleitou et al., 2018
<i>Belone belone</i>	10/2019	Ierapetra, Crete	Photos	Figures 2F,G. Nikos Petashs. About 24 juveniles in stomach
<i>L. sceleratus</i>	2019-2020	Datça and Fethiye, Turkey, Tunisia	Pers. obs.	Figures 2H,I. 6 accounts of juvenile predation, Turkey (A. Ulman) and heavy cannibalism found in Tunisia with up to 6 juveniles found inside one adult, 11 (J. B. Souissi).
(C) Predatory records on <i>P. miles</i> in the Mediterranean				
<i>E. aeneus</i>	08/2019	Larnaca, Cyprus	Photo	Figure 3A. Stelios Yiangou
<i>E. marginatus</i>	05/2017	Beirut, Lebanon	Photo	Figures 3B–D. <i>P. miles</i> in stomach
<i>E. marginatus</i>	08/2020	Kasos Island, Greece	Photo	Figures 3E,F. Giorgos Zacharis, https://cutt.ly/jjSCSck
<i>L. sceleratus</i>	06/2020	Fethiye, Turkey	Photo	Figure 3G. A. Ulman. <i>P. miles</i> spines found inside 3 <i>L. sceleratus</i> stomachs
<i>L. sceleratus</i>	06/2020	Famagusta, Cyprus	Pers. obs.	<i>P. miles</i> spines found inside one <i>L. sceleratus</i> stomach, Akbora, unpubl. data
<i>O. vulgaris</i>	02/2021	Famagusta, Cyprus	Photos	Crocetta et al., 2021

fins and spines when threatened (Galloway and Porter, 2019). Opportunistic life-history strategies such as reproduction and recruitment, age, growth, and diet may also contribute to the success of both these species in invading the Mediterranean Sea (Sabrah et al., 2006; Fogg, 2017; Ulman et al., in review). Tetraodontidae have high TTX content in their ovaries, which is then passed onto their larvae, which may presumably inhibit larval predation. *Takifugu* spp. larvae have TTX localized on their skin and can effectively deter predation (Itoi et al., 2014). In *Pterois* species, females release eggs encased inside a mucous membrane, which may inhibit predators from sensing the scent or pheromones of the eggs and larvae (Morris et al., 2011b).

Although Tetraodontidae and lionfish are preyed to some extent in all seas, it appears unlikely that predation rates are high enough control of their populations (Arias-González et al., 2011; Barbour et al., 2011; Morris et al., 2011a; Chagaris et al., 2017). Mumby et al. (2011) reported that higher grouper biomasses in fishing-prohibited reefs resulted in a sevenfold decrease in Western Atlantic lionfish biomass, but this conclusion was made from only from 12 dive surveys. Findings from studies of high predator biomasses elsewhere in the invaded Western Atlantic reefs also challenge the hypothesis that lionfish are affected by top-down control. Surveys of 71 reefs conducted in three biogeographic regions of the Caribbean found no correlation between lionfish and native predator abundances (Hackerott et al., 2013; Valdivia et al., 2014). Generally, it appears that lionfish abundances are more strongly correlated to physical and environmental conditions than to community or native predator composition (Anton et al., 2014; Bejarano et al., 2015; Hunt et al., 2019).

It is unknown to what degree *L. sceleratus* and *P. miles* compete with each other in the Mediterranean. Their niches have some

overlap, and they are both generalist predators. Fishers from Kaş (Turkey) attribute *L. sceleratus* bycatch declines in 2020 to *P. miles* abundance increases (A. K. Topuz, pers. comm.). Indeed, competition for habitat (Ellis and Faletti, 2016) and prey (Chagaris et al., 2017, 2020) may help control Western Atlantic lionfish abundances, although empirical measurements of such indirect effects are challenging (Côté and Smith, 2018). From this study, it has been revealed that *L. sceleratus* is already preying on lionfish in the Mediterranean. Further research in the Mediterranean on the extent of spatial and prey overlap of both *L. sceleratus* and its new *P. miles* potential competitor may be of interest, considering sympatry between these two species in their native Indo-Pacific. Currently, the food web and community effects of these species are largely unknown. Natural control of Western Atlantic lionfish may also be exerted by the emergence of disease or parasitism in their invasive ranges. Lionfish in the Western Atlantic initially appeared resistant to pathogens (Stevens and Olson, 2013; Stevens et al., 2016) and parasites (Sikkel et al., 2014; Loerch et al., 2015; Sellers et al., 2015; Fogg et al., 2016; Tuttle et al., 2017). However, in 2017, emergences of an ulcerative skin disease were first observed in the NGoM, with observations reported throughout the invaded Western Atlantic range (Harris et al., 2018). The NGoM lionfish populations exhibited a high prevalence of the disease and, within 18-months, their populations underwent dramatically (>50%) declines in recruitment, densities, and commercial landings (Harris et al., 2020a).

Lagocephalus sceleratus in the Mediterranean Sea and lionfish in the Western Atlantic exhibited evidence for conspecific cannibalism. Earlier reports of *L. sceleratus* diet from visual stomach analyses did not report cannibalism (Aydin, 2011; Kalogirou, 2013). However, our findings suggests that

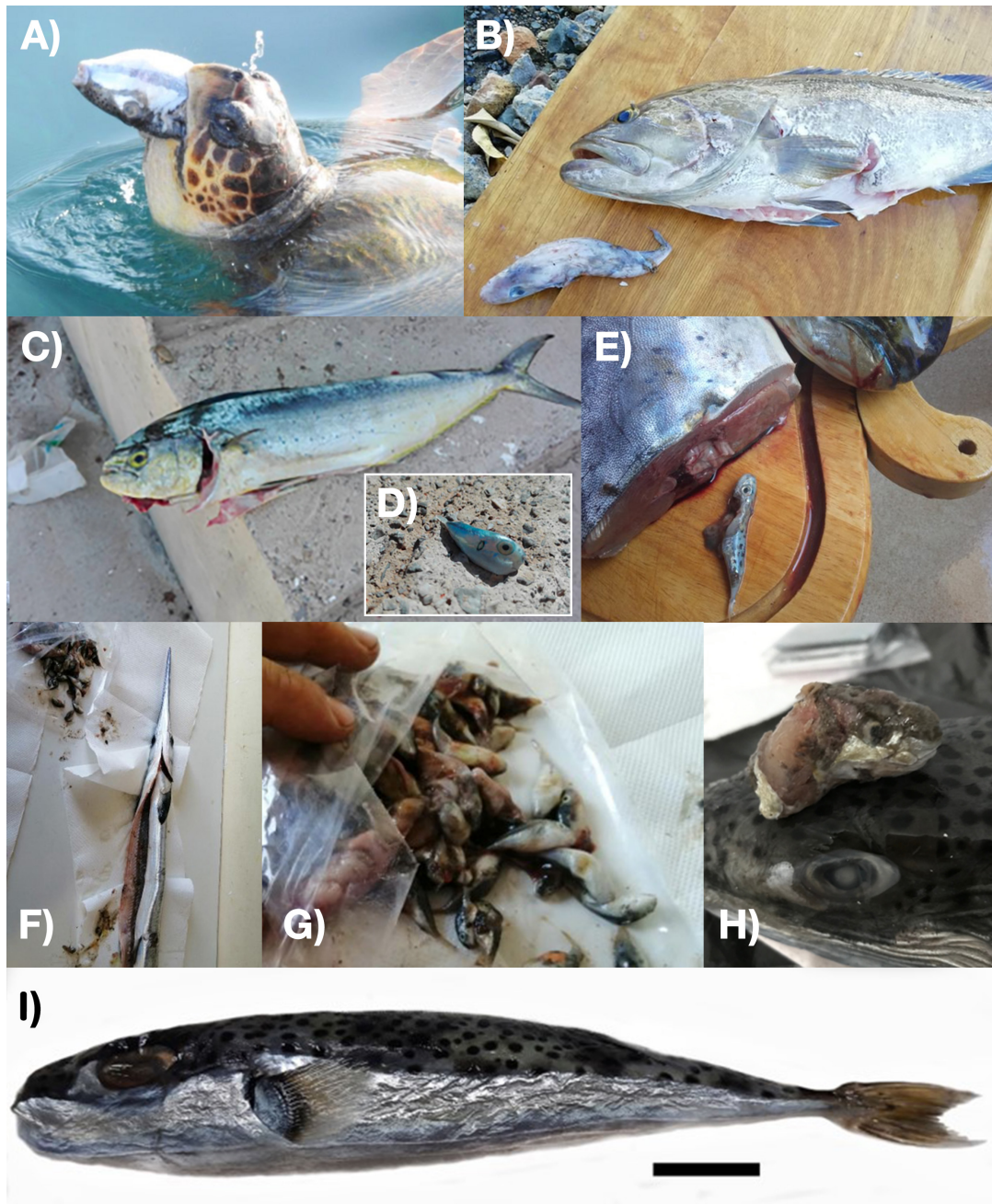


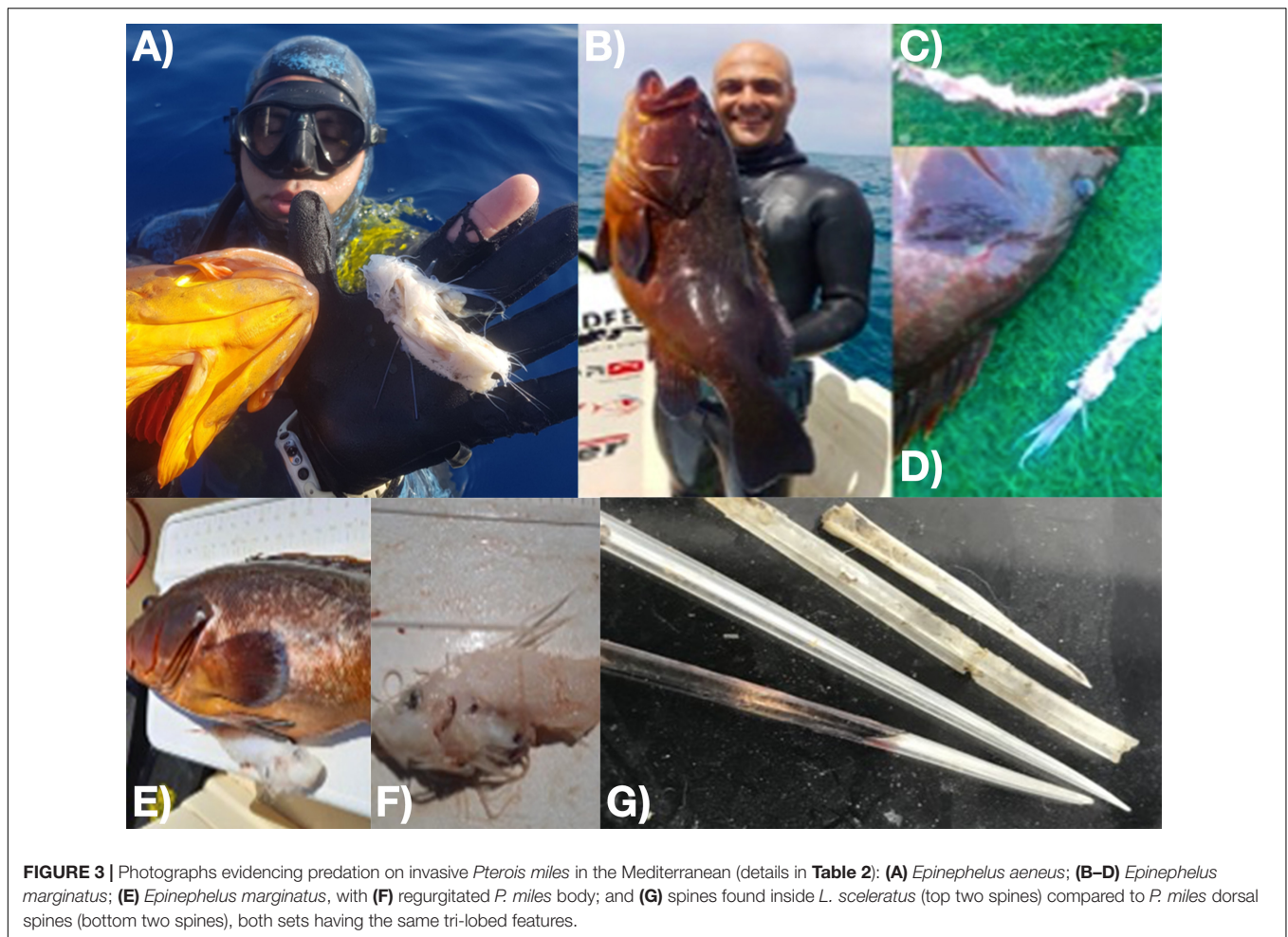
FIGURE 2 | Photographs evidencing predation on invasive *Lagocephalus sceleratus* in the Mediterranean Sea (details in **Table 2**): **(A)** *Caretta caretta*; **(B)** *Epinephelus aeneus*; **(C,D)** *Coryphaena hippurus*; **(E)** *Coryphaena hippurus*; **(F,G)** *Belone belone* with stomach full of juvenile *L. sceleratus*; **(H)** cannibalism; **(I)** well preserved specimen from cannibalism (6.4 cm total length).

density-dependent population control via cannibalism may now be occurring. Also interesting is that fishers from Datça (Turkey) conducting experimental removals of *L. sceleratus* caught hundreds of adult *L. sceleratus* using adult *L. sceleratus* as bait (Taşkıran, pers obs.). Although it is not considered a predation record, one video shows fireworms scavenging on dead pufferfish². No location was provided for this record,

²<https://cutt.ly/5krA8mc>

but the worms appear to be the bearded fireworm (*Hermodice carunculata*), which are native to the Eastern Atlantic and the Mediterranean Sea.

Lionfish cannibalism has not yet been observed in the Mediterranean, but it should be expected once DNA barcoding methods are employed. Visual identification of stomach contents can produce biased diet estimates as fish rapidly lose visually identifiable characteristics within a short period of time (Schooley et al., 2008), especially in warmer waters (Legler et al.,



2010). Although an expansive richness of Western Atlantic lionfish diet has been well-described via thousands of visually identified stomach samples from many locations throughout the West Atlantic invasion (Peake et al., 2018), high rates of cannibalism within the same populations were only revealed when DNA barcoding technology was employed (Valdez-Moreno et al., 2012; Côté et al., 2013; Dahl et al., 2017). In fact, conspecifics comprised the most frequent identified prey taxon (14.4%) in lionfish from natural and artificial reefs located within the northern sections of the Gulf of Mexico (Dahl et al., 2017, 2018) where lionfish densities are generally 10–100 times higher than from tropical Western Atlantic reefs (Green and Côté, 2009; Darling et al., 2011; Dahl et al., 2019; Harris et al., 2019). Density-dependent competition and/or prey-switching thus appears evident in the Western Atlantic lionfish populations (Pereira et al., 2017), given the observed regime changes in prey-fish abundances and diversity on NGoM reefs (Chagaris et al., 2020; Lewis et al., 2020).

This study albeit comes with its limitations, as certainly undocumented predatory events exist. This could be improved with fishers' interviews, thus it is suggested that researchers studying these species, and whom are in contact with fishers, to ask for new records and document them. Additionally,

quantitative studies could be conducted on the stomach contents of regional top predators landed in local fish markets around the invaded regions to improve predator knowledge on these new invaders. For example, a new study on the diet of the rock goby *Gobius paganellus* in the central Mediterranean showed its possible control on the invasive crab *Percnon gibbesi* (Tiralongo et al., 2021).

Records of loggerhead turtles and grouper predatory records on these invasive mesopredators should provide further support for a renewed effort toward prioritizing the rebuilding of top predators across the Eastern Mediterranean. Overfishing has driven recent declines of carnivorous fish in rocky reefs to very low levels (e.g., Sini et al., 2019), and the Mediterranean is currently considered an extinction risk hotspot for sharks and rays (Dulvy et al., 2014). There is, unfortunately, no sign of improvement over the Mediterranean International Union for Conservation of Nature (IUCN) Red List assessments of 2007 and 2016 (Dulvy et al., 2016). Marine Protected Areas (MPAs) in the Mediterranean, have proven highly effective in increasing fish biomass and restoring top predator populations (Giakoumi et al., 2017). Proposed recommendations to improve marine conservation efforts in the Mediterranean included designing effective networks of MPAs based on systematic

TABLE 3 | Predatory records on Tetraodontidae and *Pterois volitans* and *P. miles* in their Western Atlantic invaded ranges; NGoM= Northern Gulf of Mexico.

Common name	Scientific name	Date	Location	Evidence	References
(A) Predation on Tetraodontidae in the Western Atlantic					
Yellow-footed gull	<i>Larus livens</i>	2005	Florida	Video	https://cutt.ly/fkw0Sskh
Frogfish	Antennariidae	2014	(Aquarium), United States	Video	https://cutt.ly/vkw0Bwr
Blue heron	<i>Ardea herodias</i>	2017	Florida	Video	https://cutt.ly/JkwVAY8
Tri-colored heron	<i>Egretta tricolor</i>	2020	United States	Video	https://cutt.ly/SkwNIE5 ; https://cutt.ly/tkwBNEK
Osprey	<i>Pandion haliaetus</i>	2020	Florida	Video	https://cutt.ly/9kq2to7
Common octopus	<i>Octopus vulgaris</i>	2021	Bonaire	Video	https://cutt.ly/akq2pZU
(B) Predation on <i>P. volitans</i> and <i>P. miles</i> in the Western Atlantic					
Spotted moray	<i>Gymnothorax moringa</i>	2005	NE Florida	Pers. obs.	Muñoz, 2017
Tiger grouper	<i>Mycteroperca tigris</i>	2008	Bahamas	Dissection	Maljkoviæ et al., 2008
Nassau grouper	<i>Epinephelus striatus</i> x2	2008	Bahamas	Dissection	Maljkoviæ et al., 2008
Lionfish	<i>Pterois volitans/miles</i> (cannibalism)	2009	Mexico	DNA Barcoding	Valdez-Moreno et al., 2012
Greater amberjack	<i>Seriola dumerilli</i>	2012	Gulf of Mexico	Dissection	Fogg, pers. comm.
Red grouper	<i>Epinephelus morio</i> x10	2012-2020	Gulf of Mexico	Photo	Fogg, pers. comm.
Northern red snapper	<i>Lutjanus campechanus</i> x5	2012-2020	NGoM	Photo	Fogg, pers. comm.
Nurse shark	<i>Ginglymostoma cirratum</i>	2013	Cayman Islands	Video	Diller et al., 2014
Nassau grouper	<i>Epinephelus striatus</i> *	2013	Cayman Islands	Video	Diller et al., 2014
Lionfish	<i>P. volitans</i> (cannibalism)	2013-2014	NGoM	DNA Barcoding	Dahl et al., 2017, 2018
Gag grouper	<i>Mycteroperca microlepis</i>	2014	Gulf of Mexico	Photo	Fogg, pers. comm.
Black grouper	<i>Mycteroperca bonaci</i>	2014	Florida	Photo	Fogg, pers. comm.
Red grouper	<i>Epinephelus morio</i>	2015	Cayman Islands	Video	youtu.be/BSn22wqJ5mA
Nurse shark	<i>Ginglymostoma cirratum</i>	2015	Cayman Islands	Acoustic tag	Candelmo, pers. comm.
Fast predator (likely shark)		2016	NGoM	Acoustic tag	Dahl and Patterson, 2020

*Predation on *Pteroinae* observed in Diller et al. (2014) were tethered to a lead weight but otherwise healthy.

conservation planning principles, developing and implementing adaptive management plans, incorporating biological invasions in conservation plans, and prioritizing management actions to control invasive species (Mačić et al., 2018; Giakoumi et al., 2019; Katsanevakis et al., 2020a; Kleitou et al., 2020). Nevertheless, even if they are successful, rebuilding top predator populations will likely take decades.

Effective long-term control strategies for pufferfish and lionfish will require us to understand the factors that facilitate and control their population growth. For both species, their Mediterranean colonizations have been facilitated by environmental drivers, including ocean circulation, sea surface temperature, and the lunar cycle, which has been suggested for lionfish in the Western Atlantic invasion (Mostoway et al., 2020). Research and management will require regional coordination given their metapopulations are connected through larval dispersion (Johnston and Purkis, 2015). Therefore, the General Fisheries Commission of the Mediterranean announced in their Eastern Mediterranean Subregional Committee Meeting to establish a working group in early 2022 specifically for *L. sceleratus* and *P. miles*. This group would first be tasked with consolidating all available regional spatial and biological data on these species through an integrated monitoring platform. One output could be to present the mapping data in a current database similar to the mapping database for Western Atlantic lionfish (U.S. Geological Survey, 2016).

Finding ways to add commercial value to these species should further be explored to help the enablement of commercial fisheries to be established. In Cyprus, *L. sceleratus* removals have been incentivized with a financial bounty since 2009 (as well as in Turkey during December 2020), but regional-scale collaborated removal efforts are needed. Volunteer removals and recreational lionfish tournaments (often called “derbies”) have shown to be effective at immediately controlling lionfish (de León et al., 2013; Lopez-Gómez et al., 2014). Derbies are particularly successful if the lionfish population is well-established in the area and if there is a large pool of divers (Malpica-Cruz et al., 2016). With current technologies, however, lionfish removals are limited to depths accessible to SCUBA divers (generally < 40 m), although experimental traps to expand fishing capacity to deeper populations are an active area of research, development, and testing (Harris et al., 2020b). Nevertheless, removals within depths accessible to SCUBA divers can control lionfish densities in frequently harvested areas (Frazer et al., 2012; Green et al., 2014; Dahl et al., 2016). In the NGoM, commercial diving removals have been as high as 20,000 kg per year and removal tournaments have removed over 10,000 lionfish in a single weekend (Harris et al., 2020a). In the Mediterranean, however, current regulations do not permit lionfish culling using SCUBA, with the exception of permitted culls allowed in Cyprus and Egyptian Mediterranean waters.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the research was a review of natural animal processes. No fish were collected or harmed for this study. Written informed consent was obtained from the individual(s) for the publication of any potentially identifiable images or data included in this article.

AUTHOR CONTRIBUTIONS

AU and NiD contributed to the conception and design of the study. AU and TY prepared the figures. AU, NiD, HEH,

and AF prepared the tables. AU, HEH, AF, TY, and NaD provided the final article revisions. All authors participated in the contribution of data and in the drafting and revising of the manuscript, contributed to the article and approved the submitted version.

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Conflict of Interest: AU was employed by the company Mersea Marine Consulting.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The reviewer SK declared a past co-authorship with several of the authors ND, SK, PK, JH-S, and FT to the handling editor.

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