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Another One Bites the Net: Assessing the Economic Impacts of *Lagocephalus sceleratus* on Small-Scale Fisheries in Greece

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Abstract: The assessment of the economic impacts of marine invasive species is fundamental for adopting mitigation measures, yet such impacts have been underreported in the Mediterranean Sea. The silver-cheeked toadfish (*Lagocephalus sceleratus*) is a toxic pufferfish that since its introduction has seriously disturbed small-scale fisheries along the eastern Mediterranean coast. This species depredates on fishing gears, causing damage to nets, longlines and commercial catches. To quantify its economic impact on small-scale fisheries, we interviewed 141 fishers from Crete (Cretan and Libyan Sea) and the Ionian Sea (Greece) during May 2020–December 2022. The mean annual economic cost resulting from *L. sceleratus* depredation was estimated at EUR 6315 ± 2620 per vessel in Crete and EUR 258 ± 120 in the Ionian Sea. Additionally, observer surveys carried out on board small-scale fishing vessels in Crete showed that depredation probability was significantly influenced by fishing depth, sea surface temperature, gear type (nets, longlines) and region (Cretan, Libyan Sea). *L. sceleratus* was caught more frequently and in higher numbers in the Libyan Sea. In response to depredation, fishers in Crete have altered their fishing tactics in terms of fishing in deeper waters, reducing fishing time and changing the technical characteristics of fishing gears. Our results underscore the adverse impacts of *L. sceleratus* on Greek small-scale fishers, emphasizing the need for region-specific management plans where the species establishes large populations.

Keywords: *Lagocephalus sceleratus*; small-scale fisheries; depredation; economic loss

Key Contribution: This study provides the first detailed assessment of the economic losses experienced by Greek fishers due to the interaction with the invasive pufferfish *Lagocephalus sceleratus*, using the small-scale fishing fleets of Crete and the Ionian Sea as case studies. The negative impacts were much more severe in Crete where the species was abundant, forcing local fishers to change fishing tactics.

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1. Introduction

The Mediterranean Sea is a key hotspot for marine biological invasions, hosting approximately 1000 non-indigenous species to date [1]. Among these, ~13.5% have been characterized as invasive due to their adverse effects on human health, the economy of coastal communities and the structure, function and services of native ecosystems [2,3]. The economic impacts of marine invasive species relate to monetary losses to coastal human activities such as fisheries, aquaculture, tourism and marine infrastructure [4], resulting in a potential decline in living standards. Regarding fisheries, invasive species inflict losses by depleting native commercial stocks (through predation, competition, habitat degradation and disease transmission), by fouling gear and equipment and by damaging fishing gear and catches [5].

Small-scale fisheries hold substantial socio-economic importance for Mediterranean fishers, contributing significantly to sustainable livelihoods, employment and income within fishing communities, as acknowledged by the FAO [6]. In Greece (eastern Mediterranean), the small-scale fishing fleet numbers approximately 11,000 active vessels comprising >90% of the fishing fleet. Small-scale fisheries produce 35–40% of total landings, although they contribute 55% to total fish value, as they mainly target high-valued species [7]. The regions on which the present study focused were coastal areas of the Ionian Sea, the Cretan Sea and the Libyan Sea (Figure 1), where 1317, 501 and 108 active small-scale fishing vessels are registered [8]. In these regions, the most commonly used gear types are nets (mainly gillnets and trammel nets) and bottom longlines, with combined nets also used to a lesser extent [9–11]. In the Ionian Sea, net fishers mainly target the European hake *Merluccius merluccius*, the common sole *Solea solea*, the common dentex *Dentex dentex* and members of the family Mullidae (striped red mullet *Mullus surmuletus* and red mullet *Mullus barbatus*) [9,10]. In seas around Crete, net fishers mainly target members of the family Mullidae, the common cuttlefish *Sepia officinalis*, the Mediterranean parrotfish *Sparisoma cretense* and the European barracuda *Sphyraena spyraena* [11]. Longline fisheries in all regions mainly target the red porgy *Pagrus Pagrus* and species of the genera *Diplodus* and *Epinephelus* [9–11].

Depredation by marine fauna is a significant source of economic loss for small-scale fisheries in the Mediterranean Sea. To date, the most well-studied species that cause damages in the Mediterranean small-scale fisheries are dolphins and seals [12,13]. To a lesser extent, sea turtles, large fish (e.g., sharks, amberjacks, eels) and sea birds are also reported by fishers to inflict gear and catch damages [14,15]. Over the last few decades, however, the rising rate of biological invasions of Indo-Pacific marine species from the Red Sea to the Mediterranean Sea has increased the number of species negatively affecting small-scale fisheries [16]. The blue crab *Portunus segnis* [17] and pufferfish species [18] are now reported as the new gear-damaging invaders of the eastern Mediterranean.

Lagocephalus sceleratus (Gmelin, 1789), commonly known as the silver-cheeked toadfish, is the largest among the tetraodontid pufferfish introduced in the Mediterranean [19]. The species was first recorded in the Mediterranean Sea on the southwestern coast of Turkey, in 2003 [20]. In the Basin, *L. sceleratus* is found in depths ranging from 0 to 170 m and on various substrate types, including sandy, rocky and muddy areas and *Posidonia oceanica* meadows [21,22]. However, the species shows a preference for shallower waters at depths 0–50 m and sandy bottoms with patches of *Posidonia oceanica*, as stated in previous studies [23,24].

Shortly after its introduction, *L. sceleratus* gained notoriety as one of the "worst" invasive species in the Mediterranean Sea [25], primarily due to the high levels of the neurotoxin tetrodotoxin (TTX) contained in its internal organs, muscles and skin. The high toxicity of silver-cheeked toadfish has raised significant public health concerns in eastern Mediterranean countries, as several cases of TTX poisoning, including some fatalities, were linked to the consumption of this pufferfish [26–30]. In response to these health risks, the European Union, Turkey and Egypt have enacted legislation prohibiting the commercial exploitation and consumption of *L. sceleratus* along with other pufferfish species [31–33]. Additionally, *L. sceleratus* adversely affects small-scale fisheries, which is attributable to two main factors: Firstly, as consistently emphasized by numerous reports of eastern Mediterranean fishers, the species depredates on fishing gears causing damage to nets, longlines and catches due to its formidably sharp teeth [27]. Secondly, its inherent toxicity makes it a common discarded catch, rendering it commercially worthless.

In contrast to the extensive research on the toxicity of the species in the Mediterranean Sea [34–38], quantitative assessments of its economic impact remain limited. Such assessments originate exclusively from the Mediterranean coasts of Turkey, where total losses due to *L. sceleratus* were estimated at around EUR 4.5 million per year [39,40]. Another review provides semi-quantitative data, ranking the socio-economic impact of this species in the Mediterranean Sea as moderate, albeit higher compared to other invasive fish with management priority [28]. In the Greek seas, data are even more scarce and fragmentary, with only one study ranking silver-cheeked toadfish as the second most damaging species for the Cretan small-scale fisheries after dolphins, based on local fishers' perceptions [15]

The present study aims to investigate for the first time the magnitude of the economic impacts of *L. sceleratus* on small-scale fisheries in Greece and to assess how fishers adapt to this emerging economic challenge. Predictive models were also constructed to elucidate the factors affecting *L. sceleratus* by-catch, in terms of biomass and abundance, as well as the depredation by this species on fishing gears during fishing trips.

2. Materials and Methods

2.1. Interviews with Local Fishers

In this study, data were collected through interviews with fishers working on 141 small-scale fishing vessels operating in coastal areas of the Ionian Sea (54 vessels docked in 24 ports), Cretan Sea (54 vessels, 15 ports) and Libyan Sea (33 vessels, 6 ports), from May 2020 to December 2022 (Figure 1). During the interviews, fishers provided information on (a) the fishing gears they used, (b) the occurrence of catches of large ($\gtrsim$2 kg) and small ($\lesssim$0.5 kg) *L. sceleratus* individuals per depth zone (0–10, 10–25, 25–45, 45–65 and 65–100 m), (c) the total by-catch (kg) of *L. sceleratus* in the preceding year, (d) the resulting shifts in fishing tactics due to depredation by *L. sceleratus* and (e) the economic impacts they suffered from *L. sceleratus* concerning gear, labor and catch losses (Table 1). The aforementioned depth zones were set based on previous expert knowledge on the fishers' operational depths. Concerning gear-related losses, fishers were asked to explicitly report only the extra annual quantity of gear required, and its associated cost, due to interactions with *L. sceleratus*. This approach allowed for the distinction between gear-related losses caused by *L. sceleratus* from regular gear maintenance expenses (also incurred before *L. sceleratus* invasion) such as those due to native megafauna species and wear and tear. Regarding labor-related losses, fishers provided information on the extra person-hours they spend per month, typically after their fishing trips, on repairing gear damages (extra fisher's time). Additionally, fishers hire extra workers to assist in repairing gear damage (hiring of extra workers, person-months/year). We also recorded the days per month that fishers were forced to skip fishing in order to repair gear damage (lost fishing days/month). Finally, fishers provided an estimate of the monthly catch losses of commercial species (in kilograms) they experienced due to *L. sceleratus* depredation.

Table 1. Data collected through questionnaires per data type.

Data Type		Data
Presence/absence		Small/large individuals per depth zone (m)
Qualitative		Fishing tactic shifts
Quantitative	Gear-related loss	Extra cost for gear repair and/or replacement (EUR/year)
	Labor-related loss	Extra fisher's time (person-hours/month)
		Hiring of extra workers (person-months/year)
		Lost fishing days/month
	Catch loss	Loss of commercial species (kg/month)
	L. sceleratus by-catch	kg/year

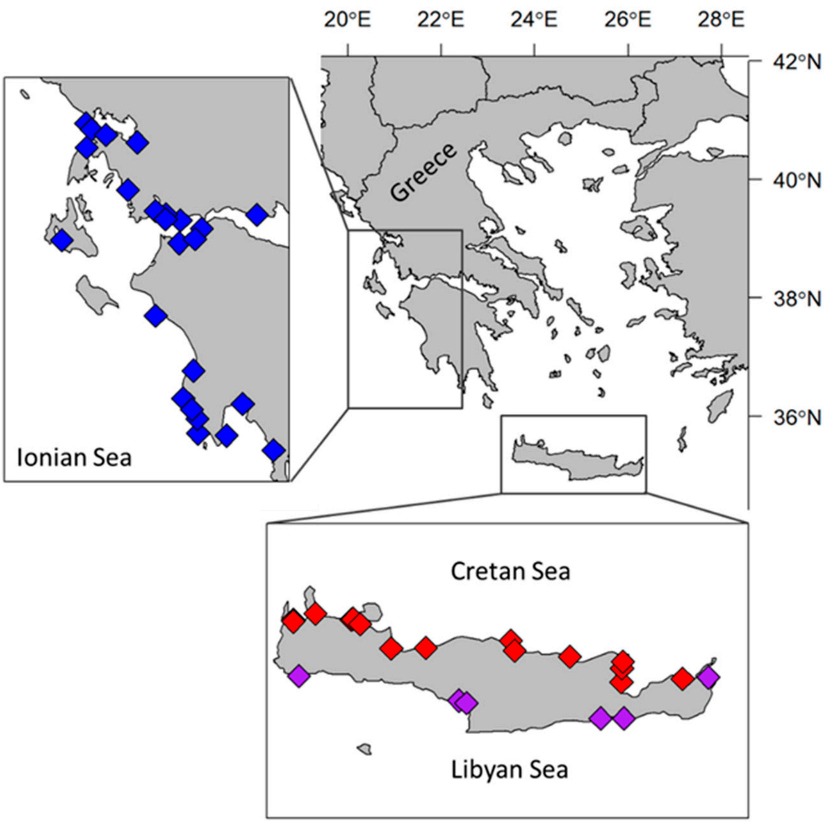


Figure 1. Fishing ports per fishing region, where interviews with fishers took place (red: Cretan Sea, purple: Libyan Sea, blue: Ionian Sea).

2.2. Onboard Sampling

On account of the impacts of *L. sceleratus* being particularly pronounced in small-scale fisheries around Crete, as shown from the fishers' reports (see Results Sections 3.1 and 3.2), additional data were gathered in situ concerning damages inflicted on gear and catches. Overall, onboard sampling from 208 fishing trips was conducted on 27 small-scale fishing vessels in the Cretan Sea (145 fishing trips) and the Libyan Sea (63), using nets (142 fishing trips) and longlines (66), during May 2020–December 2022 (Figure 2). The sampling protocol included (a) an interview with the fisher to record the target species, the technical characteristics of the fishing gear (mesh size for nets and hook size for longlines) and the fishing depth; (b) the categorization of catches into commercial, discarded and catches damaged by *L. sceleratus*; (c) the biomass (kg) caught per species; and (d) the number of gear damages inflicted by *L. sceleratus* (number of holes in nets and missing hooks on longlines). The main mesh sizes used in nets were 20 mm (24% of net fishing trips), 32 mm (12%), 19 mm (9%), 22 mm (8%) and 28 mm (8%) (knot to knot), whereas for longlines, the most common hook sizes were No. 10 (32% of longline fishing trips), 13 (17%) and 14 (15%).

Gear and catch damages were verified by the onboard observers to be related to interactions with *L. sceleratus*. Prior to deployment, the fishing gear was inspected for unrepaired damages incurred during previous expeditions, and if present, they were excluded from recording. *L. sceleratus*-related damages on catch were recognized by the typical triangular-shaped bite mark of this species (Supplementary Figure S1). Based on the fishers' descriptions, *L. sceleratus* damages on nets show two main patterns: When the species depredates on entangled fish, it creates either a cluster of holes or a single and relatively big hole in the part of the net where the fish was caught. Notably, the holes in trammel nets are mainly located in the middle net layer, while the outer layers often remain intact (Supplementary Figure S2). An exceptional feature of *L. sceleratus* depredation is damage to the relatively sturdy gear parts, such as ropes and floaters, which has only been rarely observed in dolphin–net interactions [41]. As for longlines, the sharp teeth of *L. sceleratus* inflict "clean" cuts to the branch lines and the main line, in contrast to damages of other species which leave trimmed edges at the cut lines. Moreover, several sequential cut branch lines are a typical sign of depredation by *L. sceleratus* on longlines. Damages on gear inflicted by dolphins, monk seals and sea turtles were excluded based on the unique damage patterns described for each one of these taxa in previous studies [13–15].

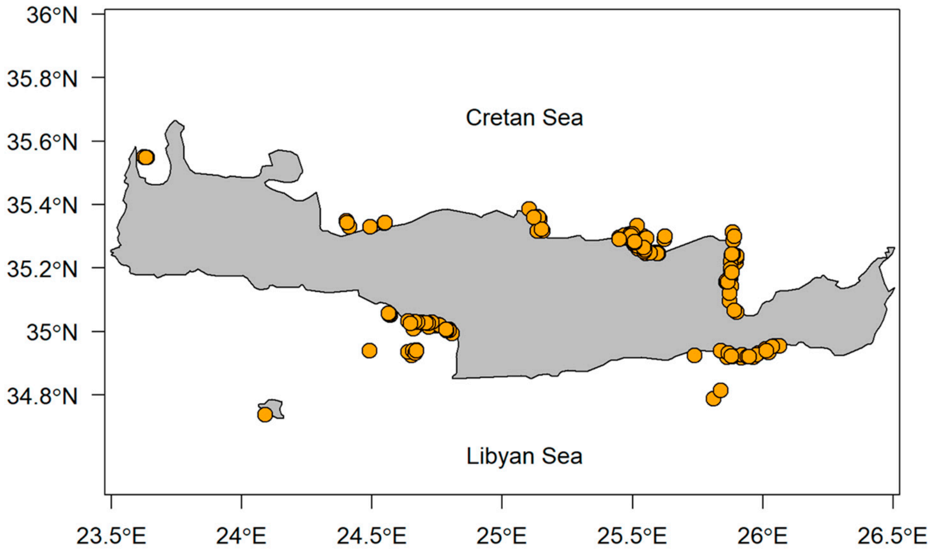


Figure 2. Locations of the fishing trips sampled by observers on board small-scale fishing vessels in coastal areas around Crete, during the period May 2020–December 2022.

2.3. Estimation of By-Catch and Impacts

To estimate the annual cost resulting from catch- and labor-related losses, the reported values were initially multiplied by the corresponding period (number of months) when impacts of *L. sceleratus* were most frequent (i.e., excluding the months with a lack of reported *L. sceleratus* interactions). These values were then multiplied by the following costs per unit as declared by the fishers: fishing day (EUR 80), person-hour (EUR 7), person-month (EUR 700), mean price of commercial catch (EUR 12 per kg).

Moreover, for each impact type, the weighted mean ($\bar{\bar{y}}$) and its variance were estimated for each gear type and for the whole Cretan small-scale fisheries (Cretan Sea and Libyan Sea fishers), as follows [42]:

$$\bar{\bar{y}} = \frac{\sum_{i=1}^{n} m_i \bar{y}_i}{\sum_{i=1}^{n} m_i}, \quad (1)$$

$$Var\left(\bar{\bar{y}}\right) = \frac{\sum_{i=1}^{n} m_i^2 \left(\bar{y}_i - \bar{\bar{y}}\right)^2}{\left[\sum_{i=1}^{n} \frac{m_i}{n}\right]^2 n(n-1)}, \quad (2)$$

where $\bar{y}_i$ is the mean value of each impact in the region i, $n = 2$ is the number of regions and m_i is the number of interviews conducted in each region. Finally, the percentage of reports per category of change in fishing tactics was calculated per region.

Quantitative data collected from the onboard sampling were utilized to estimate the frequency of occurrence of *L. sceleratus* by-catch and gear and catch damages per region and gear type. Subsequently, these variables were standardized per unit of effort (1000 m of net or 100 hooks of longlines). *L. sceleratus* by-catch was expressed both in kg and individuals per unit of effort (BPUE and NPUE, respectively). Finally, catch loss was expressed in kg per unit of effort (EPUE), and gear damage (DPUE) was expressed as the number of holes and missing hooks per 1000 m of net and 100 hooks, respectively.

2.4. Generalized Additive Models

To investigate the factors affecting three key variables (depredation on fishing gear, biomass and abundance of *L. sceleratus*) we employed generalized additive models (GAMs) on the onboard sampling data using the "mgcv" R package [43]. Prior to the GAM modeling, fishing trips performed at depths exceeding 300 m were excluded from the dataset due to their divergence from the reported depth distribution of *L. sceleratus* [22,44,45].

To estimate the probability of depredation, we constructed a model with a binary response variable (0/1), generated for each fishing trip. Fishing trips with recorded depredation indicators (e.g., gear and/or catch damages) were designated as 1, while fishing trips with the absence of depredation indicators were designated as 0. Given the binary nature of the response variable, the binomial family distribution coupled with cubic smoothing was used. The logit function was used as a link between the non-linear factor component and the binomial error. The initial model constructed was

$$\text{Depredation} \sim \text{Region} + \text{Gear} + s(\text{Duration}) + s(\text{Depth}) + s(\text{SST}), \quad (3)$$

where Duration is the time period (hours) that fishing gear remained deployed and SST is the sea surface temperature. A similar model was applied to assess the effect of these terms (i.e., region, gear, duration, depth and SST) on *L. sceleratus* biomass and abundance, assuming Tweedie distributions and utilizing the log-link between the non-linear factor component and the binomial error. To ensure the quality of the models, covariate dependencies were assessed by using the "concurvity" function and setting the elimination threshold at 0.5 [46], which excluded Duration from all models. All other terms were kept for consistency between models, resulting in the final GAM formulas:

$$\text{Depredation} \sim \text{Region} + \text{Gear} + s(\text{Depth}) + s(\text{SST}), \quad (4)$$

$$\textit{L. sceleratus}\ \text{biomass} \sim \text{Region} + \text{Gear} + s(\text{Depth}) + s(\text{SST}), \quad (5)$$

$$\textit{L. sceleratus}\ \text{abundance} \sim \text{Region} + \text{Gear} + s(\text{Depth}) + s(\text{SST}). \quad (6)$$

3. Results

3.1. Interviews

In the present study, the interviewed fishers mainly used nets (45.4% of the fishers) and alternately nets and longlines (45.4%), while 9.2% used exclusively longlines. Nearly all respondents operating in the seas around Crete reported by-catches of *L. sceleratus* (100% in the Libyan Sea and 98% in the Cretan Sea). In contrast, only 46% of the fishers in the Ionian Sea reported by-catches of the species. Based on the fishers' responses, the highest by-catch (mean $\pm$ S.E.) was recorded in the Libyan Sea (739 $\pm$ 137 kg/vessel/year), followed by the Cretan Sea (222 $\pm$ 57 kg/vessel/year) and the Ionian Sea (23 $\pm$ 10 kg/vessel/year). Regarding gear, the highest by-catch was recorded in seas around Crete by fishers using both nets and loglines (Libyan Sea: 865 $\pm$ 165 kg/vessel/year, Cretan Sea: 270 $\pm$ 94 kg/vessel/year) and the lowest by longliners (Libyan Sea: 145 $\pm$ 117 kg/vessel/year, Cretan Sea: 33 $\pm$ 24 kg/vessel/year). In the Ionian Sea, the highest by-catch was recorded by longliners (50 $\pm$ 50 kg/vessel/year) and the lowest by netters (18 $\pm$ 13 kg/vessel/year).

With regard to the occurrence of large ($\gtrsim$2 kg) and small ($\lesssim$0.5 kg) *L. sceleratus* individuals, fishers from the Libyan and the Ionian Sea reported very similar catch frequencies between large (Libyan Sea: 100% of fishers, Ionian Sea: 26%) and small *L. sceleratus* (Libyan Sea: 97% of fishers, Ionian Sea: 24%). In contrast, fewer small *L. sceleratus* were reportedly caught in the Cretan Sea (54%), in comparison to large ones (85%).

Concerning the *L. sceleratus* size distribution by depth zone, the majority of Cretan Sea fishers reported catches of large individuals in the 25–45 m zone (90%) and small ones in the 10–25 m zone (67% of the fishers). This trend remains consistent in the Libyan Sea, with large individuals between 25 and 45 m (91%) and small individuals between 10 and 25 m (87%). In the Ionian Sea, most fishers reported large and small individuals between

10 and 45 m (67%) and between 25 and 45 m (71%), respectively. Across all regions, the fewest reports for both size classes were recorded at the depth range of 65–100 m (0–18% of fishers) (Table 2).

Table 2. Reported by-catch frequency (%) of large and small *L. sceleratus* individuals per region and depth zone.

Region	Size Class	Depth Zone (m)				
		0–10	**10–25**	**25–45**	**45–65**	**65–100**
Cretan Sea	Large	42	77	90	42	13
	Small	52	67	52	3	0
Libyan Sea	Large	36	85	91	82	18
	Small	63	88	47	6	0
Ionian Sea	Large	13	67	67	13	13
	Small	14	64	71	7	7

3.2. Economic Impacts

The highest percentages of fishers who declared impacts resulting from depredation by *L. sceleratus* were recorded in the Libyan Sea (gear loss: 97%, labor loss: 85%, catch loss: 97%) followed by the Cretan Sea (gear loss: 85%, labor loss: 54%, catch loss: 91%) and the Ionian Sea (gear loss: 7%, labor loss: 7%, catch loss: 0%). Furthermore, some fishers noted that the extra time needed for repairing gear damages often led to lost fishing days and necessitated the hiring of extra workers. The highest percentages of reports concerning these extra labor-related impacts were also recorded in the Libyan Sea (58% reported lost fishing days and 21% the hiring of extra workers), and the lowest in the Ionian Sea (2% reported the hiring of extra workers, while no fisher reported lost fishing days).

The total annual economic losses due to *L. sceleratus* were estimated at EUR 6315 $\pm$ 2620 per vessel in seas around Crete (Libyan Sea: EUR 8954 $\pm$ 875, Cretan Sea: EUR 4702 $\pm$ 500) and EUR 258 $\pm$ 120 per vessel in the Ionian Sea. Based on gear type, the mean annual economic losses per loss category were higher in seas around Crete compared to the Ionian Sea (Tables 3 and 4). The same was true for the *L. sceleratus* by-catch (higher in Crete, lower in the Ionian Sea). Notably, catch losses were not reported from the Ionian Sea fishers. Additionally, net fishers operating in this region did not report any labor losses either. In Crete, the mean economic losses and *L. sceleratus* by-catch were generally higher in the Libyan compared to the Cretan Sea. However, gear- and labor-related losses of net fishers were higher in the Cretan Sea compared to the Libyan Sea (Table 3).

Table 3. Annual economic losses (mean $\pm$ S.E.) in euros (EUR) per region, gear and loss category due to *L. sceleratus*, and declared *L. sceleratus* by-catch (kg/year).

Region	Gear	N of Fishers	Economic Losses			*L. sceleratus* By-Catch
			Gear	**Labor**	**Catch**	
Libyan Sea	Longlines	2	650 ± 650	1960 ± 1960	720 ± 720	145 ± 118
	Nets	7	1364 ± 209	1662 ± 1003	2263 ± 288	477 ± 276
	Nets/Longlines	24	2495 ± 266	5348 ± 688	2649 ± 169	865 ± 165
Cretan Sea	Longlines	6	628 ± 201	1255 ± 965	444 ± 115	33 ± 24
	Nets	19	1550 ± 304	1906 ± 590	1360 ± 333	209 ± 76
	Nets/Longlines	29	1459 ± 182	1904 ± 444	1756 ± 282	270 ± 94
Ionian Sea	Longlines	5	40 ± 25	672 ± 412	-	50 ± 50
	Nets	38	8 ± 8	-	-	18 ± 13
	Nets/Longlines	11	364 ± 364	554 ± 415	-	27 ± 14

Table 4. Weighted-average (± S.E.) annual economic losses in euros (EUR) per vessel, gear and loss category due to *L. sceleratus*, and declared *L. sceleratus* by-catch (kg/year) for all of Crete.

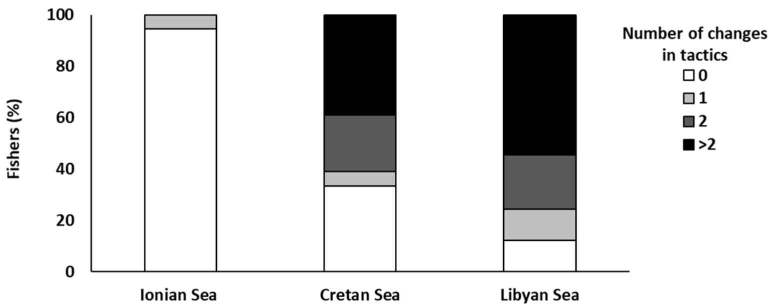
Gear	N of Fishers	Economic Losses			*L. sceleratus* By-Catch
		Gear	Labor	Catch	
Longlines	8	634 ± 6	1431 ± 262	513 ± 73	61 ± 30
Nets	26	1500 ± 52	1840 ± 68	1603 ± 251	281 ± 74
Nets/Longlines	53	1928 ± 363	3464 ± 944	2160 ± 313	540 ± 208

3.3. Adjustment in Fishing Tactics

In response to the depredation by *L. sceleratus* on fishing gears, a significant number of interviewed fishers (48%) modified their fishing tactics during periods when damages from *L. sceleratus* were more frequent. Overall, nine adjustments of fishing tactics were identified, including changes in the fishing ground (such as depth, substrate, distance from the coast and area), deployment of different fishing gear (gear type and/or technical characteristics), alterations in the fishing effort (quantity of gear deployed per operation), shifts in the gear soaking time, target species selection and a temporary pause in fishing activity during nights with high lunar illumination (e.g., full moon).

Specifically, reported changes in depth and distance entailed a preference for fishing grounds in deeper waters (50–200 m) and farther off the coast (2–5 nautical miles). Changes in substrate pertained to the shift from fishing in areas with soft substrate (mainly sandy grounds with patches of seaweeds) to areas with hard substrate (rocky grounds and crustose/coralline beds). Moreover, changes in fishing gear mainly involved the deployment of nets and longlines with larger mesh and hook sizes, respectively, as reported by 72% of the fishers who made gear adjustments. The most common change in gear technical characteristics was the shift from mesh sizes of 19–22 mm to 28–45 mm and from hook Nos. 13–14 to 9–12. Fishing effort adjustments exclusively involved deploying more fishing gear to compensate for catch losses caused by *L. sceleratus*. Furthermore, changes in gear soaking time consistently involved a reduction in fishing hours, with fishers choosing to deploy and retain their gear exclusively during nighttime hours, diverging from their previous practice of extending fishing into daylight hours (usually from dusk until dawn).

In terms of region, the highest percentage of fishers reporting changes in their tactic was recorded in the Libyan Sea (88%, 29 fishers), followed by the Cretan Sea (67%, 36 fishers) and the Ionian Sea (6%, 3 fishers). Single tactic changes were most prevalent in the Libyan Sea (12%) compared to the Cretan and Ionian seas (6%), while multiple tactic adjustments (more than two) were exclusively reported in Crete, with the highest percentage attributed to fishers operating in the Libyan Sea (55% of the fishers) (Figure 3a). For fishers operating in seas around Crete, the main adjustments included a change in depth (Cretan Sea 43% and Libyan Sea 64%), a reduction in gear soaking time (Cretan Sea 35% and Libyan Sea 55%) and changes in fishing gear (Cretan Sea 30% and Libyan Sea 39%) (Figure 3b). Additionally, 52% of the Libyan Sea fishers reported an increase in fishing effort, whereas Ionian Sea fishers adjusted their fishing tactic exclusively by changing fishing areas (6% of the fishers).



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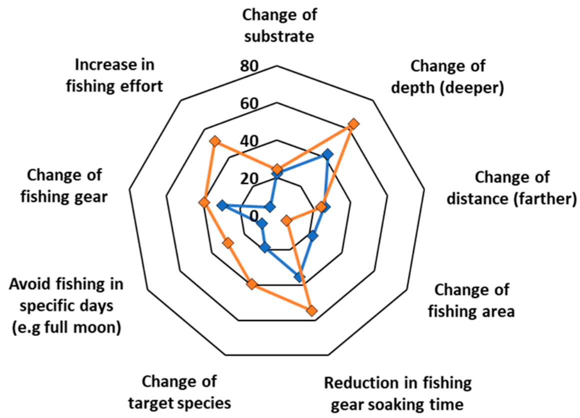

(**b**)

Figure 3. (**a**) Percentage of fishers per fishing region in relation to the number of changes in fishing tactics due to *L. sceleratus* depredation; (**b**) percentage of fishers operating in seas around Crete per category of tactic change (orange line: Libyan Sea, blue line: Cretan Sea).

3.4. Onboard Sampling

In the 208 fishing trips in Crete, the mean daily catch was 15.3 ± 12.4 kg, and the mean daily *L. sceleratus* by-catch was 0.6 ± 1.6 kg. *L. sceleratus* was recorded in 42 trips (20%). The species total by-catch was 123 kg (86 individuals), which represented 3.8% of the total catches recorded. Moreover, the contribution of *L. sceleratus* to the total catch was higher in the Libyan (4.3%) compared to the Cretan Sea (3.6%). The highest frequency of *L. sceleratus* by-catch was recorded in nets operated in the Libyan Sea (49% of the fishing trips), followed by nets (17%) and longlines (6%) operated in the Cretan Sea. The species was not caught on longlines in the Libyan Sea. *L. sceleratus* NPUE in nets was higher in the Libyan (0.6 ± 1.0 ind.) compared to the Cretan Sea (0.4 ± 1.4 ind.), although the opposite was true for the species BPUE (0.5 ± 0.8 kg and 0.9 ± 3.0 kg, for the Libyan and Cretan Sea nets, respectively). Additionally, the mean total length (TL) of individuals caught in the Libyan Sea was smaller compared to the Cretan Sea (385 ± 139 vs. 544 ± 114 mm) (Table 5).

Table 5. Frequency of occurrence (FO%) and mean values (±standard deviation) of *L. sceleratus* biomass (BPUE) and abundance (NPUE), gear damages (DPUE) and catch loss (EPUE) per unit of effort (1000 m of net and 100 hooks of longlines), region and gear type. *n* = number, TL = total length.

Region	Gear	FO%			Mean				
		L. sceleratus By-Catch	Gear Damages	Catch Damages	*L. sceleratus* BPUE (kg)	*L. sceleratus* NPUE (*n*)	DPUE (*n*)	EPUE (kg)	TL (mm)
Cretan Sea	Nets	17	11	12	0.9 ± 3.0	0.4 ± 1.4	2.1 ± 14.6	0.04 ± 0.22	544 ± 114
	Longlines	6	24	6	0.1 ± 0.3	0.03 ± 0.14	2.1 ± 5.9	0.01 ± 0.08	557 ± 74
Libyan Sea	Nets	49	19	26	0.5 ± 0.8	0.6 ± 1.0	4.5 ± 15.1	0.4 ± 2.1	385 ± 139
	Longlines	0	19	13	-	-	2.9 ± 9.0	0.004 ± 0.01	-

Overall, damages inflicted by *L. sceleratus* to gears and/or catches were recorded in 46 out of 208 fishing trips (22%). Gear damages were most frequent for longlines operated in the Cretan Sea (24%), whereas the lowest frequency of gear damages was recorded in nets operated in the same area (11%). For both gear types, DPUE was higher in the Libyan than in the Cretan Sea (Table 5). Regarding the catch damaged by *L. sceleratus*, its mean weight per fishing trip was 0.1 ± 0.8 kg. The frequency of catch damages was higher in the Libyan Sea for both nets and longlines. Finally, EPUE was an order of magnitude higher in nets operated in the Libyan compared to the Cretan Sea (0.4 ± 2.1 vs. 0.04 ± 0.22 kg), but notably, the opposite was true for longlines (0.004 ± 0.01 vs. 0.01 ± 0.08 kg).

3.5. GAMs for Depredation Probability and By-Catch of *L. sceleratus*

Regarding the depredation probability, the fitted model explained 15.8% of the total variability, with all terms tested being significant (region: $p < 0.01$, gear: $p < 0.01$, depth: $p < 0.001$, SST: $p < 0.05$) (Table 6). Depredation probability dropped with increasing depth and was higher in the Libyan Sea and for longlines. The probability also showed a general increase with increasing SST, being lowest at 16–17 °C (period from February to March when the lowest yearly temperatures were recorded, see Supplementary Figure S3) and highest at 25–28 °C (period from July to September with the highest yearly temperatures). However, a decrease in the depredation probability was shown at intermediate temperatures (21–23 °C) (Figure 4). The model for the *L. sceleratus* biomass explained 21.4% of the total variability, with depth and gear being the only significant terms ($p < 0.01$ and <0.05, respectively). *L. sceleratus* biomass showed a negative relationship with depth, and it was higher for nets than for longlines (Figure 5). Finally, the model for the *L. sceleratus* abundance explained 25.7% of the total variability and had region ($p < 0.05$), gear ($p < 0.01$) and depth ($p < 0.05$) as significant terms. As in the previous models, depth was negatively related to *L. sceleratus* abundance. Also, the species abundance was higher in the Libyan Sea as well as in nets (Figure 6). In all models, fishing depth was the term with the highest explanatory power. SST was not significant in either the *L. sceleratus* biomass or the abundance models.

Table 6. Analysis of deviance for the *L. sceleratus* depredation probability, biomass and abundance GAMs.

Explanatory Variable	Residual d.f	Residual Deviance	Cumulative Variance Explained (%)	*p*-Value
Depredation probability (binomial model)				
Mean	202.00	214.78		
Region	201.00	213.39	0.65	0.0074
Gear	200.00	211.63	1.47	0.0042
Depth	199.01	191.20	11.0	0.0001
SST	195.26	180.90	15.8	0.0305
L. sceleratus biomass (Tweedie model)				
Mean	202.00	735.87		
Region	201.00	732.06	0.52	0.2692
Gear	200.00	673.85	8.43	0.0383
Depth	197.29	597.13	18.8	0.0097
SST	194.76	578.33	21.4	0.2600
L. sceleratus abundance (Tweedie model)				
Mean	202.00	760.22		
Region	201.00	711.18	6.45	0.0261
Gear	200.00	657.02	13.57	0.0098
Depth	196.25	564.95	25.7	0.0196
SST	196.25	564.95	25.7	0.7863

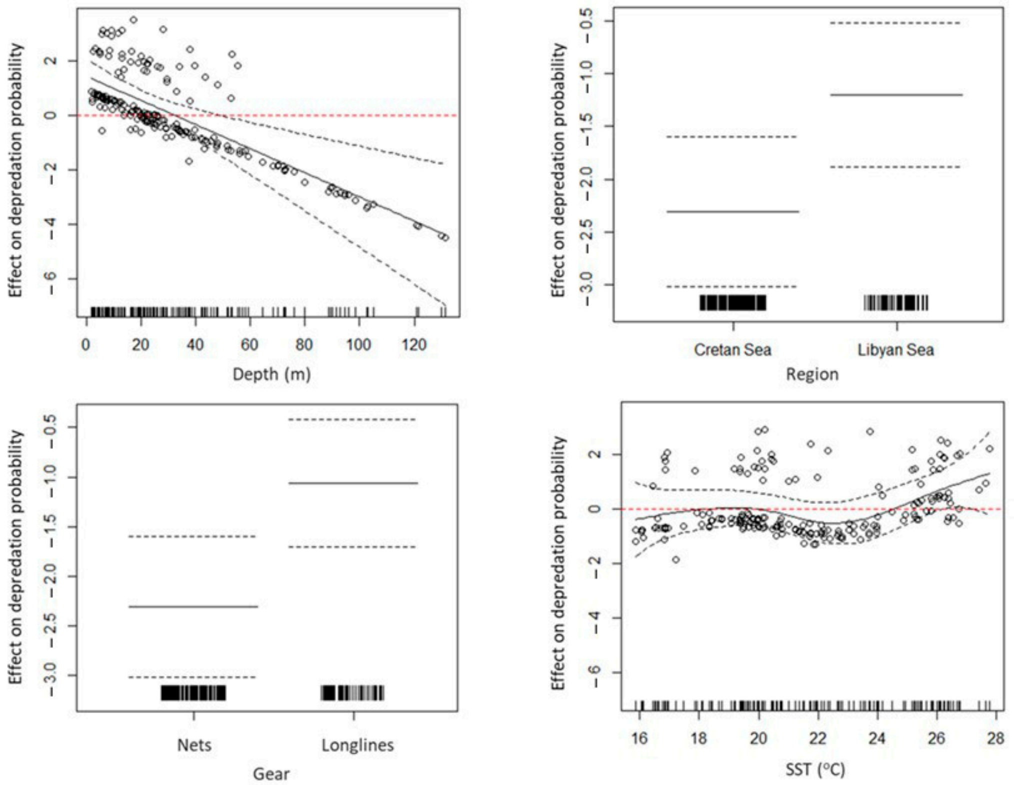

Figure 4. Effects of significant predictors on depredation probability of *L. sceleratus* in Crete. The mean model estimates are represented by the red dashed lines, while the corresponding standard errors are denoted with black dashed lines. The points in the smoothing term plots denote the residuals. The "rug" on the *x*-axis represents the relative density of data points.

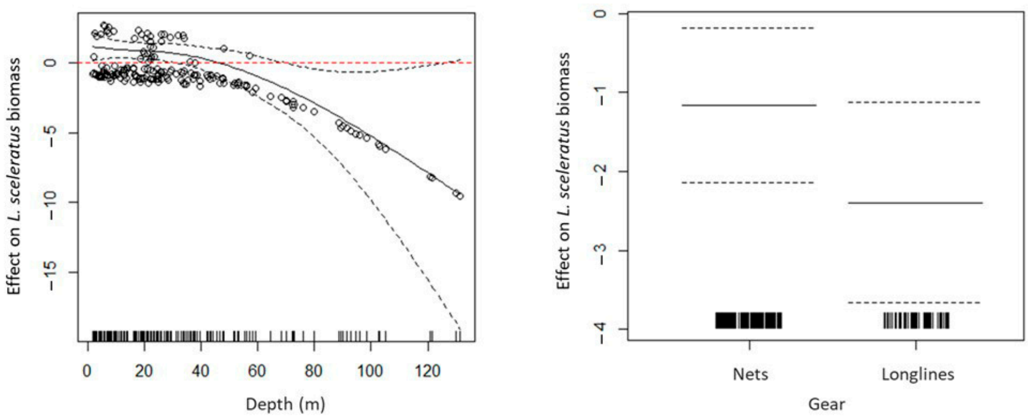

Figure 5. Effects of statistically significant predictors on *L. sceleratus* biomass in Crete. The mean model estimate is represented by the red dashed line, while the corresponding standard errors are denoted with black dashed lines. The points in the smoothing term plot denote the residuals. The "rug" on the *x*-axis represents the relative density of data points.

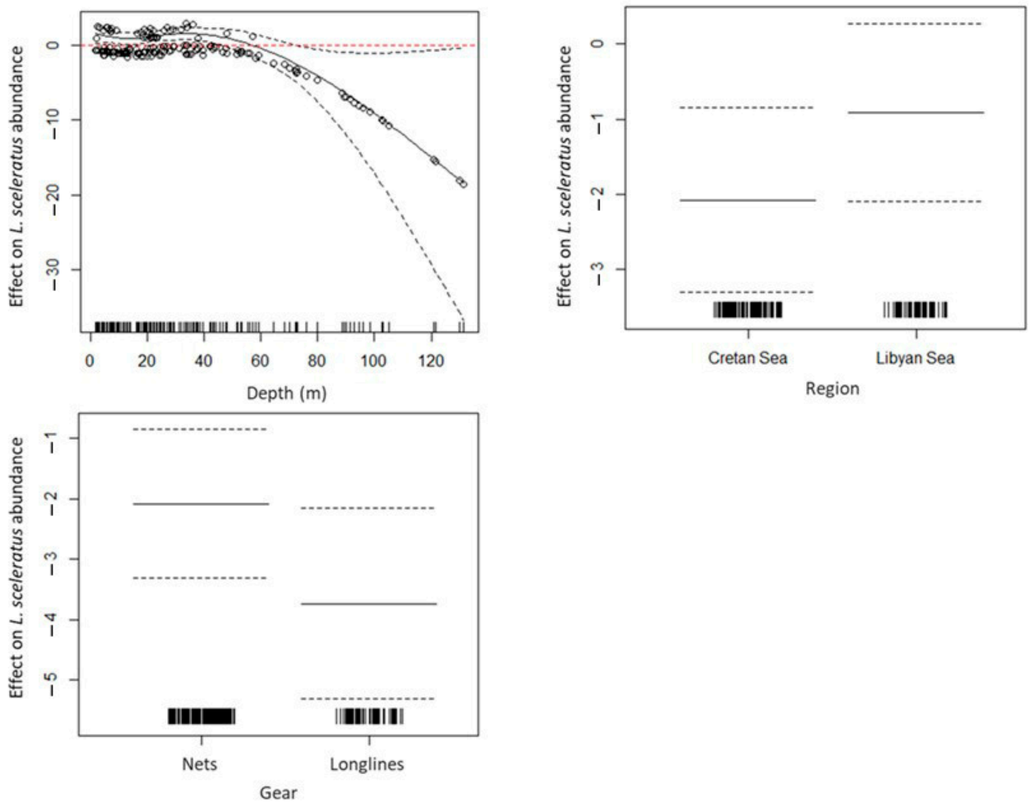

Figure 6. Effects of statistically significant predictors on *L. sceleratus* abundance in Crete. The mean model estimate is represented by the red dashed line, while the corresponding standard errors are denoted with black dashed lines. The points in the smoothing term plot denote the residuals. The "rug" on the *x*-axis represents the relative density of data points.

4. Discussion

In the present study, we evaluated the magnitude of *L. sceleratus* impacts on small-scale fisheries in the Greek seas through interviews with local fishers. A multitude of economic impacts were reported (Table 3), marking the first quantitative assessment of monetary losses suffered by Greek fishers due to this invasive species. In response to *L. sceleratus* depredation on gears, fishers reported several fishing tactic adjustments (Figure 3), particularly in Crete, where the species was more prevalent. Additionally, in order to disentangle the factors influencing the interaction of *L. sceleratus* with small-scale fisheries, generalized additive models were applied to data collected through onboard sampling on Cretan vessels.

Our study contributes to the limited literature on the impacts of *L. sceleratus* in Mediterranean small-scale fisheries (Supplementary Table S1) and, on a broader scale, to the poorly assessed economic impacts of marine invasive species in European seas [47]. It is the first to examine all sources of monetary losses due to interactions with this pufferfish (gear-, catch- and labor-related losses), thereby providing a more accurate estimation of the overall economic impact of this damaging species. In contrast, previous studies focusing on the economic impacts of *L. sceleratus*, conducted along the coasts of Turkey, mainly addressed the economic losses associated with gear damages, with limited information on labor and catch losses provided [18,39,40].

We found that the silver-cheeked toadfish adds substantial extra economic pressure to small-scale fisheries, a sector already considered marginalized and vulnerable [48]. The mean annual income of Greek small-scale fishers for the period 2012–2019 was 17,518 EUR/vessel, with little variability recorded across different years (range = 15,896–20,168 EUR/vessel) [49]. This implies that fishers in Crete experience approximately 36% losses in their total income, while those in the Ionian region experience a comparatively minor 1% reduction due to *L. sceleratus* impacts. The annual economic losses resulting from *L. sceleratus* depredation were comparable to those caused by marine mammals in Greek small-scale fisheries [50–53] (Supplementary Table S2). According to a previous study conducted in Crete in 2013, fishers had already identified *L. sceleratus* as the second most gear-damaging species after dolphins, followed by seals and turtles [15]. Additionally, the species was also reported to have a higher impact on catch compared to marine megafauna species. However, since then, the abundance of this species has substantially increased, and the impacts found are presumed to be more severe than in previous years.

Variations in the economic impact of *L. sceleratus* were observed across study areas and fishing gears. Specifically, the highest economic losses were reported by the Libyan Sea fishers operating both nets and longlines, while the lowest were reported by Ionian netters. The magnitude of the impact in each fishing region appeared to align with the reported *L. sceleratus* catch frequency and annual by-catch, which were higher in the Libyan Sea (southeastern region of this study) and markedly lower in the Ionian Sea (northwestern region of this study) (Table 3). These regional trends may be linked to the westward expansion of the species in the Mediterranean Sea, suggesting higher occurrence and population size in the southeastern regions compared to the northwestern ones. Indeed, Coro et al. [54] found that the probability of *L. sceleratus* occurrence is higher in South Turkey and South Greece (>0.8) compared to the Aegean and Ionian seas (0.4–0.6).

In Crete, the interview results agreed with findings from the onboard sampling and indicated that *L. sceleratus* is more frequent and abundant in the Libyan Sea, contributing more to the total catch compared to the Cretan Sea. However, the higher *L. sceleratus* BPUE recorded in the Cretan Sea is an indication that the species populations in south Crete included a relatively higher number of smaller individuals than those in the north. This finding is also supported by the mean total length of specimens caught, which was higher in the Cretan compared to the Libyan Sea. The potential increased presence of small-sized *L. sceleratus* in the Libyan Sea may suggest that nursery grounds of the species are mostly located in southern regions of Crete rather than in northern regions of the island.

In order to mitigate the impacts of silver-cheeked toadfish, fishers adjusted their fishing tactic to avoid interaction with this pufferfish. Fishers' tactical responses to *L. sceleratus* depredation reflect well-established knowledge regarding the species ecology (e.g., depth and substrate preferences, daily activity). Regionally, the highest percentage of fishers who changed their tactic was recorded in the Libyan Sea, where the higher abundance indices of *L. sceleratus* (annual by-catch, NPUE, catch frequency) and the higher depredation probability were estimated. The shift of fishing activity to deeper waters (>50 m) was the most frequently reported tactic adjustment of fishers operating in seas around Crete, which is justified by the fact that operations conducted in shallow waters (<40 m) are more likely to be impacted by this species (see Results Section 3.5). Similar changes in fishing tactics have also been reported for Cyprus small-scale fisheries [55], as well as for long- and handline fishers in the island of Rhodes (southeast Aegean), who shifted their effort to depths greater than 60 m [24].

The GAMs fitted in the present study revealed that interactions of *L. sceleratus* with small-scale fisheries, in terms of the species by-catch and depredation, were influenced by depth, gear, region and temperature. All dependent variables tested presented a decreasing trend with the increase in fishing depth. Specifically, depredation probability, biomass and abundance of *L. sceleratus* were higher between 0–40 m and started to steadily decrease as the fishing depth exceeded 40 m. These findings agree with the results from the interviews; the lowest catch frequencies were reported in the depth zone 65–100 m (Table 2). In a previous study in Cyprus, the highest numbers of *L. sceleratus* caught during small-scale fisheries operations were also recorded in the 10–40 m depth zone [21]. Similarly, in trawl operations conducted on the Turkish coasts, the highest catches of *L. sceleratus* were reported in the depth zone 0–25 m [56,57]. Concerning the fishing gear, *L. sceleratus* biomass and abundance were higher in nets than loglines, whereas the opposite was true for depredation probability. These findings are explained by the fact that *L. sceleratus* easily escapes when caught on longlines, as it cuts off the branch lines with its sharp teeth. Moreover, the damages may be more frequent for longlines due to the appeal of the bait used.

The effect of region indicated that depredation probability and *L. sceleratus* abundance were higher in the Libyan Sea compared to the Cretan Sea. Interestingly, region was significant in the abundance model but not in the biomass model. This is an additional indication of the presence of more and smaller specimens in the Libyan Sea and fewer and larger specimens in the Cretan Sea (see above). Conclusively, the higher abundance of *L. sceleratus* in the Libyan Sea may also justify the higher depredation probability found in this region.

Lastly, the increase in temperature positively influenced the depredation probability during a fishing trip. This trend may be driven by the increase in *L. sceleratus* metabolic rate caused by the sea temperature rise [58]. However, a drop is presented in this general increasing trend in temperatures between 21 and 23 °C (period from early to late June). This period corresponds to the peak of the spawning activity of *L. sceleratus* in Crete [59], when lower depredation on fishing gears may be related to a general restriction of food intake by the species. Such limitation of feeding activity may occur due to investment in accessory spawning activities, such as nest building, which is observed in other pufferfish species [60] but has not been confirmed yet for *L. sceleratus*.

Up to now, specific management actions for the control of *L. sceleratus* populations in the eastern Mediterranean have only been applied in Turkey and Cyprus. These actions involved the initiation of bounty programs which compensated the fishers for each specimen of *L. sceleratus* caught [61–63]. Other than the small monetary benefit for the fishers, these bounty programs have, so far, been ineffective in controlling *L. sceleratus* populations, as no evident declining trends have been observed yet [61,62]. Moreover, prior experience with the management of lionfish (*Pterois miles*/*Pterois volitans*) in the western Atlantic has shown that bounty programs are not a self-sustaining measure, as they usually do not run on a consistent basis due to their dependence on fund availability [64].

According to Giakoumi et al. [65], the most applicable and highly prioritized management actions in order to control a widely spread marine invader (such as *L. sceleratus*) are (a) raising public awareness regarding the species impacts, (b) encouraging the targeted removal of the species from commercial and/or recreational fisheries (i.e., increasing the fishing pressure on the species), and (c) promoting the commercialization of the species. A successful management example is the control of lionfish populations in the western Atlantic [64], but for the case of *L. sceleratus*, the non-edibility of the species necessitates exploring commercial applications other than human consumption.

Currently, there are no available market products from *L. sceleratus*; however, some promising advances towards the potential commercial use of this invasive species have been made. Bioactive compounds, such as collagen and TTX, have been successfully extracted from *L. sceleratus* tissues, and, moreover, successful detoxification methods have been developed [66,67]. TTX, which is predominantly extracted from pufferfish, can be used in various medical and pharmaceutical applications [68]. Additionally, the extracted collagen and TTX can have applications in the production of cosmetics, and the detoxified *L. sceleratus* tissues can be used as a fish-oil source in nutraceuticals [65,66]. The processed skin of *L. sceleratus* is also available for the production of "eco-friendly" clothing and accessories [69]. In conclusion, there is much scope for the commercial exploitation of *L. sceleratus*, which would be essential for a long-term, self-sustaining management plan.

In summary, our research significantly advances our understanding of biological invasions, particularly in the context of marine invasive species interacting with fisheries. The investigation of spatial variations in the distribution and impact of such species emerged as a crucial aspect. Region-based approaches are recommended for future studies in the field of invasion biology, as they are essential for targeted and cost-effective management schemes. The combination of fishers' perspectives, onboard sampling and the application of predictive models was proven to be a robust approach. Similar approaches can provide insights that can guide stakeholders in regions where the arrival or population growth of an invasive species, interacting with fisheries, is imminent.

5. Conclusions

Understanding the regional variations in *L. sceleratus* distribution and its impacts on small-scale fisheries is crucial for informed decision-making to adopt mitigation measures and sustain local fisheries in the eastern Mediterranean. Although *L. sceleratus* has been present in the Greek seas since 2005 [70], no studies revealing the magnitude of its impacts on small-scale fisheries have been conducted to date. The present work sheds light on the most significant sources of economic losses resulting from *L. sceleratus* depredation (gear, labor and catch losses); however, further investigation is needed to estimate indirect economic losses due to shifts in fishing tactics (e.g., extra fuel cost when operating in deeper waters and thus more distant fishing grounds, opportunity loss due to avoidance of fishing grounds with highly valuable commercial species).

The findings of this study emphasize the urgent need for management actions, particularly in Crete, where fishers face substantial economic losses. Prior knowledge on the management of marine invasive fishes suggests that raising public awareness, increasing the fishing pressure and exploiting the species commercially might be key components for the successful control of *L. sceleratus* populations. The abundance and biomass indices, as well as the catch frequency of *L. sceleratus*, provided here can offer important information for establishing targeted fisheries for this species. In this context, sustainable fishing practices could benefit from technical adjustments to fishing gears. For example, the construction of longlines with wire branches and more durable mesh panels for nets could increase the catchability of the species and minimize gear losses [71]. However, the missing link towards the successful management of *L. sceleratus* is its commercial utilization. Further research in the fields of medicine, pharmacology, nutrition and cosmetics may lead to the elaboration of high-value products from *L. sceleratus* (extraction of TTX, collagen and fatty acids) and thus create demand and motivate fishers to target the species.

Supplementary Materials: The following supporting information can be downloaded at https://www.mdpi.com/article/10.3390/fishes9030104/s1: Figure S1: Typical triangular-shaped bite mark of *L. sceleratus* on some commercial catches, recorded during small-scale fishing trips conducted in seas around Crete during the period May 2020–December 2022: (A) Mediterranean parrotfish, *Sparisoma cretense*. (B) Striped red mullet, *Mullus surmuletus*. (C) Common stingray, *Dasyatis pastinaca*. (D) Salema, *Sarpa salpa*. (E) Common dolphinfish, *Coryphaena hippurus*. Figure S2: Damages of *L. sceleratus* in small-scale fishing trips conducted in seas around Crete during the period May 2020–December 2022: (A) Cluster of holes in trammel net. (B) Cluster of holes in trammel net, around a depredated European barracuda *Sphyraena sphyraena*, with obvious triangular-shaped bite marks. (C) Single big hole in trammel net with the outer net layers being intact. (D) Damages on sturdy gear parts (net floaters). Figure S3: Mean sea surface temperature per month in coastal waters of Crete. Error bars represent standard errors. Temperature data were acquired on a year-round basis through deployments of a temperature logger (HOBO Pendant Temperature/Light 64K Data Logger UA-002-64). Table S1: Annual economic losses (mean ± S.D.) inflicted by *L. sceleratus* on small-scale fisheries operating in various Mediterranean regions per loss category, vessel and gear. Table S2: Annual gear and catch economic losses inflicted by marine mammals and *L. sceleratus* on small-scale fisheries operating in various Greek regions. NA = not available.

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