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An in-depth study of the biology, trophic ecology and catchability of the invasive pufferfish *Lagocephalus sceleratus* from southern Turkey, eastern Mediterranean Sea

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Summary: The silver-cheeked toadfish (*Lagocephalus sceleratus*) is an invasive species of highest concern. Its population must be controlled to mitigate its negative impacts on marine ecosystems, fishers, fisheries and human health. This study thoroughly investigates the biology, diet and catchability of the *L. sceleratus* stock from Finike, Turkey from March 2017 to February 2018 in order to better manage its invasion. A total of 751 specimens were sampled for this study with a M/F ratio of 1.25/1. The species becomes sexually mature at three and a half years of age, and Lm_{50} was 41.39 cm for males and 42.08 cm for females. Its spawning season in this region was from June to August, peaking in July. Its diet was mostly crustaceans in spring, fish in summer and both fish and crustaceans in winter. This species consumed a large amount of other pufferfish species, resulting in over a quarter of its fish diet. The trophic level of *L. sceleratus* was 4.41, demonstrating that it is indeed a top predator carnivore in the eastern Mediterranean Sea. Ingested fishing gear parts such as net pieces and hooks were found in about 10% of the fish. A slight modification of longlines using steel branch lines and a swivel hook resulted in double the catch per unit effort than standard longlines, so this technique can be used to target and control more of this invasive species, which is a national priority.

Keywords: non-indigenous species (NIS); pufferfish; catch per unit effort (CPUE); ageing; stomach content analysis; trophic level.

Un estudio exhaustivo sobre la biología, ecología trófica y capturabilidad del pez globo invasor *Lagocephalus sceleratus* en el sur de Turquía, mar Mediterráneo oriental

Resumen: El pez globo (*Lagocephalus sceleratus*) es una especie invasora de gran preocupación. Es necesario controlar su población para mitigar sus impactos nocivos en los ecosistemas marinos, los pescadores, la pesca y la salud humana. Este estudio investiga minuciosamente la biología, la dieta y la capturabilidad del stock de *L. sceleratus* en Finike, Turquía, desde marzo de 2017 hasta febrero de 2018, con el fin de mejorar la gestión de la invasión. Se muestreó un total de 751 ejemplares para este estudio, con una proporción de machos/hembras de 1,25/1. *L. sceleratus* alcanza la madurez sexual a los tres años y medio de edad, y la Lm50 fue de 41,39 cm para los machos y 42,08 cm para las hembras. Su temporada de desove en esta región fue de junio a agosto, alcanzando su punto máximo en julio. Su dieta consistía principalmente en crustáceos en primavera, peces en verano y tanto peces como crustáceos en invierno. Esta especie consumía una gran cantidad de otras especies de peces globo, lo que representaba más de una cuarta parte de su dieta de peces. El nivel trófico de *L. sceleratus* fue de 4,41, lo que demuestra que *L. sceleratus* es en efecto un carnívoro depredador de alto nivel en el Mar Mediterráneo Oriental. Se encontró ingestión de partes de artes de pesca en aproximadamente el 10% de los peces, como trozos de redes y anzuelos. Una ligera modificación del palangre utilizando líneas de acero y un anzuelo giratorio resultó en valores duplicados de CPUE en comparación con palangres estándar, lo que se puede utilizar para enfocar y controlar más de esta especie invasora, lo cual es una prioridad nacional.

Palabras clave: especies no autóctonas (ENA); pez globo; Captura por Unidad de Esfuerzo (CPUE); envejecimiento; análisis del contenido estomacal; nivel trófico.

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INTRODUCTION

The Mediterranean Sea is a complex region in which intensive human activities have shaped the marine biodiversity, especially over the last half century (Coll et al. 2012). As it is a nearly totally enclosed basin, it can be viewed as a model of the global oceans and a natural laboratory for studying marine ecosystems and processes and deciphering future trends through its physical, ecological and socio-economic structure. The Mediterranean Sea's biological structure and ecological processes are changing rapidly, especially in the eastern region as a result of tropicalization (Vergés et al. 2014, Gücü et al. 2021), and Indo-Pacific marine migrants are increasingly arriving through the Suez Canal vector and establishing new populations (Zenetos and Galanidi 2020). The Suez Canal, opened in 1869, connects the Red Sea and the Mediterranean Sea, linking two distinct biogeographical regions and acting as a corridor for alien species. This corridor is the main reason for the invasions of most alien species into the eastern Mediterranean (Galil et al. 2018). While some alien species provide economic, social, ecological or human health benefits, those that negatively affect human health, the economy or the biodiversity are deemed invasive (Bax et al. 2003). When invasive species successfully establish in a new area, the intensity of their effects on the economy, biodiversity or human health, or combinations of these effects, can warrant directed management for their targeted control.

Among the alien species established in the eastern Mediterranean, one of the most successful is the silver-cheeked toadfish, *Lagocephalus sceleratus* (Gmelin 1789). This species was first recorded in the Mediterranean in 2003, from Gokova Bay in southwestern Turkish waters (Akyol et al. 2005). It is both the largest (maximum weight of 10 kg; Ulman et al. 2022) and most abundant pufferfish species in many localities in the eastern Mediterranean (Farrag et al. 2015, Turan 2022). Within just ten years of its first Mediterranean record, it expanded rapidly to nearly every Mediterranean sub-region (strangely, with the exception of southern France and Corsica), and within 15 years it was also recorded in the much cooler Black Sea and the Strait of Gibraltar (Rambla-Alegre et al. 2017, Bilecenoglu and Ozturk 2018). It is easily identified by its elongated shape, a shiny silver stripe across its side and leopard-like spots on a grey background on its dorsal side (Fig. 1). It is sometimes confused with *Lagocephalus suezensis* but can be distinguished by the spots of *L. suezensis* on a brown background on its dorsal side. The first feature that makes this species invasive is its threat to human life from its tetrodotoxin (TTX, a neurotoxin) levels. TTX is found in high concentrations in all its tissues (gonads, liver, muscle, eyes, intestine, skin, etc.) and can sometimes cause human death if consumed (Katikou et al. 2009, Kosker et al. 2016). TTX is highly variable in *L. sceleratus* individuals, likely depending on its diet. Despite widespread awareness of its toxicity, ingestion of this species has caused at least a dozen human fatalities across the Mediterranean, although most intoxications are not formally recorded (Ben Souissi et al. 2014, Ul-

Fig. 1. – Photos of *Lagocephalus sceleratus* samples, Aylin Ulman.

man et al. 2022). Its second invasive trait is the economic losses that it causes to fishers, which are three-fold. First, it can cause extensive damage to fishing gear by cutting off large proportions of longline hooks and biting into fishing nets, causing major fishing gear expenses. Second, it preys on the catches on lines and in nets, reducing fishers' catches and incomes and leading to increased labour costs from attaching new hooks and repairing nets (Ünal et al. 2015). Third, due to its high invasive success in the Mediterranean (Akyol and Ünal 2017, Ulman et al. 2022), it has likely reduced favoured prey taxa in certain areas, especially, as observed in Rhodes, that of cephalopods, which were found in nearly one-third of stomachs (29% in number and frequency) over a decade ago (Kalogirou 2013), though a more recent study found cephalopods to be found in just 11% of stomachs (Ulman et al. 2021a). Another interesting development in its diet was a recent shift towards cannibalism (Ulman et al. 2021a), which was not evidenced from earlier studies and is thought to have developed through density dependence of their invasion success and the inability to locate enough other prey, as in the western Atlantic lionfish invasion (Dahl and Patterson 2014). In fact, it is now well known that fishers targeting *L. sceleratus*, for example in Turkey and Cyprus where the government has set a bounty for its control, use pieces of *L. sceleratus* for bait, which is very quickly consumed.

Before invasive species can be properly managed, their biological traits, ecological effects, stock status and catchability need to be better understood. Quantifying some of these effects, especially the ecological ones, are challenging, usually requiring in-situ controlled experiments. To help improve the research needed for this species and aid in its targeted control, a comprehensive study was undertaken to better understand the biological traits and ecological impacts of *L. sceleratus* and to test methods for improving its catch rates. For these purposes, two separate sampling studies were undertaken on *L. sceleratus* in southern Turkey, the first on its biological and ecological traits (age, growth, reproduction and diet) and the second on improving catch rates. When small-scale fishers use longlines in southern Turkey, it is common for *L. sceleratus* to bite off many of the hooks, which is costly for fishers in both materials and time. Thus, to try to improve its catch rates and reduce its impacts on longline hooks, two longline gear modifications were trialed for the second part of this study.

MATERIALS AND METHODS

Biological study

The biological sampling was conducted monthly from March 2017 to February 2018 in Finike Bay in the north-western Levant Basin (Fig. 2). Scientific fishing operations were conducted using longlines six to seven times per month to collect fish for the investigation. Additionally, extra pufferfish caught by commercial gill net and recreational handline fishers in the region were also collected. Each sampling day, the samples

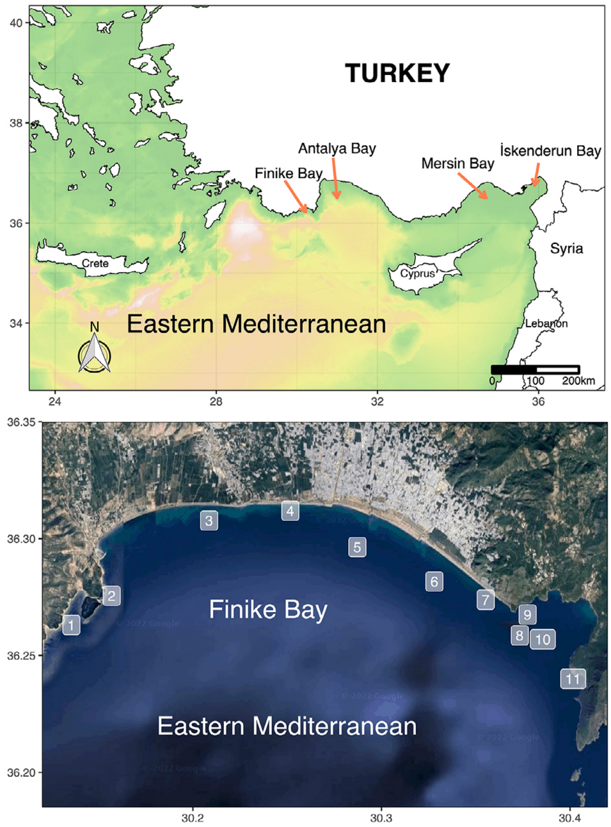

Fig. 2. – A map of southern Turkey (top panel) and the Finike Bay study area (bottom panel), with sampling locations numbered. 1, Gökliman; 2, Taşocağı; 3, Gülmezler; 4, Alakır Stream; 5, Yapraklı Stream; 6, Mavikent; 7, Aktaşlar; 8, Karaöz; 9, Papaz Bight; 10, Sazak Bight; 11, Ovacık.

were transferred to the laboratory using coolers. First the total length and total weight were initially recorded, then individuals were dissected, the gonad weights and liver weights were measured, sex was determined, and the complete digestive tracts were removed and fixed with 70% alcohol for further stomach content analyses. For the biological analysis, a total of 1310 pufferfish were collected, including four species: 751 *L. sceleratus*, 325 *L. suezensis*, 18 *L. guentheri* and 216 *Torquigener hypselogeneion* (syn. *T. flavimaculosus*). Relative abundances of the four pufferfish species in total catches were 57.3% for *L. sceleratus*, 24.8% for *L. suezensis*, 16.4% for *T. hypselogeneion* and 1.7% for *L. guentheri*. Length/weight, age, growth, mortality, condition factor, reproduction and diet were investigated for the biological studies.

Growth and mortality parameters

Total fish lengths (TL) were measured to the nearest 0.1 cm and total weights (TW) were recorded to the nearest 0.01 gram using a digital scale. The relationship between TL and TW was calculated using the equation $TW=aTL^b$. Parameters (a) and (b) were estimated by applying the ordinary least squares method with natural logarithms of TW and TL. Next, to determine fish shape with growth, 95% confidence intervals of b were calculated to test whether it was significantly different from 3, as fish become thinner as they grow if $b<3$ and plumper if $b>3$ (Pauly 1984). Then, the b values of the males and females were compared using ANCOVA to determine whether there was a difference between the allometry coefficient for both sexes.

A sclerochronologic method was employed to determine the age of the specimens (Lewis 1949). First, the 2nd to 7th vertebrae were removed from the fish by ventral dissection. Samples were taken by scalpel, slicing a portion of the vertebrae beginning above the pectoral arch and separating large flesh portions. Residual flesh was removed by boiling the samples in hot water for three to five minutes and cleaning them with a brush. Finally, the samples were washed with distilled water and air-dried. Age was determined by counting the annual age rings on the vertebrae, which are mostly clearly seen under a stereomicroscope. The vertebrae that were unclear were sliced vertically into two pieces and examined under a stereomicroscope. Figure 3 provides an example of the annual growth rings from a vertebra sample from this study.

Length at age data was fitted to the von Bertalanffy growth function (VBGF); $L_t = L_\infty\ (1–e^{-K(t-t0)})$, where L_∞ is the asymptotic fish length if the fish were to grow indefinitely, K is the growth coefficient used in the VBGF expressing the rate (1/year) at which the asymptotic length is approached (Pauly 1984) and t_0 is the hypothetical age of the fish when the length was equal to zero (Sparre and Venema 1998). Growth parameters and 95% confidence intervals were estimated separately for males, females and all individuals by using the non-linear least squares method using TropFishR library (Mildenberger et al. 2017) in R statistical language (R Core Team 2021). The difference between the growth parameters of males and females was investigated using confidence intervals. Weight-specific growth parameters, $Wt = W_\infty\ (1–e^{-K(t-to)})^b$, were then calculated using the methods detailed in Sparre and Venema (1998). Here W_∞ was calculated as $L_\infty{}^b$.

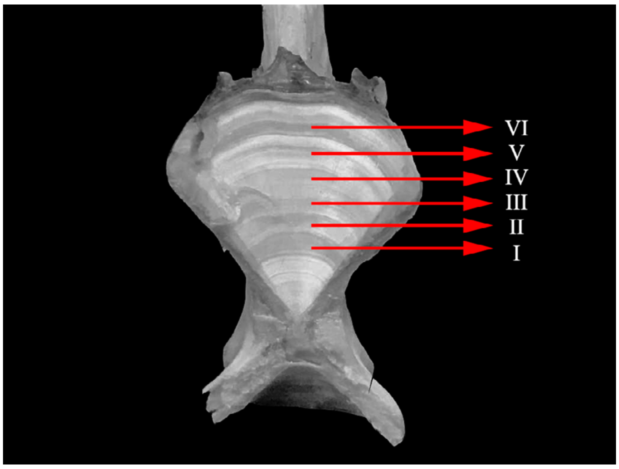

Fig. 3. – Sectioned vertebra sample of a six-year-old male *Lagocephalus sceleratus* caught with a longline on September 20, 2017. Total length is 58.5 cm. Annual growth rings are marked with red arrows.

Total mortality rate (Z) was calculated following Beverton and Holt (1993), which estimates Z from mean fish lengths as $Z = K*(L_\infty - \bar{L} / \bar{L} - L')$. L was the average fish length, and L’ the smallest fish length (Beverton and Holt 1993). Natural mortality was estimated using “Composite M: method weighting” from The Barefoot Ecologist’s Toolbox, which allows weighting of the contribution of different methods. This is an online tool compiling primary life-history–based predictors and weighting them according to input data sets. Since more than one estimator may use the same life-history data, the results are divided by the tool into the number of estimators involved. For example, there were four estimators based on maximum age, so each was weighted by 0.25 as the composite value. The tool then compiles all estimates to make a composite prior density using the empirical cumulative distribution of the point estimates. Equations and details of the composite M method can be found on the toolbox website (http://barefootecologist.com.au/shiny_m.html). Afterwards, the equation Z = M + F was used to estimate the fishing mortality rate (F). Then, the exploitation ratio was calculated from E = F/Z.

After length and weight measurements were taken, the livers and gonads were weighed to the nearest 0.01 gram. The somatic condition factor was determined using the equation $SCF= (TW-GW)/TL^3$, where GW is gonad weight. The hepatosomatic index (HSI) is used to show the stored liver energy level of individuals, which is later transferred for reproduction purposes. It is calculated using the equation HSI = (LW/TW) 100, where LW is liver weight. These indices were calculated separately for each sex.

Maturity and reproduction

To determine sex, the gonads of each specimen were examined macroscopically to identify mature specimens and stereomicroscopically to identify immature specimens. Gonads containing granular structures and plump-looking tube-shaped gonads were identified as females, and those containing a milky-white substance were identified as males.

The monthly average gonadosomatic index (GSI) values were used to understand the peak reproductive period, which coincides with high GSI values. The GSI values were calculated using the equation GSI: GW/(TW-GW)100 (Gibson and Ezzi 1978). GSI provides insights into changes in ovary size and reproductive activity through gonadal development (Lowerre-Barbieri et al. 2011). Determination of reproductive timing is recommended by assessing a combination of macroscopic-microscopic evaluation and histological analysis, but high GSI is also a useful indicator and a less-costly method than others (Lowerre-Barbieri et al. 2011).

Length at first maturity (L_{50}) is defined here as the size group at which 50% of the specimens are sexually mature. To calculate L_{50}, a binomial regression model was fitted with total lengths and sex interaction. Since sex-TL interaction was not significant, sex was dropped from the model and L_{50} was calculated for combined sexes. 95% confidence limits of L_{50} were calculated employing 10000 bootstrap resampling.

Diet

Entire digestive tracts were removed from the samples. Then, total weights of a particular food category were measured using a digital scale (0.01 g) after absorbent paper was used to soak up extra moisture for one minute. Next, the prey items in the stomach content were examined macroscopically and identified to the lowest possible taxonomic level. To analyse seasonal variations of feeding intensity, the degree of stomach fullness was assigned using an ordinal scale between 0 and 4, where 0 = empty, 1 = 1/4 full, 2 = 1/2 full, 3 = 3/4 full and 4 = full.

Numerous numerical indices have been developed to explain the importance of different food groups. Here the following indices were used: A) frequency of occurrence (%FO) from Berg (1979), B) contribution of prey items in numbers (%N) by Hyslop (1980) and C) contribution of prey items by weight (%W) from Cortés (1997). Please note that %FO is the most robust method for prey content analysis due to fundamental problems resulting from gravimetric approaches (Becker et al. 2013).

Finally, after the above measures were derived, the index of relative importance (IRI) was calculated for each prey category using the equation $IRI_i = (\%N_i + \%W_i) * \%FO_i$ from Hacunda (1981) to determine the main food groups. Then, percentage IRI values of each prey category were calculated with $pIRI_i = IRI_i/\Sigma IRI$.

The trophic level of *L. sceleratus* was then calculated based on the diet composition expressed as percentage pIRI values of each prey category using the following equation;

$$trop = 1 + \sum_{i}^{n} pIRI_i * trop_i$$

Here $trop_i$ represents the trophic level of each prey item (i=1,2,..,n), which were derived from Fishbase or Sealifebase, if available (Froese and Pauly 2022). The average values of family, order or group were inputted if no information existed about the taxon's trophic level. A bootstrap resampling procedure (9999) was performed to calculated 95% percentile confidence intervals for trophic levels using the R library boot (Canty and Ripley 2021).

Catch per unit effort (CPUE)

A longline experiment was used for the improved catch efficiency study. Two longline sets composed of 100 hooks each were used to examine CPUE differences by season and site. The main body of the longline was a 100-gauge line with 9 m distance between branch lines, each branch line was 90 cm in length, and a straight #9/0 fishing hook was attached to each branch line.

A second experiment was performed using the standard longline type and two types of modified longlines to try to improve *L. sceleratus* catch efficiencies to optimize targeted removals. The first longline gear type was the standard type as described above, using a 1 mm monofilament fishing line, which is commonly used in longline fishing, as the lead line. The catches of this standard longline were compared with two types of modified longlines to compare catch efficiencies:

– The first modified longline type used an 80-pound capacity steel fishing line as the branch line.

– The second modified longline type used an 80-pound steel fishing branch line (as above) and placed an additional steel rolling swivel #3 between the steel wire and the hook. A fishing swivel is made of two separate round, metal eyelets that are connected by a barrel fitting. The eyelets turn freely within the fitting, independent of each other. Swivels provide an axis point that allows leaders or rigs to spin yet keeps the main line still reducing the amount of torque and hence the likelihood of the fishing line breaking.

Then, the three gear types were trialled in fishing experiments and the results were compared for catch efficiencies. The catch (in kg) and CPUE (kg/100 hooks) were recorded along with the number of missing hooks (missing hooks/100 hooks). Number of missing hooks by different longline types were analysed using a one-way analysis of variance (ANOVA). As variances were not homogenous in analysing CPUE values, a Welch correction was applied. Pairwise comparisons were performed with Bonferroni correction. R package "one-way tests" were used in these analyses (Dag et al. 2018).

Experimental longline fishing operations were carried out specifically at the 11 main fishing sites in Finike. A total of 89 standard longline fishing operations were performed over the year-long study to test CPUE. Additionally, three longline gear type modifications were tested using ten trials each to determine whether the modifications could improve catch efficiencies for pufferfish. All longline operations were carried out between 7:00 and 14:00 during the day, with soak times ranging between two and three hours. In the study, the effect of three different snood types on the CPUE was examined. For this purpose, three different longlines, whose snood characteristics are given below, were prepared. A total of 100 snoods were used in each of these longlines. All technical features except the snood type were kept the same in the longlines (main line thickness, 1 mm; distance between snoods, 9 m; snood length, 90 cm; fishing hook No, 9/0). With these three longlines, ten operations were performed in March. CPUE (kg/hook) was calculated for each operation using the weights of individuals obtained in these ten operations. Then, it was statistically tested whether the CPUE obtained for different snood types differed. Also, the number of lost (broken) snoods in each operation was recorded. Thus, it was tested whether there was a difference in the number of lost snoods per operation according to snood types.

Temporal and spatial assessment of CPUE

For each longline fishing operation, the CPUE index was used as the number of caught pufferfish per

100 hooks from each longline vessel. The CPUEs from the different fishing sites were compared using the Kruskal-Wallis test. Monthly changes in CPUE values were also compared using the Kruskal-Wallis test. The seasons were organized by assigning the last month of each season to the subsequent seasonal group (1st group, November-December-January; 2nd group, February-March-April; 3rd group, May-June-July; 4th Group, August-September-October). Of the 89 operations carried out during the 12 months, 12 were carried out in the first group, 27 in the second, 25 in the third and 25 in the fourth. The Tamhane and Dunnett T3 statistical post-hoc tests were used to examine variations by season.

RESULTS

Sex ratio, size and length class distribution by gear type

Of the 751 *L. sceleratus* samples, 414 were male, 328 female and 8 unknown (juveniles). The M/F ratio was 1.25:1, which was significantly different from 1:1 (χ^2= 9.97, p <0.01). Total length of specimens ranged from 10.2 cm to 73.4 cm. The median lengths (Wilcoxon W= 65420, p=0.39) and weights (Wilcoxon W=65091, p=0.33) of males and females were not significantly different. The mean length of individuals was 27.30±11.40, 32.34±14.90 and 49.65±8.88 cm (±standard deviation) for set nets, handlines and longlines, respectively. Based on a Kruskal-Wallis test and pairwise comparison tests with Bonferroni correction, longliners caught significantly larger specimens than set nets and handlines (p<0.05). This is because the #9/0 size hook used in this study is generally used to target medium to large gamefish, as smaller fish cannot bite larger hooks, so a standard size selectivity was applied when the hook sizes were chosen.

From Figure 4, which shows the length-frequency distribution of the samples caught by different fishing gear methods, two distinct peaks are shown, one 20 cm and the second one around 48 cm length. Clearly, the 20 cm peak is from samples caught by handlines and set nets, and the 48 cm peak is from samples caught by longlines.

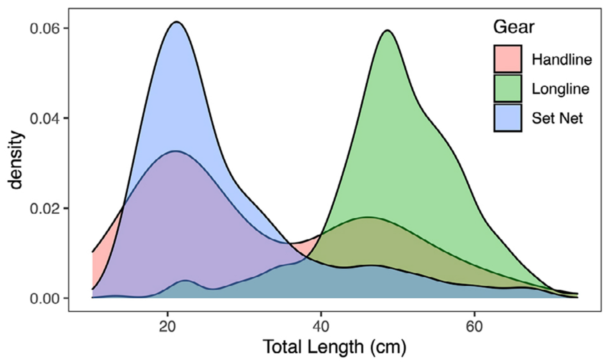

Fig. 4. – Length-frequency distribution of *Lagocephalus sceleratus* by sampling gears.

Table 1. – Growth and mortality parameters for *Lagocephalus sceleratus* from this study. The values in parentheses are 95% confidence intervals. L_∞ and W_∞, von Bertalanffy growth functions, asymptotic total length and weight; K, VBGF growth coefficient; t_0, hypothetical age of the fish when the length was equal to zero; Ø', the growth performance index; L_{50}, length at first maturity; a, b and R^2, the coefficients of allometric length-weight relationship; Z, M and F, exponential rates of total, natural and fishing mortality; E, exploitation rate.

Sex	♂	♀	♂+♀
# samples	414	328	750
L_∞ (cm)	103.78 (94.84–115.95)	107.97 (97.71–122.49)	113.97 (105.55–124.77)
W_∞ (g)	12088.17 (11804.31–12378.84)	13623.13 (13294.02–13960.38)	15877.34 (15595.83–16163.93)
K ($year^{-1}$)	0.13 (0.11–0.15)	0.12 (0.10–0.15)	0.11 (0.10–0.13)
t_0 ($year^{-1}$)	-0.47 (-0.60–-0.35)	-0.54 (-0.68–-0.41)	-0.62 (-0.71–-0.53)
Ø'	7.26	7.26	7.28
L_{50}	-	-	41.86 (39.73–44.08)
a	0.0114 (0.0105–0.0124)	0.0116 (0.0107–0.0126)	0.0119 (0.0112–0.0125)
b	2.989 (2.967–3.011)	2.986 (2.962–3.007)	2.979 (2.964–2.994)
R^2	0.994	0.995	0.995
Z ($year^{-1}$)			0.94
M ($year^{-1}$)			0.34
F ($year^{-1}$)			0.60
E			0.64

Age and growth

Based on the ANCOVA results, the length-weight relationship parameters of each sex were not found to be significantly different. The coefficients of allometry were not significantly different from 3 in males and females, suggesting that this species retains the same body shape as it grows, but a very weak trend was detected when both sexes were combined, suggesting that some get thinner (Table 1). Somatic condition factor gradually began to decrease from April to July, coinciding with the spawning season. Except for t_0, males and females had similar von Bertalanffy growth parameters based on 95% confidence intervals (Table 1, Fig. 5). Natural mortality estimations ranged between 0.165 (Jensen method) and 0.703 (Roff method), with a mean score of 0.34 using the weighted values of both methods.

A total of nine year classes were found in this study from the vertebrae readings, ranging from 0 to 8 years. The frequency of year classes were 0.6% from the 0-age class, 17% in the first year, 15% in the second year, 10% in the third year, 26% in the fourth year (the dominant age class), 19% in the fifth year, 7% in the sixth year, 5% in the 7th year and only 0.4% in the eighth year. The frequency of older individuals present in the samples decreased after four years in age. Longlines caught much larger fish on average (see Fig. 4), while handlines and set nets caught mostly immature ones. This is likely due to longliners targeting larger fish, hence using larger hooks able to catch larger specimens.

Reproduction

GSI values started to increase in March while somatic (SCF) and hepatic condition (HSI) and feeding index (FI) started to decrease at the same time (Fig. 6). There were strong negative correlations between GSI and HSI (Pearson's r=–0.64, p<0.01) and SCF (Pearson's r=–0.81, p<0.01). In addition, a week negative correlation with FI (Pearson's r=–0.36, p=0.08) was found. These negative correlations are strong arguments that *L. sceleratus* is a capital breeder. GSI peaked in July and then rapidly declined until September, suggesting that the main reproductive period in Finike Bay is between June and August, peaking in July (Fig. 6). Total length-maturity relationship parameters were not significantly different between sexes, and length at first maturity (L_{50}) was calculated as 41.86 cm (39.73–44.08 cm; 95% confidence intervals) for combined sexes, corresponding to an age of 3.5 years (Table 1).

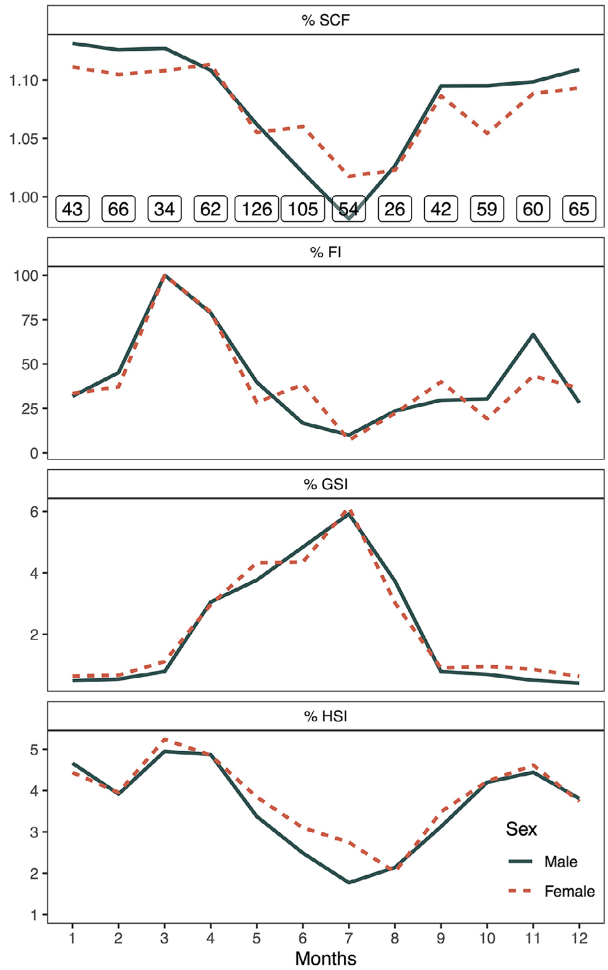

Fig. 6. – Monthly changes of somatic condition factor (% SCF), feeding intensity (% FI), gonadosomatic index (% GSI) and hepatosomatic index (% HSI) values of *Lagocephalus sceleratus*. Labels in the upper panel show number of samples per month.

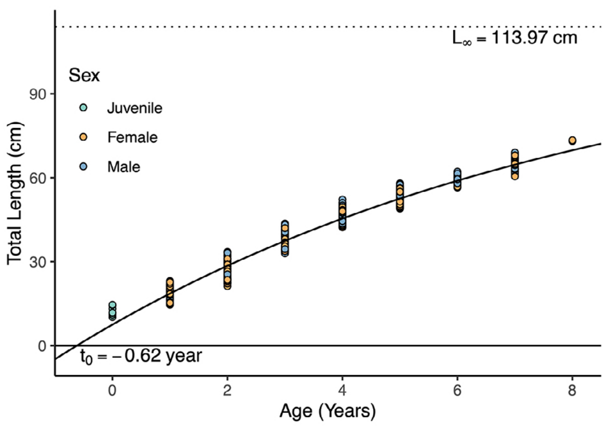

Fig. 5. – Length at age values of juveniles, females and males and von Bertalanffy growth curve calculated for combined sexes.

Diet

Of 751 individuals, 287 (38%) underwent stomach content analysis. A total of 39 different species belonging to 29 families, including 15 bony fishes, 7 crustaceans, 6 molluscs and 1 echinoderm were found as prey items (Table 2). The most important prey group was crustaceans (54%), followed by bony fish (44%). The proportion of molluscs and echinoderms was negligible compared with crustaceans and fish. There were considerable seasonal differences in prey content in terms of %IRI; crustaceans had a higher value (83%)

Table 2. – Diet of *Lagocephalus sceleratus*: N, number of prey item; W, weight of prey item; F, number of stomachs with the prey item; %N, %W and %FO, percentage of N, W, and FO; IRI, index of relative importance; %IRI, percentage index of relative importance; trop, trophic level.

Group/species	N	W	F	%N	%W	%FO	IRI	%IRI	trop
Mollusca									
Bivalvia									
Flexopecten glaber	4	33.08	4	0.77	0.67	0.53	0.77	0.13	2.10
Gastropoda									
Naticarius stercusmuscarum	2	3.55	2	0.39	0.07	0.27	0.12	0.02	2.37
Turritellinella tricarinata	3	1.07	2	0.58	0.02	0.27	0.16	0.03	2.37
Gastropoda spp.	8	11.97	7	1.54	0.24	0.93	1.66	0.28	2.37
Cephalopoda									
Loligo vulgaris	9	163.56	9	1.74	3.30	1.20	6.04	1.02	4.50
Octopus vulgaris	7	173.68	7	1.35	3.50	0.93	4.53	0.76	3.74
Sepia officinalis	5	40.10	5	0.97	0.81	0.67	1.18	0.20	3.71
Cephalopoda spp.	10	60.48	7	1.93	1.22	0.93	2.94	0.50	3.98
Crustacea									
Decapoda									
Callinectes sapidus	1	1.85	1	0.19	0.04	0.13	0.03	0.01	3.35
Charybdis longicollis	80	322.91	31	15.44	6.52	4.13	90.65	15.31	3.45
Goneplax rhomboides	4	45.47	2	0.77	0.92	0.27	0.45	0.08	2.50
Ixa monodi	4	58.17	3	0.77	1.17	0.40	0.78	0.13	2.50
Macrophthalmus graeffei	6	128.33	4	1.16	2.59	0.53	2.00	0.34	2.00
Portunus pelagicus	1	3.78	1	0.19	0.08	0.13	0.04	0.01	3.54
Brachyura spp.	56	321.21	33	10.81	6.48	4.39	75.99	12.83	3.45
Parapenaeus longirostris	5	61.35	4	0.97	1.24	0.53	1.17	0.20	3.68
Penaeus kerathurus	14	256.67	14	2.70	5.18	1.86	14.69	2.48	3.54
Penaeus semisulcatus	24	359.64	23	4.63	7.26	3.06	36.42	6.15	2.92
Processidae spp.	6	54.24	5	1.16	1.09	0.67	1.50	0.25	2.60
Dendrobranchiata spp.	11	26.72	9	2.12	0.54	1.20	3.19	0.54	3.19
Decapoda spp.	22	185.45	22	4.25	3.74	2.93	23.40	3.95	3.06
Stomatopoda									
Erugosquilla massavensis	7	62.82	7	1.35	1.27	0.93	2.44	0.41	3.62
Crustacea spp.	43	224.98	17	8.30	4.54	2.26	29.07	4.91	3.10
Teleostei									
Clupeiformes									
Etrumeus golanii	3	39.05	2	0.58	0.79	0.27	0.36	0.06	3.45
Sardinella aurita	7	85.52	6	1.35	1.73	0.80	2.46	0.42	3.40
Clupeidae spp.	12	125.31	9	2.32	2.53	1.20	5.81	0.98	3.43
Engraulis encrasicolus	1	8.12	1	0.19	0.16	0.13	0.05	0.01	3.12
Gobiiformes									
Oxyurichthys papuensis	5	91.54	5	0.97	1.85	0.67	1.87	0.32	3.50

Group/species	N	W	F	%N	%W	%FO	IRI	%IRI	trop
Holocentriformes									
Sargocentron rubrum	4	79.48	3	0.77	1.60	0.40	0.95	0.16	3.58
Mulliformes									
Mullus barbatus barbatus	6	119.42	4	1.16	2.41	0.53	1.90	0.32	3.14
Mullus surmuletus	5	91.61	3	0.97	1.85	0.40	1.12	0.19	3.45
Mullus spp.	4	78.81	3	0.77	1.59	0.40	0.94	0.16	3.30
Perciformes									
Chelidonichthys lucerna	2	5.11	1	0.39	0.10	0.13	0.07	0.01	3.98
Lepidotrigla cavillone	1	11.95	1	0.19	0.24	0.13	0.06	0.01	3.33
Serranidae spp.	1	12.69	1	0.19	0.26	0.13	0.06	0.01	3.82
Diplodus annularis	1	4.02	1	0.19	0.08	0.13	0.04	0.01	3.06
Pagellus erythrinus	1	11.12	1	0.19	0.22	0.13	0.06	0.01	3.48
Sparidae spp.	3	34.64	3	0.58	0.70	0.40	0.51	0.09	3.27
Spicara maena	1	6.42	1	0.19	0.13	0.13	0.04	0.01	3.21
Nemipterus randalli	13	183.16	11	2.51	3.70	1.46	9.09	1.53	3.82
Pomadasys stridens	5	52.26	5	0.97	1.05	0.67	1.34	0.23	4.02
Pleuronectiformes									
Bothus podas	3	18.75	3	0.58	0.38	0.40	0.38	0.06	3.37
Soleidae spp.	4	77.16	3	0.77	1.56	0.40	0.93	0.16	3.25
Scombriformes									
Scomber colias	2	91.77	2	0.39	1.85	0.27	0.60	0.10	3.91
Tetraodontiformes									
Lagocephalus guentheri	4	58.17	3	0.77	1.17	0.40	0.78	0.13	3.60
Lagocephalus sceleratus	2	7.28	2	0.39	0.15	0.27	0.14	0.02	3.70
Lagocephalus suezensis	10	64.56	9	1.93	1.30	1.20	3.87	0.65	3.47
Torquigener flavimaculosus	4	11.77	4	0.77	0.24	0.53	0.54	0.09	3.33
Lagocephalu sspp.	9	146.53	5	1.74	2.96	0.67	3.13	0.53	3.59
Teleostei spp.	73	838.07	62	14.09	16.91	8.26	255.97	43.22	3.48

than bony fish (15%) in spring, but this pattern reversed in summer months when more bony fish (73%) than crustaceans (19%) were found. The %IRI difference between fish and crustaceans was reduced in autumn and almost stable in winter (Table 3). The bony fish with the highest IRI were represented by the Clupeidae, Mullidae, Nemipteridae and Tetraodontidae families. The two most common decapod families were Penaeidae and Portunidae.

The stomach fullness rate was highest in March, gradually decreased to its lowest rate in July, and then increased until September. This indicates that the fish entered an intense feeding period before the spawning period; the feeding intensity decreased with the development of the gonads and intensified again after the spawning period (Fig. 6).

Table 3 shows that there is a clearly distinguishable change in either seasonal prey preferences or availability. Crustaceans were the dominant prey group in spring (March-May), but bony fish were dominant in summer, with fish and crustaceans having similar contributions in winter. Molluscs played a much more minimal role in *L. sceleratus* diets than fish and crustaceans.

Regarding the target fish groups, interestingly, *L. sceleratus* was found to prey on both pelagic (Clupeidae) and benthic families (Mullidae; Table 2). Among the fish species which could be classified to species level (n=112), predation on other pufferfish occurred in 29 cases, or 26% of the identified consumed fish prey, while cannibalism of other *L. sceleratus* was only found in two cases.

L. sceleratus was found to prey on 39 different families/species, clearly showing that it is an opportunistic carnivorous predator with a very wide ecological niche. The trophic level of *L. sceleratus* was 4.41, demon-

Table 3. – Importance of prey groups by season. N, number of prey item; W, weight of prey item; F, number of stomachs with the prey item; %N, %W and %FO, percentage of N, W and FO; IRI, index of relative importance; pIRI, percentage index of relative importance.

Season	Prey groups	N	W	F	%N	%W	%F	IRI	%IRI
Spring	Bony fish	40	524.03	37	21.74	32.13	29.37	1581.73	15.36
	Crustacea	129	933.81	85	70.11	57.25	67.46	8591.40	83.43
	Mollusca	12	168.59	9	6.52	10.34	7.14	120.41	1.17
	Echinoderm	3	4.79	3	1.63	0.29	2.38	4.58	0.04
Summer	Bony fish	32	478.60	25	45.71	67.80	67.57	7669.69	73.32
	Crustacea	28	111.78	13	40.00	15.83	35.14	1961.75	18.75
	Mollusca	10	115.55	10	14.29	16.37	27.03	828.49	7.92
Autumn	Bony fish	48	761.11	39	39.67	58.72	62.90	6188.95	59.28
	Crustacea	54	372.43	29	44.63	28.73	46.77	3431.39	32.87
	Mollusca	19	162.65	18	15.70	12.55	29.03	820.18	7.86
Winter	Bony fish	65	793.01	50	43.62	58.51	80.65	8236.80	53.87
	Crustacea	77	521.38	48	51.68	38.47	77.42	6979.19	45.64
	Mollusca	7	40.90	6	4.70	3.02	9.68	74.67	0.49

Table 4. – Number of broken lines and CPUE (kg pufferfish/100 hooks) results for the three longline types. ± values show standard deviation. Different superscript letters indicate significant difference at 0.05 confidence level.

Gear type	Number of broken lines	CPUE
Standard longline	7.40±3.98	$1.65{\pm}1.11^{a}$
Steel wire branchline	5.50±4.09	$1.85{\pm}0.78^{a}$
Steel wire branchline and steel swivel	3.90±3.35	$4.00{\pm}1.90^{b}$

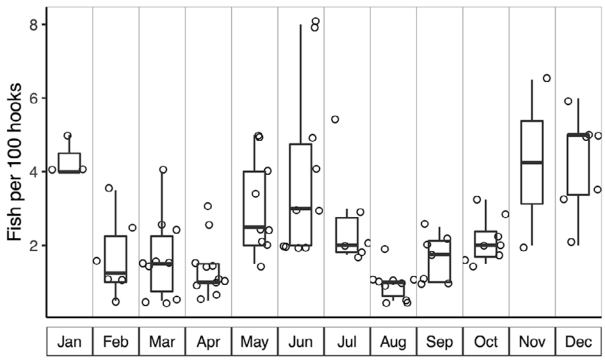

Fig. 7. – Monthly variability of CPUE values in longlines.

strating that it has assumed the role of a top predator carnivore in its invaded Mediterranean Sea region.

Catch per unit effort

Although there was no significant difference between the number of broken lines between the three types of longlines tested here, the highest CPUE values were attained using the second modification of the steel wire branch lines with the steel swivel hook system ($p<0.05$) (Table 4).

To examine spatial differences of CPUE from the 89 longline operations trialled at 11 fishing sites throughout one year, only the first fishing site had higher CPUE values (Aktaşlar with 3.6 pufferfish per 100 hooks) than the other sites, while the other ten sites had similar CPUE values (mean 2.12 pufferfish per 100 hooks; $p>0.05$). When the CPUE values were compared by month, catch rates were highest from November to January and May to July, and lowest from February to April and August to October (Fig. 7).

DISCUSSION

This study on the biology and catchability of *L. sceleratus* from Finike Bay in the north-western Levant Basin investigated some new topics for the first time. We discuss these new contributions and then briefly compare our results to other relevant studies on *L. sceleratus*, which contribute to a more thorough understanding of the biological and ecological characteristics of this highly invasive species and its impacts in the eastern Mediterranean.

When the results of the age analysis are interpreted along with the length at first maturity, we learn that *L. sceleratus* becomes sexually mature at about 42 cm and 3.5 years of age. The asymptotic length for both sexes of 114 cm and the asymptotic weight of 14 kg are quite close to maximum recorded sizes and to those modelled based on extreme value theory (Ulman et al. 2022, Ulman et al. 2021b).

The length-weight relationship for both sexes was $W = 0.0115L^{2.9875}$. The growth coefficient of K=0.11 year^{-1} shows that they can reach their asymptotic length at about ten years, which is averaged for faster growing juveniles and slower growing adults (Sibly et al. 2015). The allometry coefficient being very close to 3 shows that its growth is isometric, so its size and weight increase in equal proportions.

The findings of the catchability study may serve as a model for improved targeted control of this species. So far Cyprus (both states) has had a bounty for pufferfish since 2010, and Turkey since 2020, which shows that targeted control is indeed prioritized by governments in its regions of high abundance. This information may be useful to other Mediterranean regions if this species becomes more abundant in the central or western basins, warranting directed management. This is also the first time that longline modifications have been tested to explore ways to reduce the number of broken branch lines and increase CPUE values.

This study trialed three different types of longline fishing gear with the aim of minimizing broken longline branches and severed hooks, which are common occurrences with pufferfish, and of increasing its CPUE. We found that the addition of a steel swivel with a conventional longline resulted in significantly higher CPUEs. This is likely the result of the higher resistance of the thicker steel in the swivel to the sharp teeth of pufferfish. After a fish is caught, it normally swims around the fishing gear trying to break loose, causing higher torque of the fishing line which can result in breakage. With the addition of the swivel shackle, the fluttering movements resulted in reduced torque of the line and hence a lower number of broken lines and higher catches. Thus, the addition of a swivel shackle may reduce the economic losses incurred by fishers targeting pufferfish for the bounty programme launched by the Turkish Government and also those targeting other species with strong teeth and jaws. Due to the low monetary compensation of the Turkish bounty programme, which was 5 TL (=.26 USD) in 2020 and increased to 12.5 TL (=.65 USD) in 2022, it has not yet proven effective at controlling this invasive species as fishers have not been specifically targeting this species for this price. However, to verify whether the use of the swivel hook is beneficial, an economic analysis should be performed to assess the average time spent re-attaching longline hooks, along with the CPUE of both pufferfish and other target and discard species using this method compared with the traditional longline gear.

Another novel finding from this study is that the CPUE and feeding index showed similar seasonal variations. CPUE values were highest in early winter from November to January and late spring/early summer from May to July. A slightly earlier peak was found in the feeding index by month; feeding intensity was highest in March and April (>95%, and 75%, respectively) before the spawning season, with a small secondary peak in November (>50%). A proximate study on *L. sceleratus* also showed stomachs to have fed less during the spawning season (Ulman et al. 2021b). A similar study on feeding intensity of the smaller orange-spotted pufferfish *T. hypselogeneion* showed spatial variations in its feeding intensities, with one stock feeding much less during their spawning season and another stock feeding less intensely at the end of their spawning season (Ulman et al. 2023). These two pufferfish species follow similar patterns, and it has been suggested that the stomach cavity area is reduced to make room for gonad enlargement during the peak spawning season along with their lower feeding intensities, a trend that has been documented in many other fish species (Dulčić et al. 2014, Jardas et al. 2004, Ulman et al. 2023).

The economic losses caused by *L. sceleratus* are mainly related to its feeding activities, as it damages fishing gear by cutting longline hooks, biting fishing nets or consuming catch (Ünal et al. 2015). Therefore, understanding its foraging behaviour has important implications for reducing its economic impacts.

L. sceleratus stores lipids in its liver which are then used in gonadal development, as the HSI peaked in March, then gradually decreased during the entire spawning season and increased again in November. The HSI and GSI trends show a strong inverse relationship supporting this explanation, suggesting that *L. sceleratus* is a capital breeder. The condition factor results are highly interesting, as immature fishes also had a decrease in HSI values in summer months along with matured individuals, and had a very strong peak in November, which must be due to food availability as spawning is ruled out here.

The length-frequency and growth analyses fed the calculations for the total mortality rate, natural mortality and fishing exploitation rate for *L. sceleratus*. Natural mortality can only be calculated for unfished species, which are increasingly difficult to find. Here the natural mortality was M=0.34 year^{-1}, the fishing mortality was F= 0.60 year^{-1}, and thus the total mortality (F+M) was at Z=0.94 year^{-1}. Natural mortality of about 29% is interesting, because this species has few natural predators owing to its high toxicity and ability to puff (Ulman et al. 2022, Gücü et al. 2021, Ulman et al. 2021a). Juveniles, however, were found to have more predators, such as garfish and groupers (Ulman et al. 2021a), but cannibalism likely plays a huge role in natural predation and seemingly developed more recently in the invasion due to density dependence of this species. These rates relate highly to those calculated from the Egyptian Mediterranean (Farrag et al. 2015), which found M=0.35 year^{-1}, F=0.66 year^{-1} and Z=1.01 year^{-1}. Since pufferfish were prohibited from being fished in Turkey during this study period (2017-2018), the fishing mortality rate of 45% of the stock being removed through fishing can be explained through their by-catch. However, not all fishers who incidentally catch this fish kill it, so potentially even a higher number are caught as by-catch. Since the exploitation rate is above 0.5, targeted fishing pressure on this species seems to be beneficial for its abundance control, but more targeted control is needed to help decrease its negative effects on biodiversity, fishers and the economy. What is clear from the high incidence of fishing gear pieces found in their stomachs (10% of samples) is that *L. sceleratus* is indeed targeting fish caught in nets and longlines, thus increasing its chances of being caught along with its exploitation rate. Those caught by handlines and set nets were mostly juveniles, whereas those caught by longlines were mostly adult fish.

The increase in pufferfish preying on fish in the summer could be attributable to pufferfish targeting fishing set nets and longlines more in these months, as more part-time fishers work in the months with more amenable weather. Over 10% of pufferfish had ingested a piece of fishing gear, either nets or hooks, but we did not investigate these trends seasonally.

Being a medium-lived fish species, *L. sceleratus* has a rapid growth performance in the first years of its life. This highly invasive species has demonstrated basin-wide success and without a doubt can be considered a top predator in the region, especially with its new trophic level estimation of 4.41, which is higher than that of a previous study that estimated a trophic level of 4.1 (Ulman et al. 2021b), owing to a larger sample size in this study. It is highly unique in its TTX content, its puffing ability and its very strong jaw, which combined make it an excellent predator with very low predatory pressure of its own (Ulman et al. 2021a). It is certainly an opportunistic predator that targets both pelagic and demersal fish, as well as an assortment of crustaceans. It has even recently turned to cannibalism to fill nutritive demands, as has been well documented by fishers using *L. sceleratus* as bait to catch them. It is suggested by fishers that it is also increasingly preying on fish already caught by fishers, which reduces the energy needed but also increases its chances of getting caught. To help improve targeted catching of pufferfish, which is highly recommended to help reduce their negative impacts to human health, the economy, fishers' livelihoods and marine biodiversity, the addition of a steel swivel next to the hook in longlines proved very successful in improving their catch rates.

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