Journal of
Marine Science and Engineering

MDPI

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The Dynamics of Maximum Lengths for the Invasive Silver-Cheeked Toadfish (*Lagocephalus sceleratus*) in the Eastern Mediterranean Sea

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Abstract: The Eastern Mediterranean Sea is the most invaded sea on the planet, with 666 non-indigenous species now recorded in the region. However, not all of these become successful in their new environments. Success here is defined by wide geographical spread, increased abundances, and larger maximum sizes than their native range. The silver-cheeked toadfish *Lagocephalus sceleratus* (Gmelin 1789) was first recorded in the Mediterranean Sea in 2003. It has now spread to all corners of the basin and is increasingly abundant in the Eastern Mediterranean Sea where it reaches monstrous sizes compared to the maximum sizes reported from its native range. This contribution presents three well-documented new weight records from the Dodecanese Islands, Greece: one specimen weighing 8.5 kg from 2012, and two specimens weighing 8 and 9 kg, respectively, from 2021. The latter is also confirmed with other well-documented larger-size records, along with a physiological hypothesis suggesting how such large sizes are reached.

Keywords: length records; top predator; Tetraodontidae; extreme value theory; oxygen supply

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Citation: Ulman, A.; Kalogirou, S.; Pauly, D. The Dynamics of Maximum Lengths for the Invasive Silver-Cheeked Toadfish (*Lagocephalus sceleratus*) in the Eastern Mediterranean Sea. *J. Mar. Sci. Eng.* **2022**, *10*, 387. https://doi.org/10.3390/jmse10030387

Academic Editor: Jean-Claude Dauvin

Received: 1 February 2022
Accepted: 2 March 2022
Published: 8 March 2022

1. Introduction

The Eastern Mediterranean Sea is currently undergoing 'tropicalization', i.e., the transition to a tropical sea with similar biotic and abiotic characteristics to the Red Sea [1]. This phenomenon has been mainly attributed to increased sea surface temperatures (SSTs), as an effect of climate change and the increased establishment of Lessepsian, or non-indigenous species (NIS), of tropical origin. Most NIS in the Eastern Mediterranean arrived as a result of the man-made construction of the Suez Canal, clearing a natural barrier in 1869 [2]. Warming of the Mediterranean Sea from 1985 to 2006 led to an overall SST increase of approximately 1 °C for the eastern basin [3], which likely facilitated tropical invasions. The number of detected NIS correlates with proximity to the Suez Canal [4], from which NIS spread, possibly aided by the north-east direction of surface currents [5] and increased SST [3]. The rate of introductions during the period 2017–2019 was estimated to be eight species per year for the whole Mediterranean, and four species per year which entered through the Suez Canal [3]. Until 2019, 666 NIS (excluding Foraminifera) became established in the Mediterranean basin [3], with the Eastern Mediterranean being more highly affected due to the Suez Canal, which is the principal pathway for Lessepsian invasions from the Red Sea and Indo-Pacific region. A study on Lessepsian fish trends from southern Turkey during the period from 2004 to 2015 demonstrated that NIS comprised 27% of the species richness, 62% of the total biomass, and 85% of the total abundance. It also indicated that these three indicators were annually increasing by 1.9%, 2.8%, and 1.4%, respectively [6].

For an NIS to be classified as invasive, it has to negatively affect biodiversity, the economy, or human health [7]. Invasiveness is recognized to be the propensity of an NIS to invade a recipient ecosystem, with its expected determinants including introduction history, species traits, and ecological and evolutionary processes [8].

The silver-cheeked toadfish *Lagocephalus sceleratus* (Gmelin 1789) was first recorded from Gökova Bay in south-western Turkey in 2003 [9–11] and has since expanded its geographical distribution to the entire Mediterranean Sea [12]. *Lagocephalus sceleratus* is probably the most invasive species encountered in the Mediterranean Sea, as it meets all three criteria proposed by Bax et al. [7,11], in addition to affecting human livelihoods. Specifically, *L. sceleratus* causes substantial economic losses, particularly to the small-scale fishing sector, due to fish depredation (i.e., consumption of entangled fish in nets), as well as extensive damage to fishing nets (i.e., biting and cutting off parts) and longlines (i.e., cutting off 20–80% hooks in longline fisheries). These impacts lead to increased labor and equipment costs for the fisheries sector, in addition to catch losses [13,14].

As for its effects on biodiversity, *L. sceleratus* is classified as a generalist predator on a combination of crustaceans, fish, and cephalopods. One earlier study from 2008–2009 on its Mediterranean diet found molluscs (gastropods and cephalopods) and crustaceans to be their main prey, with fish having only a small contribution of about 5% [15]. Meanwhile, a study one decade later (2019–2020) found 26% of stomachs to contain crustaceans, 24% to contain fish, and 11% cephalopods [11]. The increasing abundance of *L. sceleratus* has been linked to a marked reduction in cephalopod abundance around the Dodecanese Islands, which the latter study supports, as cephalopod abundances had most likely already declined, (reflective in their smaller contributions) in localities with high *L. sceleratus* abundances [15]. *Lagocephalus sceleratus* has been shown to be capable of massively expanding in a wide range of coastal habitats outside the scope of its native ecological ranges [16,17]. It was recently assigned a trophic level of 4.15 [11], which is within the range assigned to top predators and *Lagocephalus sceleratus* can now be considered one of the major top predators in the Eastern Mediterranean Sea. Finally, because of its high contents of tetrodotoxin (TTX), a neurotoxin found in all its tissues [18–20], and despite frequent warnings by governments, ingestion of any part of *L. sceleratus* has been causing dozens of human deaths in countries bordering the Eastern Mediterranean Sea, notably in Turkey [11]. However, human fatalities have not yet been reported in Greece, and it is commonly sold in Egyptian fish markets [21].

Of 11 pufferfish species currently established in the Mediterranean Sea [11], *L. sceleratus* is by far the one whose body reaches the greatest lengths and weights. Having accurate maximum length and weight record data is very important in fisheries science, as these parameters are often used to calculate growth and other modelling parameters. They also provide unique information relating to the species' overall condition in the invaded territory which indicate overall health, success, and thus, its invasiveness. Maximum fish sizes convey certain ecological processes the species are capable of, and also reflect the quality of the habitat (for growth, feeding, and reproduction) in affecting the fish's condition. Previously reported maximal sizes from other parts of its range include weights up to 7 kg in the Indian Ocean coast of South Africa [22], and lengths up to 110 cm in Japanese waters [23].

Here, we report on lengths and weights recorded from the Eastern Mediterranean Sea that were well beyond the asymptotic length of 78.5 cm and the corresponding weight of 5.7 kg reported in Ulman et al. [11]. We also present a tentative prediction of maximum length based on extreme value theory [24], and a hypothesis for the physiological mechanism likely used by large individuals of *L. sceleratus* to reach even larger sizes under the conditions currently prevailing in the Eastern Mediterranean Sea. Lastly, we discuss the relevant factors which support its high invasiveness.

2. Materials and Methods

The materials examined here are the lengths and weights of three large specimens of *L. sceleratus*. Two of these three records were collected via direct communication with fishers and one from a citizen-science Facebook group on alien species in Greece [25]. All other records provided here were collected in 2019 during a fisheries survey in southern Turkey (AU; from Fethiye to Bodrum). The lengths were measured using a measuring tape and the weights were recorded using either analog or digital scales.

The three studied lengths were entered in a routine of FiSAT software by Gayanilo et al. [26] that implement 'extreme value plots' as originally described by Formacion et al. [27]. This routine, based on successive size records from a limited number of samples, provides an estimate of the maximum length (and its 95% confidence intervals) that may be expected given a very large sample size.

Additionally, based on the demonstration in Ulman et al. [11], the biology of *L. sceleratus* is compatible with the Gill-Oxygen Limitation Theory [GOLT; 27], we estimated the extent of routine metabolism reduction required by large individuals to reach even larger sizes. The logic applied here is based on the fact that as fish grow in weight and volume, i.e., in three dimensions, the surface area of the gills supplying them with oxygen grows with a lower dimension, as expressed by the equation:

$$dw/dt = Hw^d - kw \quad (1)$$

where dw/dt is the growth rate, Hw^d is the rate of protein synthesis (requiring oxygen diffused across the gills), with $d < 1$, and kw is the rate at which proteins are being spontaneously denatured (a process not requiring the consumption of oxygen) [27,28]. The parameter d is the exponent in a relationship linking gill surface area (S) and body weight (W) of the form $S = \alpha \cdot W^d$, where S determines the extent of the oxygen supply. The parameter d is always <1 in adult fish, and this also applies to *L. sceleratus*, where $d \approx 0.8$ [11]. Equation (1) implies that maximum weight (W_{max}) and the corresponding maximum length (L_{max}) are reached when $Hw^d - kw = 0$, which must occur at some point given that $d < 1$. Thus, any reduction of kw, as occurs at lower temperatures [29], will increase the maximum size an individual fish can reach. Similarly, any decrease in oxygen (or 'energy') expended during searching for prey will lead to an increased size (see, e.g., [30,31]).

The extent of the reduction in oxygen consumption (Q) relative to the oxygen consumption at a given maximum length (Qmax1, occurring at Wmax1) that is required for a heavy fish to be able to reach an even larger weight (Wmax2) via reduced oxygen requirements Qmax2, was estimated following Soriano et al. and Pauly [30,31]:

$$Q_{max2}/Q_{max1} = (W_{max1}/W_{max2})^{1-d} \quad (2)$$

d was estimated from the Supplementary Material of Ulman et al. [11].

3. Results

In 2012, an 83 cm long *L. sceleratus* specimen weighing 8.5 kg was caught off Rhodes Island in Greece (Figure 1A). Another very large specimen (slightly over 8 kg in weight) was caught by the fisher Christos Pastras in Lagana Bay (Zakynthos Island, Greece) during trolling at a depth of 35 m at 13:30 on October 3, 2021 (Figure 1B). The length was estimated to be ~120 cm, but a precise measurement was not performed. Rather, its length was assessed based on a comparison with his height of 178 cm (Figure 1C). Mr. Pastras reported his catch to the Greek NGO iSea Facebook group called "Is alien to you, share it" [25,32]. In the summer of 2021, a 9 kg specimen with a total length of ~80 cm was landed off Kos, Greece, caught between 10 and 40 m depth by a longline fisher, Petros Papasevastos, who reported it to the second author of this study (S.K.; Table 1).

Figure 1. Evidence for large specimens of *Lagocephalus sceleratus*. (**A**) 8.5 kg specimen caught off Rhodes, Greece in 2012; (**B**) 8 kg specimen caught on October 3rd 2021 in Zakynthos, Greece; (**C**) The same specimen, with fisher Christos Pastras (178 cm).

Table 1. Lengths and weights of large specimens of silver-cheeked toadfish, *Lagocephalus sceleratus* in the Eastern Mediterranean. TL = total length (cm); W = live weight (in kg).

TL	W	Location information	GPS Coordinates
78.5	6	Caught in Fethiye, Turkey (Ulman et al. 2021) [11]	36.64038 and 29.12758
~80	9	Caught off Kos, Greece, Summer 2021	36.89150 and 27.28772
83	8.5	Caught off Rhodes, Greece in 2012 (Figure 1A)	36.44597 and 28.21724
~120	8	Caught off Zakynthos, Greece, 3 October 2021 (Figure 1B,C)	37.79999 and 20.74999
-	10–12	Five records reported by various fishers from Turkey and Cyprus in 2019; not used here due to poor documentation	-

The first three maximum lengths provided in Table 1, inserted in the 'extreme value plot' of the FiSAT software [26], led to a 'best' predicted maximum length of 110 cm for *L. sceleratus* in the Eastern Mediterranean Sea, with a 95% confidence interval ranging from 87.3 to 132 cm total length (Figure 2).

Figure 3 shows the percentage (%) weight-specific (or relative) oxygen supply of *L. sceleratus* individuals from 1 g to 10 kg, assuming that their gill surface area (S) grows according to $S = a \times W^d$, with $d = 0.8$ [11,31,33]. This illustrates that to reach a maximum weight of 10 kg, an individual weighing 6 kg needs, according to Equation (2), to reduce its oxygen demand by only 10% (dotted horizontal line in Figure 3).

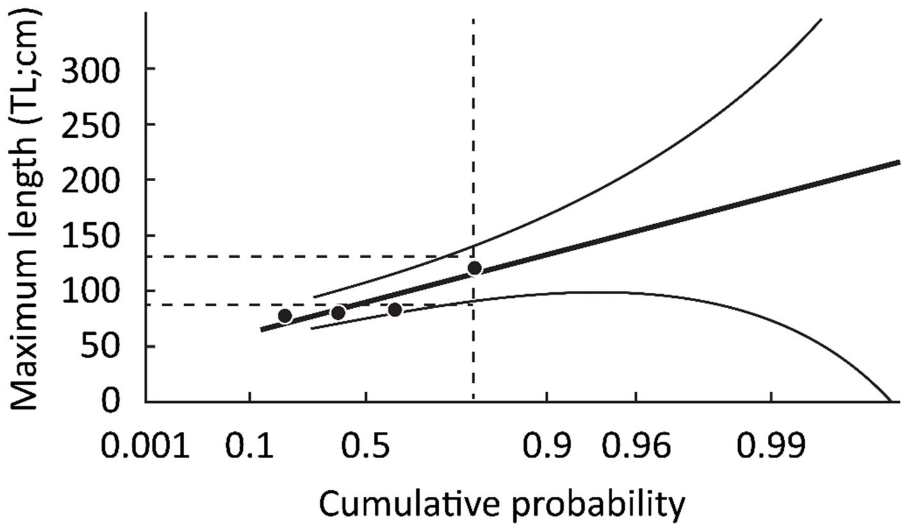

Figure 2. 'Extreme value plot' based on the first 4 maximum length estimates in Table 1, as outputted by FiSAT software [25]. The most probable potential maximum length was 110 cm, with a 95% confidence interval ranging from 87.3 to 132 cm total length.

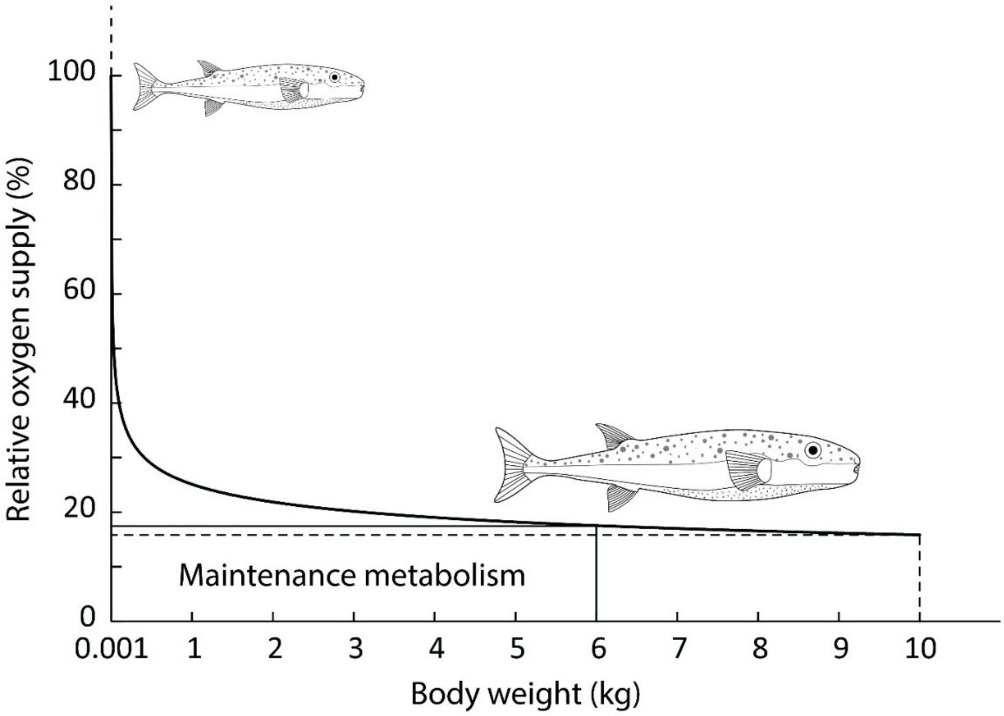

Figure 3. Weight-specific (or relative) oxygen supply of individual *Lagocephalus sceleratus* of 1 g to 10 kg body weight, in % of their relative oxygen supply at 1 g, given a gill surface area (S) growing according to $S = a \cdot W^{0.8}$. The horizontal dotted line shows that to reach 10 kg, an individual of 66 kg needs only a small reduction (10%) in its maintenance metabolism.

4. Discussion

This study reports three new weight records for *L. sceleratus* (8, 8.5, and 9 kg), considerably larger than previously reported (7 kg). The results from the extreme value plot (Figure 2) revealed 110 cm to be largest size that this species can reach, suggesting that our estimation of ~120 cm in length (Table 1) was probably an overestimation.

These size records demonstrate that *L. sceleratus* is thriving in the Mediterranean marine environment. These larger sizes probably do not affect potential predators, since only loggerhead turtles (*Caretta caretta*) have been found preying on adults. However, they could possibly extend their prey options, increasing the impact on native species and possibly further affecting the biodiversity of the marine environment.

The success of invasive species can be explained by two different types of factors: intrinsic factors that make some species inherently good invaders, such as their unique adaptations; and extrinsic differences in ecological or evolutionary processes that differ between native and introduced ranges [34]. *L. sceleratus* was found to have better fitness in its invaded Mediterranean range compared to its native Indo-Pacific range. This is more related to eco-evolutionary differences between the two ranges than intrinsic factors, the latter of which would result in the species having similar fitness levels in both environments. However, quantifying the contributing factors and features that lead to this higher fitness is difficult. Here, we present the supporting eco-evolutionary and intrinsic features that most likely contributed to its high invasiveness.

Eco-evolutionary factors:

- The Eastern Mediterranean Sea had an empty ecological niche as a result of a long distance to the more speciose and productive eastern Atlantic, which, prior to the opening of the Suez Canal, was the main source for biodiversity enrichment [2]. This was amplified by dams, resulting in a shortage of nutrient inputs in the Eastern Mediterranean, thus reducing its productivity [35];
- *Lagocephalus sceleratus* has very few predators in the Eastern Mediterranean Sea. This is possibly amplified by its aposematism, which may deter some potential predators. Only loggerhead turtles have been found preying on adult *L. sceleratus* in the Mediterranean Sea, while groupers, dolphinfish (*Coryphaena hippurus*), garfish (*Belone belone*), and *L. sceleratus* (through cannibalism) have been found preying on juveniles [36];
- Cannibalism has only recently been detected. Earlier studies of *L. sceleratus*' Mediterranean diet composition have not indicated such behavior [11,14,37,38], suggesting that cannibalism possibly develops in response to an increased density of *L. sceleratus*;
- Ontogenetic diet shift, whereby *Lagocephalus sceleratus* has been shown to possess the ability to change habitats with increased size to fulfil the increased demands for food [15,16];
- The genome of *L. sceleratus* has a higher percentage of repeated content of transposable elements (16.5%) than other pufferfish species [39]. A high percentage rate of transposable elements in various species has been shown to correlate to rapid adaptations to new environments, suggesting they may aid with invasiveness [40];
- Tolerance to a wide range of temperatures, which is suggested by the fact that, despite being native to the warmer Indo-West Pacific region [22], *L. sceleratus* has been found in the Black Sea, which experiences near freezing temperatures during winter [12].

Intrinsic features:

- From the Tetraodontidae (four-toothed) family of pufferfish, as the name suggests, it has four very strong regenerative fused teeth that provide it access to very tough-shelled animals such as crabs, gastropods, and sea urchins [11,15];
- Its inflation ability can further deter predators. For example, a tiger shark died of asphyxiation from a blown-up pufferfish that blocked its gill slits in the Western Atlantic Ocean [11,37];
- They are inedible due to their high toxicity and consequent threat to human health. Therefore, *L. sceleratus* is not targeted by fisheries, aside from bounty initiatives from Cyprus during the last decade, and very recently from Turkey (commencing in 2021), which rewards fishers for caught specimens [11,37,41];

We suggest that changes in diet and temperature may be the reasons for some individual *L. sceleratus* growing to exceptionally large sizes. Figure 3 shows that once a relatively large size is attained, only a small reduction in oxygen demands by the fish's body is required for even larger sizes to be reached. In our case, a reduction of about 10% of metabolic rate is all that is required for *L. sceleratus* to be able to increase its maximum size from 6 to

10 kg. Such a reduction in oxygen demand can be easily achieved by the largest fish seeking deeper, cooler water [26,30], and/or relying on larger, energy-dense prey captured with less effort, as enabled by the large size of the predator. Although a generalist predator, many local fishers and scientists understand that *L. sceleratus* is increasingly targeting fishing nets and longlines where prey is denser. This adaptation, although an eco-evolutionary factor, is successful in this case due to their strong fused teeth—an intrinsic feature that allows them to easily escape by chewing their way out of the net. Earlier stomach content analyses of *L. sceleratus* in south-eastern Greece revealed 55 hooks in 33 stomachs, but with a low proportion of fish to their total diet [15]. A more recent diet study found roughly 60 pieces of fishing gear (fishing hooks and pieces of nets) and a much higher proportion of fish, increasing from 5% to 24% in a decade. This suggests that *L. sceleratus* is gradually learning to target fish in longline and net fishers, as fish obviously appear less effort-demanding for them to feed upon, especially when already caught. If the cause for the high fitness is eco-evolutionary, as suggested here, fishery management could adopt measures to control them, for example by laying much tougher nets in high-abundance areas that the predators are unable to chew through.

Another invasive species of Indo-Pacific origins, *Pterois miles,* has also reached much larger sizes in the Mediterranean than in their native range: 43 cm TL (total length) in Turkey, A, Ulman unpublished data, compared to 35 cm SL (standard length) in its native range [42]. One factor suggested for the success of *P. miles* has been attributed to prey naivety [43], in which native species do not yet perceive it as a predator. As a result, it is able to easily select from a smorgasbord of unsuspecting native species. Having richer food is further exemplified by "exceptionally big individual perch (*Perca fluviatilis* L.)" in Windermere, U.K. [44], and by Nile perch (*Lates niloticus*) in Lake Chad. Like *P. fluviatilis* at 30 cm, these both switch at 40–50 cm from feeding on zooplankton (an energy-poor food that is costly to acquire) to preying on individual fish (energy-rich and easy for larger predators to hunt). Using Equation (2), this switch leads, in Nile perch, to a reduction in their oxygen requirement of 17%, and renewed growth [30,31], which is in the same order of magnitude as the 10% estimated here for *L. sceleratus* to grow from the asymptotic weight estimated by Ulman et al. [11] to the 'monster' sizes reported in Table 1.

5. Conclusions

This contribution has provided new maximum size records and an estimation of maximum lengths that *L. sceleratus* can reach. These new records can be used to better understand its growth potential in the Mediterranean Sea [22]. The previous reported maximum length of 110 cm reported from Japan by Masuda et al. [23] is identical to estimated lengths reached in this study. This contribution also suggests that the damages this fish is capable of causing to the Mediterranean's biodiversity and fisheries are probably still underestimated. Their high fitness and invasiveness could be the product of their Mediterranean adaptation to feed on captured fish from nets. High abundances that lead to damages of fishing nets have not been revealed yet from their native range, although it may also occur there.

Author Contributions: Conceptualization, A.U.; Methodology, All authors; Software, D.P.; Validation, All authors; Formal Analysis, D.P.; Resources, NA (Not applicable); Data Curation, A.U. and S.K.; Writing—Original Draft Preparation, All authors; Writing—Review and Editing, All authors; Visualization, D.P. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable for this study.

Informed Consent Statement: Informed consent was obtained from all subjects involved in the study.

Data Availability Statement: Not applicable.

Acknowledgments: We thank Elaine Chu for Figures 2 and 3, and the fishers for providing the records. We also thank our friends at iSea Environmental Organisation for the Preservation of the Aquatic Ecosystems from Thessaloniki, Greece, for creating their Facebook group titled 'Σε ξενίζει Μοιράσου το μαζί μας-Is it Alien to you? Share it!!!', and for providing the first size record that inspired this study.

Conflicts of Interest: The authors declare no conflict of interest.

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