Biol Invasions (2023) 25:983–990
https://doi.org/10.1007/s10530-022-02972-7

INVASION NOTE

The invasive silver-cheeked toadfish (*Lagocephalus sceleratus*) predominantly impacts the behavior of other non-indigenous species in the Eastern Mediterranean

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Received: 7 June 2022 / Accepted: 15 November 2022 / Published online: 1 December 2022

Abstract Marine invasive species are pervasive across the world's coastal regions. Nevertheless, empirical quantification of their ecological effects remains limited. Here, we elucidate the interaction of the invasive silver-cheeked toadfish, *Lagocephalus sceleratus,* with the fish community of the Eastern Mediterranean Sea, a hotspot for marine biological invasions. We deployed 88 underwater stereo-video systems across the Israeli continental shelf and upper slope. From this data, we quantified the change in fish behavior in the absence and presence of *L. sceleratus*. We further supported our findings by analyzing *L. sceleratus* gut contents. Our results indicated that the presence of *L. sceleratus* significantly deterred other non-indigenous species (NIS) and we recorded multiple NIS escape behaviors (fleeing, covering beneath sand or algae, or using camouflage). However, indigenous species (IS), for the most part, remained indifferent to *L. sceleratus'* presence. Furthermore, analysis of gut contents supported the visual surveys and revealed that *L. sceleratus* primarily feed on NIS, including other non-indigenous pufferfish species. Our findings suggest that harmful invasive species may not necessarily be detrimental to IS. At the same time, the apparent threat by *L. sceleratus* may have ecological impacts on other NIS, especially invasive pufferfishes which are highly poisonous and are suspected to have few predators in the Mediterranean Sea.

Keywords Mediterranean Sea · Invasive species · Naïveté · Lessepsian species · Stereo-BRUVs · Fish

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10530-022-02972-7.

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Introduction

Invasive species impact virtually every part of the globe (Seebens et al. 2017). This is specifically noticeable in the oceans, and the majority of the world's coastal regions are impacted (Molnar et al. 2008). Despite the increasing prevalence of invasions, the actual ecological effects of most marine non-indigenous species (NIS) are often unknown (Anton et al. 2019; Gurevitch and Padilla 2004; Katsanevakis et al. 2014; Watkins et al. 2021), as only a few marine NIS have been studied in-depth and determined to be harmful (e.g., lionfish and rabbitfish; Green et al. 2012; Vergés et al. 2014). Thus, the impact of marine NIS on the abundance and behavior of indigenous species (IS) and other NIS remains relatively understudied.

Behavioral responses are often found to be more sensitive indicators of a threat than actual changes in abundance (Goetze et al. 2017). If a NIS is perceived as a threat, we may expect impacted species to respond behaviorally to that species (Brown et al. 2018). Thus, recording the change in behavior in response to a specific NIS may help determine whether that species impacts other NIS or IS. However, some IS may not respond to the presence of a potentially detrimental NIS due to a lack of previous acquaintance, and this naivety may increase IS vulnerability to predation or competition (Champneys et al. 2022; D'Agostino et al. 2020; Paolucci et al. 2013).

The Eastern Mediterranean Sea is a hotspot for marine biological invasions (Edelist et al. 2013; Galil 2008), containing a growing number of NIS, mostly arriving via the Suez Canal. To date, there are ~115 Indo-pacific fish species in the Eastern Mediterranean (Kovacic et al. 2021), and in some habitats, NIS are at least as abundant as IS (Edelist et al. 2011; Mavruk et al. 2017). This situation is suggested to facilitate the establishment of further invasions (i.e. invasional meltdown; Givan et al. 2017).

One of the most notorious recent invasive species in the Mediterranean Sea is the silver-cheeked toadfish, *Lagocephalus sceleratus* (Gmelin 1789). First recorded in Turkey in 2003, this pufferfish rapidly spread in the Eastern and Western basins of the Mediterranean Sea, including some parts of the Black Sea (Akyol et al. 2005; Coro et al. 2018; Ulman et al. 2021a). The species *L. sceleratus* is a large (~100 cm total length; Ulman et al. 2022) predator with a known economic impact (e.g. damaging fishing gear) and can be lethally toxic if consumed (Ulman et al. 2021b). In this study, we use underwater observations to assess the behavioral effect of *L. sceleratus* on both IS and NIS. Further, we correlate our findings with gut content analyses. We find that the presence of *L. sceleratus* dramatically alters fish behavior, but, surprisingly, the impact was much stronger on other NIS while IS were relatively oblivious to *L. sceleratus* presence. These findings underscore the importance of quantifying in situ impacts of NIS on fish communities, and suggest that in some cases, NIS may have strong impacts on other NIS.

Methods

Video surveys

To assess the effect of *L. sceleratus* on species behavior we used baited remote underwater stereo-video systems (stereo-BRUVs; Langlois et al. 2020). The usage of stereo-BRUVs allows the estimation of species relative abundance, richness, length measurements, and behavior while surveying fishes from diverse trophic levels with a reduced observer bias (Harvey and Shortis 1995). We deployed 88 stereo-BRUVs in the northern Israeli continental shelf and upper slope spanning depths of 8–151 m. Each deployment consisted of a 60-min videos (equivalent to a total of 5,280 filmed minutes). The stereo-BRUVs were deployed within a variety of habitats (e.g. sand, gravel, silt, macroalgae, and rocky reef) and seasons to account for variation in environmental conditions (Supplemental Fig. 1). Samples were collected during daylight hours (i.e. between an hour after sunrise and an hour before sunset) to avoid possible crepuscular variation in fish assemblages. Stereo-BRUVs samples spanned the years 2019–2022 and follow the settings detailed in Supplemental Table 1.

Species- and community-level effect size

To estimate the effect of *L. sceleratus* presence on species-level behavior, we classified each deployment into two distinct periods: (1) *Absence* of *L. sceleratus* in the video frame; (2) *presence* of *L. sceleratus* in the video frame. As juvenile *L. sceleratus* are not expected to prey on other fishes, we only included samples in which non-juvenile *L. sceleratus* were present (fork length $\geq$ 25 cm). In each period, we estimated each species' relative abundance using the video frame with the maximum number of individuals (i.e. MaxN; Langlois et al. 2020). Then, we calculated an effect size to estimate the change in species abundance by subtracting each species' abundance in the *absence* period from its abundance in the *presence* period. Thus, negative values denote a decrease in relative abundance during *L. sceleratus* presence, and positive values denote an increase in relative abundance during *L. sceleratus* presence. Species that tend to occur in larger numbers will have potentially larger effects. To deal with this we standardized the effect size by dividing each effect size estimate by

Table 1 Species-level prey items and their relative abundance across 125 dissected specimens

Species	Taxonomic group	Origin	n	Relative abundance
Charybdis longicollis	Decapoda	NIS	60	0.465
Torquigener flavimaculosus	Teleostei	NIS	22	0.171
Dorippe quadridens	Decapoda	NIS	10	0.078
Upeneus moluccensis	Teleostei	NIS	8	0.062
Charybdis feriatus	Decapoda	NIS	5	0.039
Erugosquilla massavensis	Stomatopoda	NIS	5	0.039
Portunus segnis	Decapoda	NIS	3	0.023
Myra subgranulata	Decapoda	NIS	2	0.016
Equulites klunzingeri	Teleostei	NIS	2	0.016
Plotosus lineatus	Teleostei	NIS	2	0.016
Mugil cephalus	Teleostei	Cosmopolitan	2	0.016
Arcania brevifrons	Decapoda	NIS	1	0.008
Charybdis hellerii	Decapoda	NIS	1	0.008
Saurida lessepsianus	Teleostei	NIS	1	0.008
Stephanolepis diaspros	Teleostei	NIS	1	0.008
Medorippe lanata	Decapoda	IS	1	0.008
Pagurus anachoretus	Decapoda	IS	1	0.008
Squilla mantis	Stomatopoda	IS	1	0.008
Pagellus acarne	Teleostei	IS	1	0.008

the maximum MaxN across both the *absence* and *presence* periods. Thus, the Standardized Effect Size (SES) ranges between -1 (i.e. a complete disappearance of a species with the occurrence of *L. sceleratus*) and + 1 (i.e. species that occur only with the presence of *L. sceleratus*). We did not find any pattern or directionality in the relationship between the SES and species occurrences or mean MaxN (Supplemental Fig. 2).

To test the effect of species origin (i.e. IS and NIS) on the SES (i.e. the response variable) across species, we used linear models (LM) with the number of occurrences as a weighting vector. Hence, species that were assessed only a few times (i.e. rare species) received a lower weight in the model compared to more common species. To ensure that our results were not biased by rare species, we also ran our model only for species that occurred at least three times in our samples. This analysis also eliminated species for which video identification is challenging (e.g. *Decapterus russelli,* Gobiidae spp.).

To examine the community-level impact of *L. sceleratus* we calculated an effect size for each stereo-BRUVs deployment for the entire NIS and IS communities. Here, we summed the total MaxN per period across all species and calculated the SES in the same manner explained above. We applied generalized linear mixed effect models (GLMM) with the community-level SES as a response using the "glmmTMB" R package (Bolker et al. 2017). Origin was used as a two-level fixed predictor (NIS/IS), and stereo-BRUVs IDs were used as a random intercept. The family was set to Gaussian. To estimate the effect of *L. sceleratus* across depths, we ran separate models (SES ~ depth) for IS and NIS with the same above-mentioned settings. Models were tested for the validity of underlying assumptions (e.g. homoscedasticity, normality of residuals).

Gut contents

To strengthen the ecological and behavioral information from the stereo-BRUVs, we also examined the gut contents of 125 *L. sceleratus* specimens. Fish were collected from fisher catch (e.g. anglers, bottom trawls) across the Israeli coast between May 2018 and July 2020. To minimize the representation of food items from the actual fishing activities (e.g. anglers' bait, fishes that were caught within the trawlers haul) we examined the food items from each specimen's stomach and intestine only (i.e. avoiding the pharynx that may represent newly consumed prey). Food items were identified to the lowest possible taxonomic level and counted. Multiple small body parts may bias the true number of ingested prey items. For these cases, only body parts that had clear evidence regarding the number of prey items were taken into account (e.g. chelipeds, eyes). We note that this method is conservative and may underestimate the true number of ingested prey items.

Results

Species-level effects

Out of 88 stereo-BRUVs deployments, 43 recorded adult *L. sceleratus*, and their abundance did not change between the sampled months (Supplemental Fig. 3). Our surveys documented 55 species that co-occurred with *L. sceleratus* of which 39 were IS and 16 were NIS (Fig. 1A). Calculating the species-level SES, we found a significant origin-dependent change in abundance with the presence of *L. sceleratus* ($t=4.06$, $P<0.001$, $R^2=0.24$; Fig. 1B). This result suggests that with the appearance of *L. sceleratus*, NIS decreases, on average, in relative abundance while IS do not change. Here, 13 out of 16 (81%) NIS had a negative SES, including some other abundant invaders (e.g. *Siganus luridus, Siganus rivulatus, Lagocephalus suezensis, Lagocephalus guentheri,* and *Torquigener flavimaculosus*; Fig. 1A). Conversely, only 16 out of 39 (41%) of the IS displayed a negative response to the appearance of *L. sceleratus*. We found the same effect when we ran our model with an occurrence cutoff of ≥ 3 ($t=3.41$, $P<0.01$, $R^2=0.35$).

In addition to the quantitative evidence for the effect of *L. sceleratus* on species relative abundance, we also note that several NIS commonly displayed an escape behavior a few seconds before the arrival of *L. sceleratus*. These records were numerous and include *T. flavimaculosus* (e.g. Video 1), *Nemipterus randalli* (e.g. Video 2), *L. suezensis* (e.g. Video 3), and juvenile *L. sceleratus* (e.g. Video 4). We also found that *T. flavimaculosus* commonly attempt to bury itself in the sand a few seconds before *L. sceleratus* arrives (Video 5), or camouflage to blend in with nearby gravel (Video 6), a behavior that was previously suggested as a predator avoidance strategy (Bilecenoğlu 2005). These flight behaviors suggest that the occurrence of *L. sceleratus* intimidates other NIS.

Community-level effects

At the community level, we found that when *L. sceleratus* occurred, the invasive community decreased in relative abundance in comparison to the native community (GLMM: $z=2.87$, $P<0.01$, $R^2_m=0.07$, $R^2_c=0.45$). In our study site, *L. sceleratus* displayed a bimodal depth niche and occurred in depths of 8–114 m with an optimum of 29 m and a central depth niche range of 18–69 m deep (Fig. 1D, Supplemental Table 2, see supplemental methods for more details). We found that the SES of both the NIS and IS communities did not change with depth (slope coefficient for depth for the NIS based on the GLMM: 0, $P=0.28$, $R^2_m=0.03$, $R^2_c=0.82$; for the indigenous community slope: 0, $P=0.46$, $R^2_m=0.02$, $R^2_c=0.61$).

Gut contents

Across all 125 *L. sceleratus* specimens, 38 (30%) had empty stomachs. For the remaining 87 specimens, we found 401 prey items, of which 272 (68%) could not be identified at the species level, 123 (31%) were NIS, only four (1%) were IS, and two (<1%) were of the cosmopolitan mullet *Mugil cephalus* (Fig. 2A, Table 1). The four most dominant species were NIS, including the lesser swimming crab (*Charybdis longicollis*, 49%), the yellow-spotted puffer (*T. flavimaculosus,* 18%), the porter crab (*Dorippe quadridens*, 8%), and the goldband goatfish (*Upeneus moluccensis*, 7%; Fig. 2B). Among these prey, *T. flavimaculosus* and *U. moluccensis* were also found in our video analysis and had a negative SES (Fig. 1A). We note that gut content analyses from other regions in the Mediterranean found a considerable occurrence of cephalopods (e.g. >40%, Kalogirou 2013), yet in this study, they occurred only within 2 stomachs (1.6%).

Discussion

Marine invasive species have the potential to inflict severe damage on the recipient community, yet empirical measurements of this impact are scarce, thus leaving their impact on biodiversity speculated

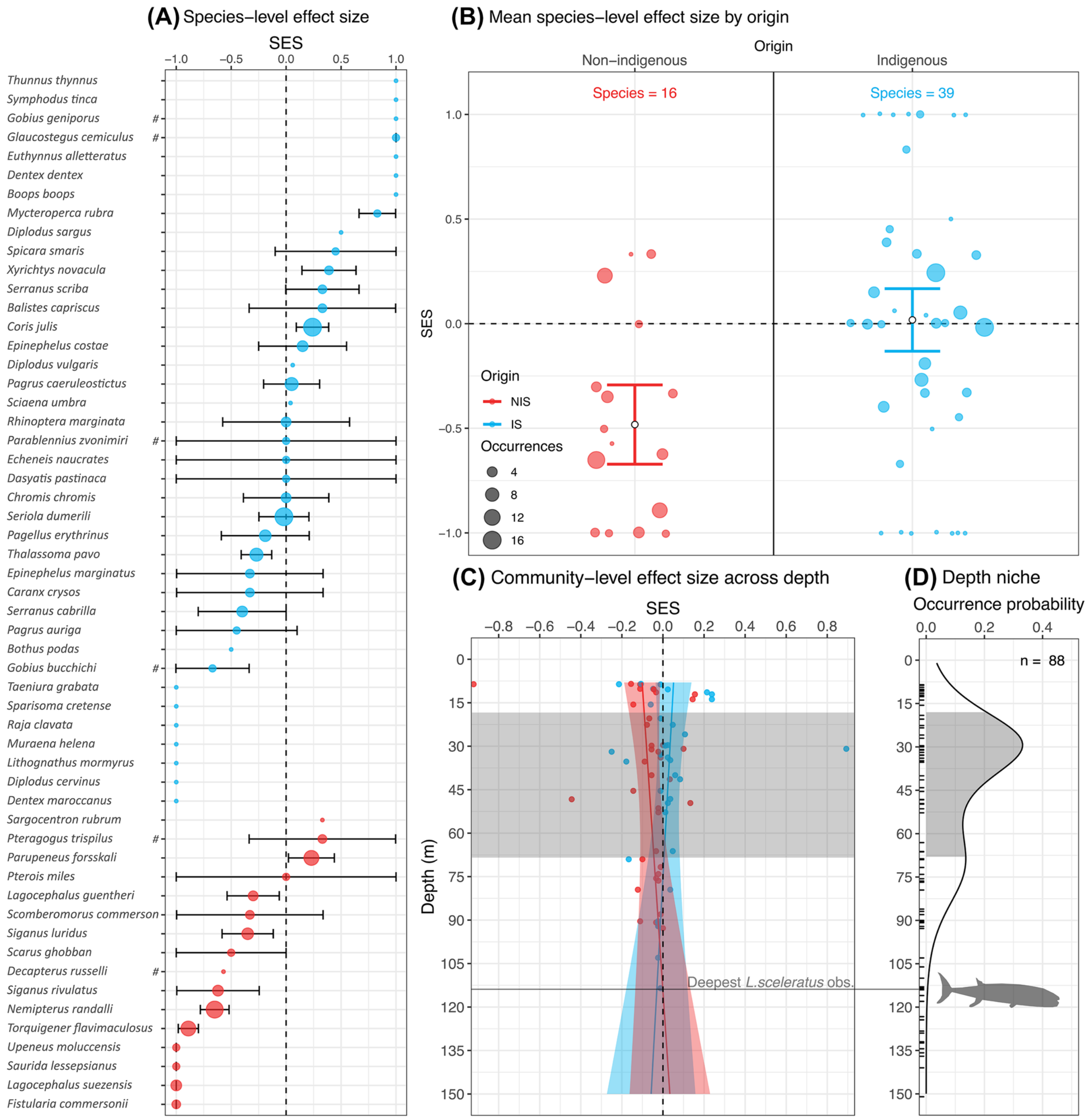

Fig. 1 The impact of *L. sceleratus* on Eastern Mediterranean fishes. **A** Species-level standardized effect sizes (SES). Positive SES denote abundance increase and negative values denote abundance decrease with the presence of *L. sceleratus*. Each dot represents a species and larger dots represent species with higher occurrences. Species are ordered by their origin (IS/ NIS; colors) and effect size. The dashed line represents zero SES, and the error bars are standard error of the mean. Hashtags represent species whose identification is challenging and excluded for sensitivity analysis. **B** SES across species origins (NIS/ IS, X-axis). White points are the average values. The dashed line represents zero SES, and the error bars are 95% CI of the mean. **C** The community-level SES across depth. Each point represents a stereo-BRUVs deployment for either NIS (red) or IS (blue). Solid lines represent the linear model prediction with polygons as 95% CI. The gray horizontal line denotes the deepest *L. sceleratus* observation of this study. **D** *L. sceleratus* depth-niche estimated from a HOF model. Here, the X-axis denotes the probability of *L. sceleratus* occurrence and black ticks represent stereo-BRUVs deployments. The shaded gray polygon denotes *L. sceleratus* central depth niche and is projected into panel C for comparison

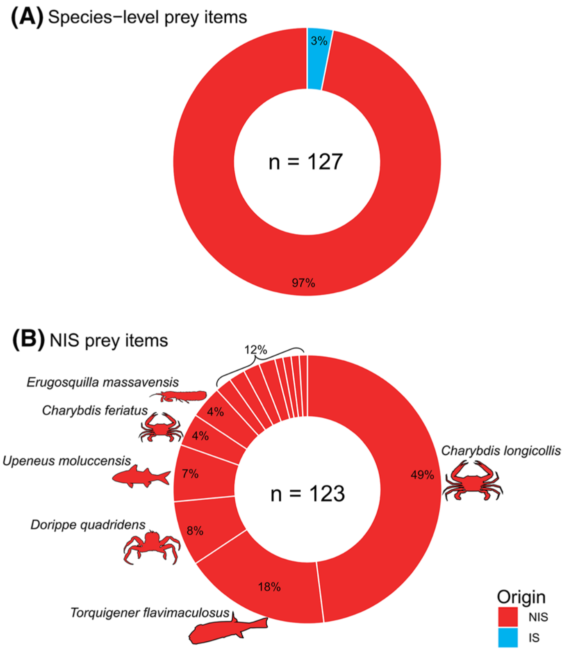

Fig. 2 Species-level prey items among 125 dissected *L. sceleratus* specimens. **A** total proportions of IS and NIS prey items. **B** NIS prey items. Each section in panel B denotes a unique prey item (i.e. species). Silhouettes denote the six most abundant prey species. For each pie, n is the number of prey items. For more information see Table 1

or unknown (Watkins et al. 2021). We focused on the invasive fish, *L. sceleratus*, in the Mediterranean Sea and quantified its in situ impact on IS and NIS fish behavior. We found that *L. sceleratus* presence induces behavioral avoidance in other NIS (Fig. 1B), which, in combination with gut content analysis, suggests that NIS are targets of predation by this species (Fig. 2B). However, on average, we found poor evidence that *L. sceleratus* impacts IS behavior. This could be either because IS are naive to predation (similarly to previous suggestions for invasive lionfish in the Eastern Mediterranean, D'Agostino et al. 2020) or because this species has little impact on IS, a hypothesis that is supported by their relative paucity in *L. sceleratus'* diet (Fig. 2A). Consequently, in the Eastern Mediterranean, *L. sceleratus* may have stronger impacts on other NIS than on IS.

In both the NIS and IS communities, different species presented negative and positive SES (Fig. 1A). In fact, for IS, we found variable responses even within species that are similar in size and habitat preference. For instance, negative SES was found for *Thalassoma pavo* and positive SES for *Coris julis* and *Xyrichtys novacula*. Yet, the majority of the NIS and their average responses were negative, while the average response of the IS were not significantly different from zero (Fig. 1B). This result suggests that for IS, *L. sceleratus* presence does not alter behavior, which can be explained by two different mechanisms. First, IS may simply be naive to *L. sceleratus* predation. However, analysis of gut contents revealed that *L. sceleratus* do not systematically prey upon IS (Table 1; we note that 68% of the prey items could not be identified so these percentages are somewhat uncertain). In support, Ulman et al. (2021b) dissected *L. sceleratus* specimens from Turkey and found that they prey upon a wide range of other NIS including fish, mollusks, and echinoderms. Thus, we postulate a second more plausible hypothesis for the indifferent behavior of IS which is that they are simply not the main targets of *L. sceleratus*.

On average, NIS had negative SES, indicating a perception of threat by *L. sceleratus* predation. Combining this result with the behavioral observations (e.g. escape, hiding within algae, entrenching in the sand, and camouflaging in the face of *L. sceleratus* arrival; Video 5, Video 6), it is evident that some NIS are undoubtedly intimidated by the presence of *L. sceleratus*. Interestingly, even species of the same family or genus as *L. sceleratus* were found to behaviourally avoid *L. sceleratus*. Indeed, *L. sceleratus* off the coasts of Turkey prey upon *T. flavimaculosus*, *L. suezensis*, and juvenile conspecifics (Ulman et al. 2021b). In support, we commonly recorded the above-mentioned species fleeing, including juvenile *L. sceleratus,* by exceptionally fast swimming a few seconds before the arrival of *L. sceleratus*. Several species in the family Tetraodontidae are highly poisonous, specifically those that have invaded the Mediterranean (e.g. *L. sceleratus*, *L. suezensis*, and *T. flavimaculosus*; Kosker et al. 2018, 2019) and it is suspected that these NIS have very few predators in the Mediterranean (Ulman et al. 2021a). Hence, the apparently strong threat by *L. sceleratus* on other Tetraodontidae may constitute one of the only potential top-down population regulation processes.

Other NIS that displayed negative SES in the study were also documented within *L. sceleratus* gut contents, including *U. moluccensis, T. flavimaculosus, and Saurida lessepsianus* from this study, and *T. flavimaculosus*, *L. suezensis, Siganus spp.,* and

Tetraodontidae spp. in other studies (Ulman et al. 2021b; Kalogirou 2013). This suggests widespread predation by *L. sceleratus* on other NIS. However, we further note that three NIS had a positive SES (Fig. 1A). Two of these, *Sargocentron rubrum* and *Pteragogus trispilus* are cryptic species that inhabit rocky crevices and macroalgae (respectively). Video recordings show that their SES did not decrease as they simply hid in the presence of *L. sceleratus*. Another species, *Parupeneus forsskali,* tended to increase in relative abundance with the presence of *L. sceleratus*, and we assume that this pattern is related to its opportunistic nature as a scavenger.

We recorded video observations of *L. sceleratus* and estimated its impact on fish behavior down to 114 m. Beneath these depths, *L. sceleratus* was completely absent. Based on stereo-BRUVs and logistic regression models (see supplemental methods), we were able to model the depth niche of *L. sceleratus*. Its central depth niche ranged from 18 to 69 m with an optimum at 29 m (Fig. 1D), suggesting that it is common in shallow to mid-mesophotic habitats above both rocky and sandy seabeds. We tested whether *L. sceleratus'* behavioral impact on the fish community was limited to its central depth niche. We found that there was no relationship between the SES and depth for either IS or NIS. Thus, NIS are still negatively behaviorally impacted at the deeper habitats of the continental shelf and upper slopes (Fig. 1C).

Our findings suggest that some harmful invasive species with strong ecological impacts on other NIS, such as *L. sceleratus,* may not necessarily be detrimental to IS. The Eastern Mediterranean Sea is commonly referred to as an extension of the Red Sea due to the increasing number of NIS (Galil 2008; Givan et al. 2017; Kovacic et al. 2021). Hence, the large number of NIS in the Eastern Mediterranean Sea may mean that NIS are likely to interact with other NIS. If this is true, then despite the strong ecological impacts, the effect of *L. sceleratus* on the sub-community of IS may actually be small (see Diga 2021 for non-indigenous bivalves). However, we note that the link between escape behavior and the larger population-level impact is not trivial. For example, it may be that species that can escape *L. sceleratus,* and hence demonstrate negative SES, may not be actually preyed upon. Therefore, additional information is needed to elucidate the population-level demographic impacts and the community-level diversity impacts of this species.

Acknowledgements We thank Shahar Malamud for his assistance at sea and logistic support throughout the field work. We thank James Seager for his technical support and rapid response with CAL, EventMeasure, and the design of camera frames. We thank Dr. Shevy Bat-Sheva Rothman for her dedicated help in identifying some of the species in the videos. We thank Prof. Bella S. Galil for her assistance in gut content identification. We thank Daphna Shapiro Goldberg for her comments on the manuscript.

Author Contributions SC collected the data, conceived the study, and planned it. SC and GDB analyzed the videos. SC conducted the statistical analysis. SC, GDB, and JB wrote the first draft. NY and NS conducted the gut contents analysis. JB supervised the findings of this work. All authors read, commented on, and approved the final manuscript.

Funding SC received partial funding from the Mediterranean Sea Research Center of Israel (SC). JB received funding from the Grant for Tel-Aviv University center for Artificial intelligence and Data science (TAD) in collaboration with Google.

Data availability The datasets in this current study have not been released as they are part of an ongoing field work. They may be requested from the corresponding author.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

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