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Trophic positioning among native and non-indigenous species in the eastern Mediterranean Sea

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Abstract

The substantial influx of non-indigenous species (NIS) into the eastern Mediterranean Sea from the Suez Canal has prompted questions about the mechanisms enabling their establishment and the resulting impacts on native species. We focus on the trophic level dynamics of the dominant native red mullet (*Mullus barbatus*) and the four NIS *Pomadasys stridens*, *Upeneus moluccensis*, *U. pori*, and *Parupeneus forsskali*. Using various methods, including trophic level estimations, intestine length analysis, and monthly trophic level variations, we assessed their trophic positions and flexibility. The results indicate that compared to *M. barbatus*, *P. stridens* occupies a lower trophic level due to its omnivorous nature, potentially facilitating its biomass increase. This lower trophic position is further supported by its lengthy intestine relative to size. Conversely, *U. moluccensis*, *U. pori*, and *P. forsskali* position themselves consistently at higher trophic levels than *M. barbatus*. Monthly trophic level variations suggest temporal dietary changes, which point to seasonal impacts on NIS success. *M. barbatus*'s resilience, including its preference for polychaetes, may explain its sustained dominance amid competition. This study sheds light on NIS-native species coexistence, further suggesting that NIS success could stem from exploitation of vacant niches and adaptation to new food sources.

Keywords: Trophic level; Red mullet; NIS; stomach content; relative intestine length.

Introduction

Non-indigenous species (NIS) are considered one of the major threats to marine biodiversity, and their presence can resonate beyond ecological disruption to cause profound socio-economic impacts (Edelist, 2013). These impacts jeopardize the livelihoods of coastal communities (Bacher *et al.,* 2023). In the complex and dynamic marine environment, this poses a daunting challenge, especially given the escalating threats that the world's oceans are currently facing. Therefore, understanding the mechanisms that facilitate the spread of NIS is crucial for developing effective strategies to control the process and mitigate its adverse consequences.

This understanding becomes particularly pertinent when examining regions like the Mediterranean Sea, which is acutely impacted by the influx of NIS. This is especially true in the eastern part of the sea, where the Suez Canal provides an inlet for these organisms. For over a century, this influx has been radically altering ecosystem dynamics, affecting not just ecological balances but also the socio-economic fabric of the region (Ben-Tuvia, 1985; Golani & Appelbaum-Golani, 2010). NIS may constitute over 85% of the biomass along the eastern Mediterranean coasts, prompting a dramatic shift in food web dynamics and increasing competition for native species (Gücü *et al.,* 2010; Mavruk *et al.,* 2017). The situation is further exacerbated by environmental stressors, such as overfishing and rising temperatures, which are leading to a significant shift in ichthyofaunal diversity on the upper continental shelf, favouring non-indigenous species over native ones (Goren *et al.,* 2016).

The substantial increase in biomass brought about by NIS inevitably exerts heightened pressure on native populations, predominantly via intensified competition for the same limited food resources within the Mediterranean ecosystem, which is often classified as oligotrophic (Gücü & Ok, 2018). Postulated cases of this pressure include the invasive lizardfish (*Saurida lessepsianus*), which might have played a role in the decline of native hake (*Merluccius merluccius*) populations (Ben-Yami & Glaser, 1974), and the possible pressure of *Nemipterus randalli* on the native common pandora (*Pagellus erythrinus*) in the eastern Mediterranean Sea (Yapici & Filiz, 2019). Another theory has been put forth that native species shift to greater depths as a result of NIS pressure (Chaikin & Belmaker, 2023).

Given these changes, the eastern Mediterranean marine environment has emerged as a prime natural laboratory for the study of NIS dynamics (Azzuro *et al.,* 2022). The interplay of invasive species with established native ones can be keenly observed in the region's soft-bottom demersal habitats. Here, the red mullet (*Mullus barbatus*), one of the historically dominant species (Vassilopoulou & Papaconstantinou, 1992; FAO, 2016, 2020), has shown remarkable resilience in the face of both environmental changes and intense fishing pressures. This resilience suggests an adaptation finely tuned to the eastern Mediterranean environment, yet the introduction of con-familial species such as *Upeneus moluccensis* and *U. pori* in the 1950s brought new dynamics to the ecosystem. These NIS thrived, and *U. moluccensis* became a commercially harvested fish (Gücü *et al.,* 1994). Nonetheless, the data indicate that their abundance has not eclipsed that of *M. barbatus* (TurkStat, 2023). Concurrently, *Parupeneus forsskali*, a species with similar nutritional requirements as *M. barbatus* (Vagenas *et al.,* 2023), has been observed within the same habitats but has failed to outcompete *M. barbatus*, showing a more selective habitat and depth preference. In contrast, *Pomadasys stridens*, a more recent arrival observed first in 2009 (Bilecenoğlu *et al.,* 2009), has shown an extraordinary increase in regional biomass, achieving up to 2000 kg/km^2 by 2020 (Eşkinat *et al.,* 2023). This figure is unprecedented for species living on the soft-bottom continental shelf. Interestingly, red mullet populations have remained robust with no significant signs of depletion despite the increasing competition for resources among the various species and the intensive fishing activities in their habitat (FAO, 2020).

These changes in the ecosystem of the eastern Mediterranean Sea have prompted two questions regarding the NIS. The first is how NIS are able to establish themselves amid the long-standing dominance of native species with well-adapted biological traits. The second is how NIS, especially *P. stridens,* obtain the energy to produce greater biomass than *M. barbatus* in oligotrophic seas like the Eastern Mediterranean.

For decades, scientists have grappled with similar questions of why certain species become successful invaders while others do not, and the consensus points to a multifaceted answer. The issue has also been examined from the perspective of resource exploitation, with studies indicating that trophic flexibility and opportunistic feeding behaviours are key factors in the establishment and success of NIS (Kostrzewa & Grabowski, 2003; Golani, 2010; Arndt *et al.,* 2018). This is further highlighted by the findings of Tüzün and Gücü (2023) on the stomach contents of *P. stridens*, which revealed that its ability to adapt to different food sources may be just as critical as other factors in explaining the species' dramatic increase in biomass in the Mediterranean.

One key factor influencing dietary preferences in fish is the ratio of intestine length (IL) to total body length (TL), often calculated as relative intestinal length (RIL). The allometric relationship between TL and IL provides insights into dietary preferences, with a negative value typically indicating a carnivorous diet and values greater than 1 suggesting an omnivorous one (Karachle & Stergiou, 2010a). Research suggests that longer intestines, typically with RILs between 2 and 21, are associated with herbivores, which have evolved to digest tougher materials such as cellulose or lignin (Kapoor *et al.,* 1975; Cleveland & Montgomery, 2003). In contrast, carnivores generally have shorter intestines (Kapoor *et al.,* 1975; Wootton, 1990; Kramer & Bryant, 1995a).

In an attempt to understand and assess the red mullet's susceptibility to NIS pressure, we compared its trophic position and flexibility with four NIS of similar trophic levels. We examined the diets and compared trophic positions of the selected species using four different approaches: trophic level estimations based on prey items in the stomach contents and the relationships between TL, total body weight (TW), and IL.

Materials and Methods

Five species were selected based on their habitat and dietary preferences (carnivorous, mainly preying on crustaceans, bottom and sub-bottom feeders, and mostly preferring sandy–muddy substrates). These species are *Pomadasys stridens, Mullus barbatus, Upeneus moluccensis, U. pori* and *Parupeneus forsskali.* Specimens of these species were collected between November 2021 and March 2023 off the coasts of Mersin, Turkey (northeast Levantine) (Fig. 1). The specimen samplings were carried out using trawl nets on board the R/V Lamas, at depths of 10 m to 200 m.

All fish were measured to determine total length (TL, cm) and total weight (TW, g) before dissection. For a proportion of each species, the guts were removed and uncoiled (without stretching), and measured for intestine length (IL, mm) from pylorus to anus. The stomachs were also removed and their contents were examined under a stereomicroscope. Plant fragments and unidentified organic material extracted from the stomach contents were also weighed and categorised separately as "plant material" and "organic material", respectively. The diets of the fish were assessed based on the index of relative importance (IRI), which accounts for the percentages of abundance (Ni%), weight (Wi%), and frequency of occurrence (Fi%) of the prey groups. IRI is calculated as Fi% × (Ni% + Wi%) (Pinkas *et al.,* 1971).

IL as a function of TL and TW is used to evaluate trophic positions; hence the relative intestinal length, RIL (calculated as IL/TL), and intestinal weight–length (IWL) {Zihler's index, ZI = intestine length (mm) / 10 [TW (g)$^{1/3}$]; Zihler, 1982} were used for intra- and interspecific comparisons. Differences in RILs, IWLs, and trophic levels among species were tested with one-way analysis of variance (ANOVA) for cases where parametric test conditions were applicable, while the Kruskal–Wallis test was used otherwise.

Trophic levels (Troph) were calculated using weight percentages (Wi%) of each prey item in the stomach content by using the *dietr* package (Borstein, 2020) of R Software v.4.3.0 (R Core Team, 2023). This package uses food item data to calculate trophic levels following procedures in TrophLab (Pauly *et al.,* 2000). We emphasized the significance of seasonal impact on trophic levels by following the approach established by Karachle and Stergiou (2008). This impact was attributed to variations

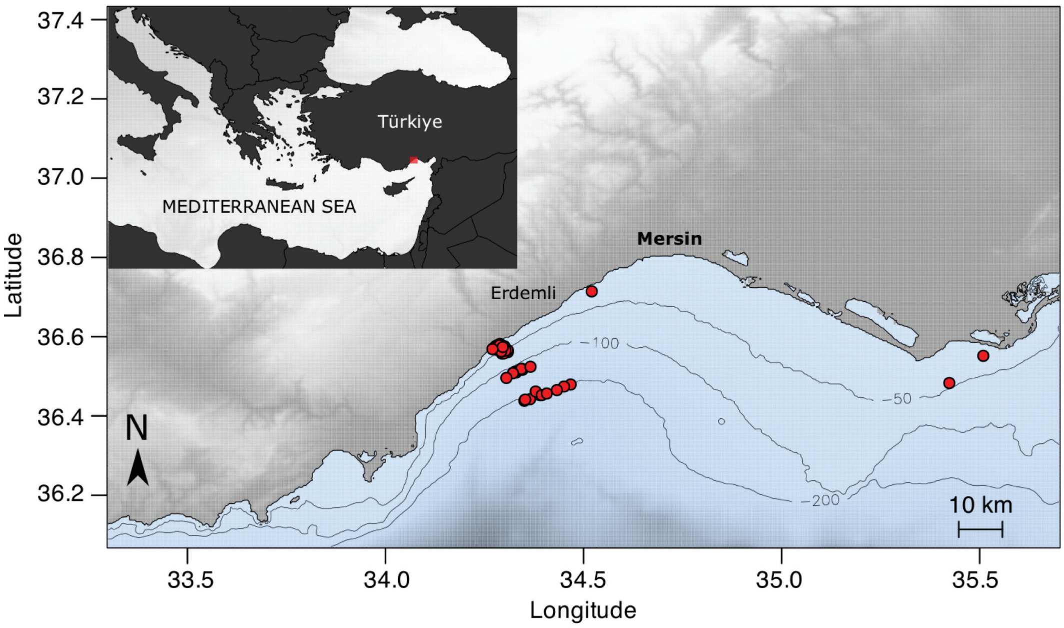

Fig. 1: Sampling area with trawl stations represented by red dots.

in food availability and the stages of the biological cycle, as previously demonstrated by Albert (1994). To assess the monthly variations in trophic levels, we employed the Kruskal–Wallis test, a non-parametric method suitable for our data analysis.

The linear relationship between TL and IL, and its implication on the feeding strategy, was investigated following the approach detailed by Kramer and Bryant (1995b). The approach was expanded by incorporating a 'random effect' term to assess species-specific variability. To achieve this, we conducted the analysis utilizing a random intercept–slope model from the *lme4* package of R Software v.4.3.0 (Bates *et al.,* 2015).

Results

In total, 2436 individuals of five species were obtained, measured, and examined for their diet (Table 1). Organisms that were found in the stomach content were classified into 19 taxa belonging to six phyla. Based on the IRI percentages of the prey groups found in the stomach contents (Fig. 2), *P. stridens* mainly consumed copepods (81%) and relatively small amounts of polychaetes (7%). Polychaetes (36%) played a major role in the diet of *M. barbatus*, followed by copepods (24%) and decapods (24%) (See Appendix for the Ni%, Wi%, Fi%, and IRI% values of the prey groups for all species). The *Upeneus* species had similar diets primarily comprising copepods and decapods, with variations in percentages among species; *U. moluccensis* showed a preference for copepods (70%), while *U. pori* consumed significant amounts of both decapods (41%) and copepods (54%). *P. forsskali* had the most diverse diet among the examined species, including copepods (33%), decapods (29%), amphipods (11%), cumaceans (10%), polychaetes (6%), and ostracods (5%) (Fig. 2).

A comparison between species revealed that *P. forsskali* and *U. pori* occupied the highest trophic level, followed by *U. moluccensis*, *M. barbatus*, and lastly, *P. stridens* (Fig. 3). The differences in trophic levels among the species was significant (Kruskal–Wallis, $p < 0.05$), except for between *P. forsskali* and *U. pori* ($p = 0.39$). When compared to the TL values given in FishBase, the mean trophic levels of all species except *M. barbatus* appear to be relatively low. However, it is worth noting that the confidence intervals

Table 1. Number (N), body length (TL) and body weight (TW) measurements of examined species (Min: Minimum, Max: Maximum, SD: Standard deviation).

		TL, cm		**TW, g**	
Species	**N**	**Min-Max**	**Mean ± SD**	**Min-Max**	**Mean ± SD**
P. stridens	785	5.3-17.6	13.3 ± 2.43	1.7-67.3	32.3 ± 15.25
M. barbatus	896	4.0-24.6	14.9 ± 4.14	0.4-165.1	45.3 ± 31.91
U. moluccensis	420	5.6-17.8	9.6 ± 2.71	1.3-62.5	10.4 ± 11.31
U. pori	231	6.6-18.5	11.2 ± 1.91	2.5-62.4	4.1 ± 7.93
P. forsskali	104	5.6-25.3	10.9 ± 3.63	1.0-195.3	18.0 ± 29.97

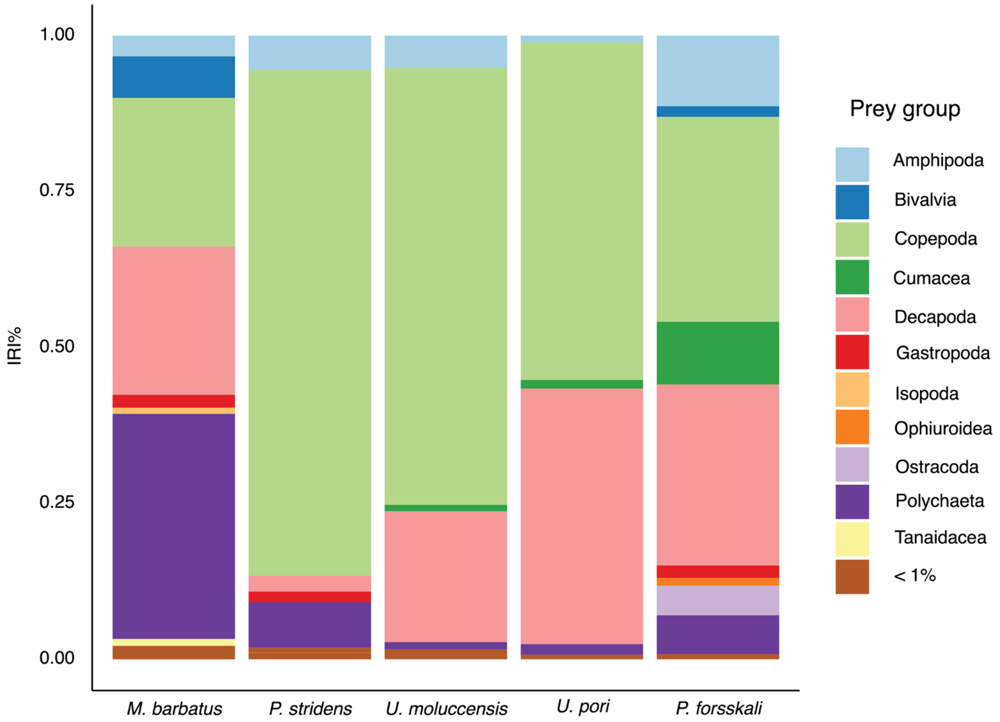

Fig. 2: Index of relative importance percentages (IRI%) of the prey groups comprising the stomach content of *M. barbatus*, *P. stridens*, *U. moluccensis*, *U. pori*, and *P. forsskali*. Prey groups with IRI% < 1 are not included.

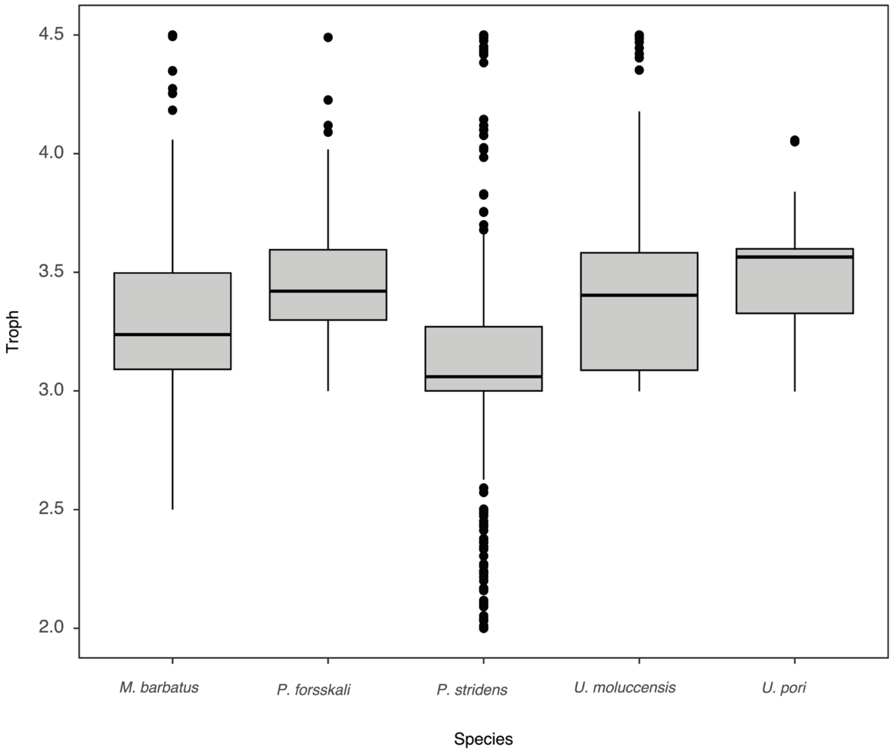

Fig. 3: Trophic levels (Troph) of examined species calculated with *dietr*. The lines in boxes represent medians, the error bars are 95% confidence intervals, and the outliers are shown as dots.

(calculated using SE values) overlap (Table 2).

Monthly changes in trophic levels were significant for all species (Kruskal–Wallis, $p < 0.05$). A general peak in late spring to early summer (April–June) was observed in all species, followed by a decrease in mid-summer to early autumn (July–September) (Fig. 4). *M. barbatus* and *P. stridens* followed a similar trend throughout the year. Their trophic levels continued to stay relatively low towards the end of the year, while the trophic levels of the other species increased. The presence of *P. forsskali* populations showed seasonal variation in the area; some months had none, while others had low numbers (Table 3).

Table 2. Trophic levels (Troph) calculated for each species based on stomach content data, along with TROPH levels obtained from FishBase (N: Number of fish, SD: Standard deviation, SE: Standard error, CI: Confidence interval).

	This study				Fishbase		
Species	N	Troph	SE	95% CI	Troph	SE	95% CI
M. barbatus	818	3.30	0.009	3.28 - 3.32	3.14	0.13	2.88 - 3.39
P. forsskali	102	3.47	0.026	3.42 - 3.52	3.54	0.26	3.03 - 4.05
P. stridens	620	3.09	0.016	3.06 - 3.13	4.02	0.67	2.71 - 5.33
U. moluccensis	407	3.39	0.015	3.36 - 3.42	3.63	0.27	3.10 - 4.16
U. pori	229	3.44	0.016	3.42 - 3.48	3.51	0.49	2.55 - 4.47

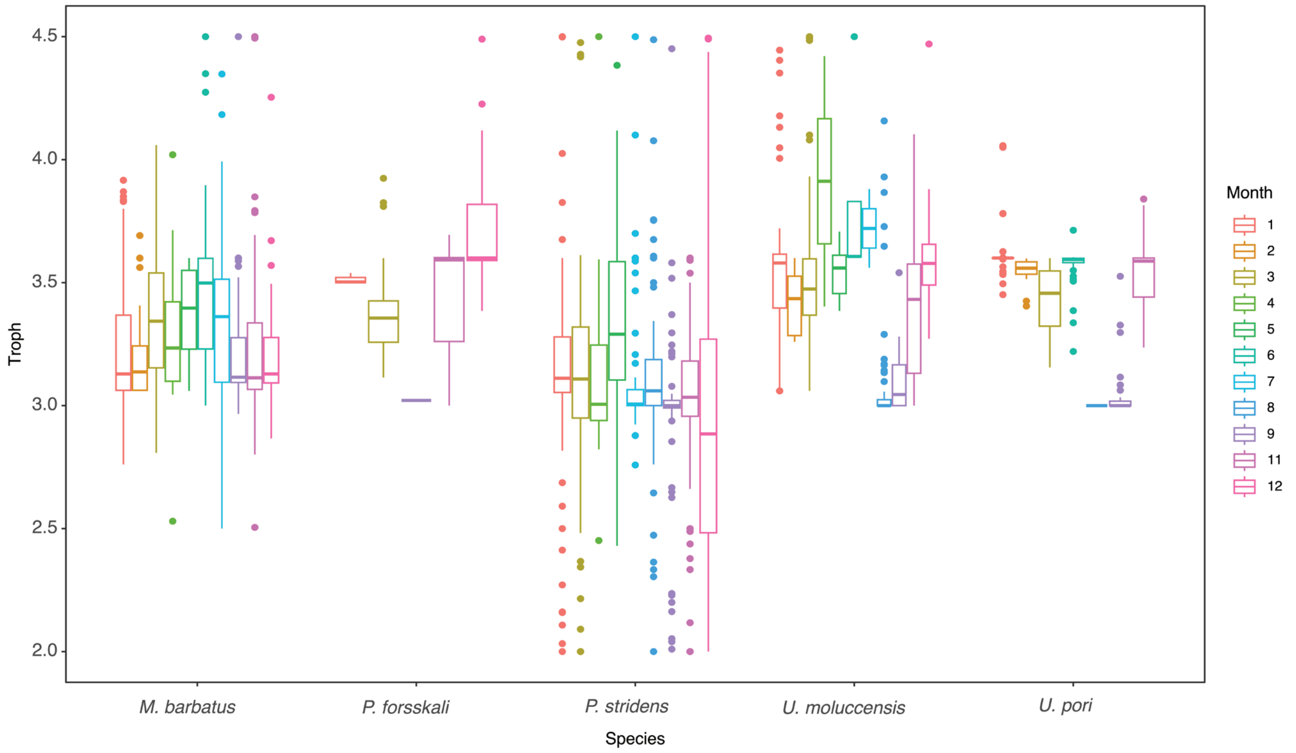

Fig. 4: Monthly variations in trophic levels (Troph) among species. The lines in boxes represent medians, the error bars are 95% confidence intervals, and the outliers are shown as dots.

Our results showed that *P. stridens* exhibited the greatest RIL, followed in order by *M. barbatus*, *P. forsskali*, *U. pori* and *U. moluccensis* (Fig. 5, Table 4). Statistically significant differences in mean RIL values among species were observed (ANOVA, $p < 0.001$). A similar rank order was observed from Zihler's indices (IWL) (Table 4), with the exception of *P. forsskali*, which had a higher IWL than *M. barbatus*. However, the difference between the mean IWL values of these two species was found to be insignificant (t test, $p = 0.87$).

An examination of the relationship between IL and TL for each species revealed that *P. stridens* has the most rapid intestinal growth relative to body size, as shown by its steep slope in Figure 6. In contrast, *M. barbatus* presents a relatively flat slope (b) despite having an intercept above the random model.

Discussion

In any ecosystem, the survival of each species, whether native or NIS, depends on its ability to access the necessary energy within the ecosystem. Their position in the food web is determined by the source of the energy they acquire. From the perspective of NIS survival, examining where they successfully establish themselves and where they face challenges within the food chain can offer valuable insights into the dynamics of the ecosystem. In this context, we compared the dominant species (red mullet) of the soft-bottom continental shelf of the Mediterranean Sea with three confamilial non-indigenous mullids and a haemulid NIS that share the same habitat. Among the three mullid species, *U. pori* and *U. moluccensis* have been present in the Mediterranean Sea for over half a cen-

Table 3. Monthly trophic level (Troph) values of each species (N: Number of specimens, SD: Standard deviation, SE: Standard error, CI: 95% confidence interval).

Species	Month	N	Troph	SD	SE	CI	Species	Month	N	Troph	SD	SE	CI
M. barbatus	1	126	3.24	0.248	0.022	0.044	*P. stridens*	1	93	3.13	0.415	0.043	0.085
	2	18	3.21	0.207	0.049	0.103		3	91	3.11	0.413	0.043	0.086
	3	127	3.37	0.266	0.024	0.047		4	23	3.13	0.380	0.079	0.164
	4	79	3.27	0.218	0.025	0.049		5	46	3.36	0.361	0.053	0.107
	5	14	3.37	0.201	0.054	0.116		7	97	3.15	0.298	0.030	0.060
	6	80	3.43	0.286	0.032	0.064		8	70	3.11	0.375	0.045	0.089
	7	168	3.33	0.254	0.020	0.039		9	63	2.95	0.375	0.047	0.094
	9	56	3.22	0.242	0.032	0.065		11	89	3.00	0.324	0.034	0.068
	11	117	3.23	0.292	0.027	0.053		12	48	2.93	0.644	0.093	0.187
	12	33	3.22	0.257	0.045	0.091	*U. pori*	1	41	3.62	0.113	0.018	0.036
U. moluccensis	1	60	3.56	0.305	0.039	0.079		2	19	3.55	0.053	0.012	0.026
	2	19	3.41	0.126	0.029	0.061		3	39	3.42	0.142	0.023	0.046
	3	113	3.50	0.247	0.023	0.046		6	57	3.57	0.069	0.009	0.018
	4	2	3.91	0.719	0.509	6.464		8	3	3.00	0.000	0.000	0.000
	5	10	3.54	0.109	0.035	0.078		9	41	3.04	0.105	0.016	0.033
	6	4	3.83	0.448	0.224	0.713		11	29	3.54	0.132	0.025	0.050
	7	2	3.72	0.226	0.160	2.034	*P. forsskali*	1	3	3.51	0.023	0.013	0.057
	8	76	3.08	0.221	0.025	0.051		3	64	3.36	0.162	0.020	0.041
	9	28	3.10	0.126	0.024	0.049		9	1	3.02	NA	NA	NA
	11	72	3.37	0.251	0.030	0.059		11	6	3.44	0.288	0.118	0.302
	12	21	3.61	0.237	0.052	0.108		12	28	3.74	0.253	0.048	0.098

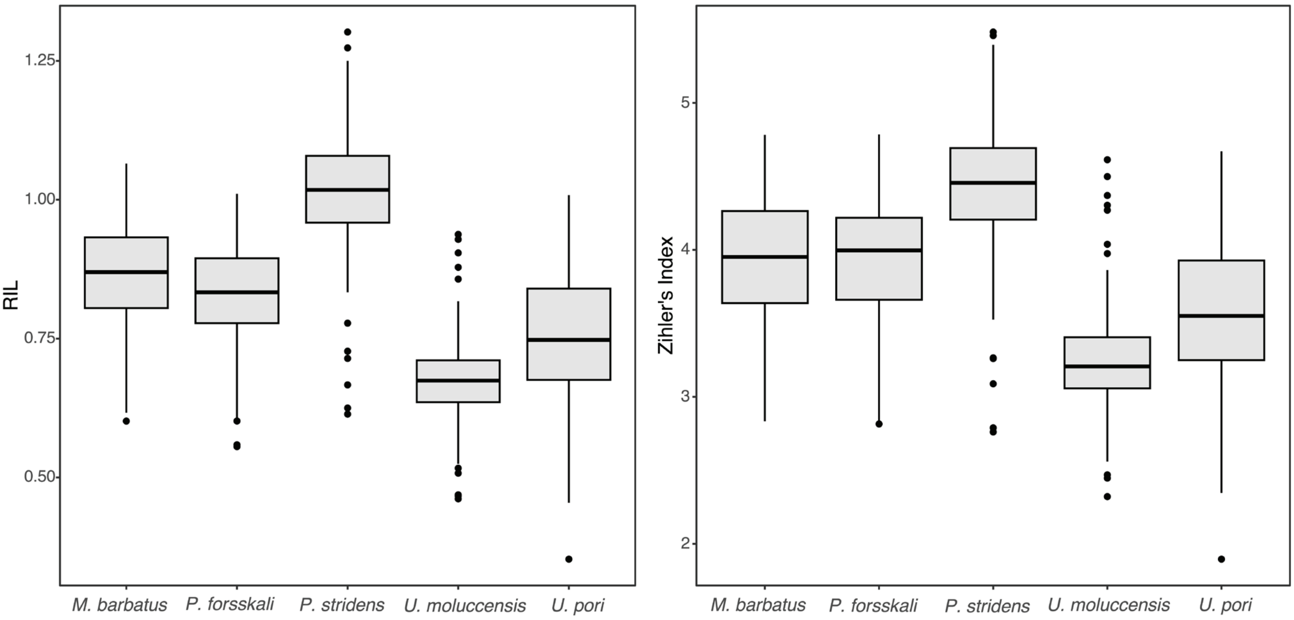

Fig. 5: Relative intestine length (RIL) and Zihler's Index of the examined species. Lines in boxes represent medians, error bars are the 95% confidence intervals and outliers are shown as dots.

tury, yet they have never held the same commercial significance as the red mullet, as indicated by catch statistics (FAO, 2020; TurkStat, 2023). The third species, *P. forsskali*, is relatively new to the Mediterranean Sea, having appeared in the last two decades (Çınar *et al.,* 2006) and recently progressed in its dispersal (Evagelopoulos *et al.,* 2020). The inclusion of the fourth species (*P. stridens*) in this study was based on its remarkable biomass expansion, which started sometime after 2012 on the eastern Mediterranean coasts of Turkey and reached a substantial

Table 4. Relative intestine length (RIL) and Intestinal weight-length for each species (N: Number of fish, SD: Standard deviation, SE: Standard error, CI: Confidence interval).

		RIL (Gut Length/Total Length)				IWL (Intestinal Weight-Length, Zihler)			
Species	**N**	**Mean**	**SD**	**SE**	**95 % CI**	**Mean**	**SD**	**SE**	**95 % CI**
M. barbatus	182	0.87	0.097	0.007	0.85 - 088	3.92	0.406	0.030	3.86 - 3.98
P. forsskali	106	0.82	0.094	0.009	0.80 - 0.84	3.93	0.421	0.041	3.84 - 4.01
P. stridens	187	1.02	0.109	0.008	1.00 - 1.03	4.44	0.427	0.031	4.37 - 4.50
U. moluccensis	131	0.68	0.082	0.007	0.66 - 0.69	3.27	0.385	0.034	3.20 - 3.33
U. pori	141	0.75	0.114	0.010	0.73 - 0.76	3.54	0.499	0.042	3.45 - 3.62

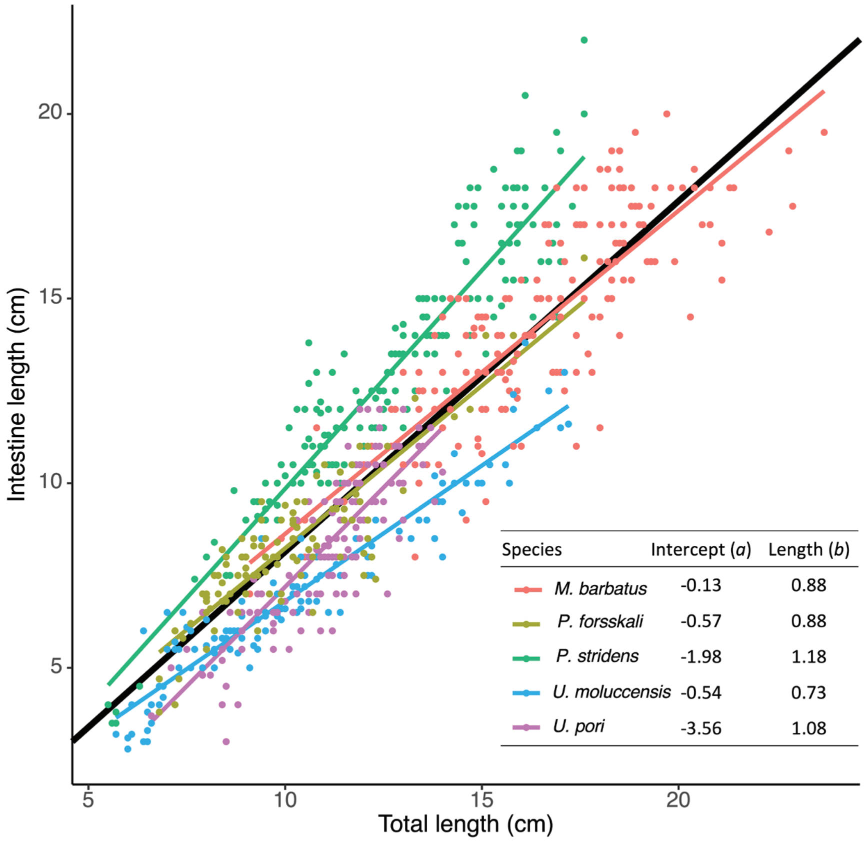

Fig. 6: IL–TL correlations for *P. stridens*, *M. barbatus*, *U. moluccensis*, *U. pori* and P. *forsskali*. The black line represents the random slope model, and the inset table shows the intercept (a) and slope (b) of each species' IL–TL relationship.

biomass level by 2016 (Eşkinat *et al.,* 2023). The results reveal that, qualitatively, all of the studied species feed on the same prey groups, as was previously documented by Golani (1993) for *M. barbatus*, *U. moluccensis*, and *U. pori*. Karachle and Stergiou (2008), on the other hand, pointed out the significance of the temporal availability of food sources and suggested that the trophic levels of the fish within an ecosystem are likely to display seasonal variability. Indeed, the species investigated in this study occupy different levels due to temporal changes in their preferences and/or the availability of their prey (Figs 3 & 4).

Trophic level calculations are based on the Troph values of the prey items that constitute a species' diet. These values fundamentally depend on the length of the food chains linking that species to autotrophs (Ginzburg & D'Andrea, 2001). Therefore, an organism's trophic level can vary significantly depending on the ecosystem which it inhabits. This study relied on the trophic levels of prey items provided by FishBase, although their relevance to the study area is subject to question. Nevertheless, the two supporting indicators applied to address this concern yielded quite similar results. RIL is proposed as an indicator of a species' feeding behaviour, with different RIL ranges being associated with various diet types (Kramer & Bryant, 1995a; German & Horn, 2006; Karachle & Stergiou, 2010b). In the Mediterranean Sea, fish species with RILs less than 1 are typically carnivorous, whereas RILs greater than 1 suggest an omnivorous diet (Karachle & Stergiou, 2010a). In light of these classifications, *P.*

stridens, which has the longest intestinal length among the studied species (mean RIL: 1.02, IWL: 4.44), appears to exhibit an omnivorous feeding nature and is positioned at a lower trophic level.

Based on the RILs, the allometric correlations in gut development, and the Troph values, the similarities observed between the rankings of the species indicate that the trophic positions of the species within the study area have been estimated with reasonable accuracy. Notably, *P. stridens*, achieving high biomass, is positioned below the native *M. barbatus*, while less abundant non-indigenous mullids, especially the pioneering *U. pori* and *U. moluccensis* that arrived significantly earlier, are positioned above it.

Considering the trophic level as proximity to autotrophs in the food chain, the ecosystem's capacity to support biomass diminishes as levels move further away from autotrophs due to ecotrophic efficiency (Odum, 1971). From this perspective, the lower trophic position of *P. stridens* may provide a clue as to how this fish can reach a biomass value above *M. barbatus* while others cannot.

In his 1993 study, Golani examined successful NIS in the eastern Mediterranean Sea, including species addressed in this study. He identified the vacant niches in the Mediterranean Sea as one of the key factors behind their success. It is suggested that both temporal and depth-related vacant niches have emerged as a result of the reproductive calendars of native species and their bathymetric preferences related to hydrography, and NIS have benefited from these gaps. The same study argues that food competition between native and NIS is negligible (Golani, 1993).

Similarly, in a comparative study based on the settlement patterns of native and non-indigenous herbivorous fish, Bariche *et al.* (2004) highlighted the significance of the absence of competition, especially for *Siganus rivulatus*, drawing attention to vacant niches within the ecosystem of the eastern Mediterranean Sea. Considering that native species in the Mediterranean Sea originated from the temperate Atlantic and therefore had to adapt to the suboptimal conditions of the eastern Mediterranean Sea, the existence of vacant niches facilitating the success of NIS should not be disregarded.

The scope of this study does not allow definitive determination of whether non-indigenous mullid species in the Mediterranean Sea prefer diets similar to those in their original habitats. It also remains unclear whether they have adapted their dietary preferences to minimize competition with the dominant native species in their new ecosystem. It was recently demonstrated that *P. forsskali* can undergo significant changes in its food sources as a NIS compared to its native Red Sea population (Tsadok *et al.,* 2023). This finding suggests strong adaptive behaviour, highlighting the need for close monitoring of its progress in the shallow waters along the Mediterranean coasts.

The fact that the stock of the native dominant demersal fish species remains unaffected despite all the pressures and competitive NIS is intriguing from a trophic interaction perspective. Such a situation is typically observed when a new food source emerges that was not previously available, or when native competitors disappear (Wootton, 1990; Rodriguez, 2006). Analysis of the red mullet's diet reveals a predominance of polychaetes; that this contrasts with the lesser importance of this prey in the diets of competing NIS provides clues to the mullet's resilience against NIS. Polychaetes are known to be resistant to eutrophication and increase in abundance during transitions from oligotrophic to eutrophic states (Dauvin *et al.,* 2016). Evidence also suggests recent increases in the diversity and biomass of polychaetes in the region (Çınar *et al.,* 2021). Alongside the implemented five-month breeding period fishing ban for the protection of mature mullets and recruits (TFR, 2020), these increases could be contributing to the success of the red mullet.

In conclusion, the results of this study offer valuable insights into the positioning of certain NIS in new environments, their successful establishment, and the effects on native species. The native species in focus, *M. barbatus*, has successfully maintained its populations at its trophic level, while the examined NIS appeared to be strategically positioned in relation to it. Notably, the species below the trophic level of *M. barbatus*, namely *P. stridens*, demonstrated a higher biomass attributed to ecotrophic efficiency. However, confamilial NIS positioned above *M. barbatus* could not achieve a similar success. The dietary preferences of *M. barbatus*, particularly its inclination towards polychaetes, may play a pivotal role in sustaining its populations, as this preference aligns with the advantage of polychaetes in coastal eutrophic hotspots within the generally oligotrophic Mediterranean marine ecosystem.

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APPENDIX

Abundance (Ni%), weight (Wi%), frequency of occurrence (Fi%) and Index of relative importance (IRI%) percentages of prey groups in the stomach content of *P. stridens*, *M. barbatus*, *U. moluccensis*, *U. pori* and *P. forsskali*

		P. stridens				*M. barbatus*				*U. moluccensis*				*U. pori*				*P. forsskali*			
Prey groups		N%	W%	F%	IRI%	N%	W%	F%	IRI%	N%	W%	F%	IRI%	N%	W%	F%	IRI%	N%	W%	F%	IRI%
Annelida	Polychaeta	3.54	6.62	40.3	7.28	18.3	6.65	70.9	36.1	0.88	2.59	27.5	1.16	3.25	3.2	24.5	1.7	4.57	3.08	54.9	6.26
	Sipuncula	0.13	0.05	2.58	0.01	1.17	0.17	10.4	0.29	0.03	0	1.23	0	-	-	-	-	-	-	-	-
Arthropoda	Pycnogonida	0.02	0	0.32	0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Arthropoda (Crustacea)	Amphipoda	8.9	0.92	31.6	5.52	6	0.48	24.9	3.3	8.77	1.51	41.5	5.16	2.37	0.75	32.8	1.1	12.2	1.65	54.9	11.3
	Copepoda	77.3	8.59	53.1	81	43.7	4.6	24.2	23.8	79.4	19.7	58.5	70.1	73.2	10.7	59.8	54.1	36.2	2.61	56.9	32.9
	Cumacea	3.07	0.23	16.9	0.99	1.59	0.14	9.78	0.35	1.81	0.64	34.2	1.01	3.34	1.12	28.8	1.39	10.7	2.13	52.9	10.1
	Decapoda	0.89	8.26	15.7	2.55	9.17	12	55	23.8	5.18	25.3	57	21	13.7	30.4	86	41	13.4	12.4	75.5	29
	Isopoda	0.25	0.04	4.68	0.02	2.38	0.12	19.9	1.01	0.27	0.03	8.6	0.03	0.07	0.01	2.62	0	0.17	0.12	3.92	0.02
	Mysida	0.18	0.2	3.39	0.02	2.87	0.75	6.23	0.46	0.4	0.22	9.09	0.07	0.32	0.98	6.11	0.09	0.47	0.08	4.9	0.04
	Ostracoda	0.11	0	2.26	0	0.26	0.01	3.3	0.02	0.24	0.02	6.39	0.02	0.58	0.04	12.2	0.08	10.2	0.32	30.4	4.75
	Stomatopoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.09	0.31	1.96	0.01
	Tanaidacea	0.4	0.04	5.32	0.04	2.62	0.28	18.8	1.11	0.2	0.04	6.14	0.02	0.36	0.11	8.3	0.04	1.28	0.08	16.7	0.34
Bryozoa	Bryozoa	0.51	0.06	10.3	0.1	0.77	0.07	11	0.19	0.09	0	3.19	0	-	-	-	-	-	-	-	-
Teleostei	Teleostei	0.17	6.43	3.06	0.36	0.48	1.75	4.16	0.19	0.21	4.21	8.6	0.46	0.07	0.36	2.62	0.01	0.6	2.11	9.8	0.4
Echinodermata	Echinoidea	0.05	0.17	1.13	0	0.02	0.02	0.24	0	0.01	0	0.25	0	-	-	-	-	-	-	-	-
	Ophiuroidea	0.63	0.3	11.3	0.19	1.7	1.51	10.2	0.66	1.62	0.76	31	0.89	0.12	0.06	6.11	0.01	2.14	1.22	24.5	1.23
Mollusca	Bivalvia	0.71	0.27	9.03	0.16	5.06	5.72	30.3	6.67	0.19	0.13	6.14	0.02	0.17	0.09	6.99	0.02	3.29	2.49	19.6	1.69
	Gastropoda	3.15	0.39	27.1	1.7	3.8	0.57	23.2	2.07	0.55	0.14	10.6	0.09	2.39	0.32	17	0.5	4.57	0.73	25.5	2.01
	Scaphopoda	0.03	0.01	0.65	0	0.2	0.04	2.08	0.01	0.2	0.02	5.41	0.01	0.01	0	0.44	0	0.21	0	3.92	0.01
Plant material			0.6	38.6			0.08	9.9			0.01	3.93			0.04	6.11			0.06	9.8	
Organic material			66.8				65.1				44.7				51.8	0			70.6		