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Abstract

The feeding habits of the invasive alien devil firefish (*Pterois miles*) and the indigenous scorpaenids *Scorpaena porcus*, *Scorpaena scrofa*, and *Scorpaena notata* in the eastern Mediterranean Sea were investigated based on stomach content analysis. Furthermore, we examined whether these confamiliar species feed upon similar prey. Specimens were captured by professional fishers using trammel nets on the southwestern coast of Türkiye in the winter and summer of 2021. A total of 608 stomachs (286 *P. miles*, 112 *S. porcus*, 136 *S. scrofa*, and 74 *S. notata*) were investigated. The results demonstrate that the diet of *P. miles* included a total of 45 taxa, with 33 identified at the species level (27 indigenous, 6 non-indigenous), while those of the three congeneric scorpaenids included a total of 46 taxa and 37 identified species (30 indigenous, 7 non-indigenous). For *P. miles*, the highest index of relative importance (%IRI) values were determined for fish in both seasons (83.44% in winter, 93.82% in summer), with the damselfish *Chromis chromis* being the most preferred species. *S. scrofa* fed mainly on fish in winter and cephalopods in summer, whereas the diets of *S. porcus* and *S. notata* included mainly crustaceans in both seasons. In winter, *P. miles* exhibited a higher percentage of empty stomachs, demonstrating a significant difference in the vacuity index in different sampling seasons, while other scorpaenids did not exhibit statistically significant differences. This study also provides the northernmost record of the non-indigenous crab species *Gonioinfradens giardi* and the second record of the squat lobster *Dactylonida curvimana* in Türkiye. It also provides new reports of rarely observed fish species for the eastern Mediterranean, including *Bellottia apoda* and *Odondebuenia balearica*.

Keywords: stomach content; diet; marine invasion; scorpaenids; lionfish; *Gonioinfradens giardi.*

Introduction

Studies on the feeding ecology of fish species are important for stock assessment, trophic models, and the provision of fundamental information to better understand the complex nature of aquatic ecosystems (Başçınar & Sağlam, 2009). Furthermore, studies related to the feeding habits of non-indigenous species (NIS), particularly invasive alien species (IAS), contribute to a better understanding of their impacts on food webs in invaded environments (David *et al*., 2017). Notably, IAS not only cause ecological problems such as radical changes in food webs and the loss of biodiversity but they have also been reported to cause economic and even cultural losses (Bonanno, 2016; Galanidi *et al*., 2023). The problem of biological invasions in aquatic ecosystems has been evaluated at the global scale and has been noted as a major threat in recent years –especially in the Mediterranean basin (e.g., Çinar *et al*., 2021; Zenetos *et al*., 2022).

The Convention on Biological Diversity (CBD), the European Union (EU), and various conventions such as the Barcelona Convention and state regulations in the Mediterranean region have long recognized the need to address the issue of IASs through international cooperation, legislation, and management strategies (Shine, 2007). For example, the EU Regulation on the Prevention and Management of the Introduction and Spread of Invasive Alien Species (No. 1143/2014) came into force in 2015 (Anonymous, 2014). This regulation provides a framework for preventing, minimizing, and mitigating the adverse impacts of IASs on biodiversity and ecosystems within the EU. From 1990 to 2017, the observed cost of biological invasions was calculated at approximately US$3.6 billion, while the projected cost was approximately $27.3 billion for Mediterranean countries (Kourantidou *et al*., 2021).

Türkiye's Mediterranean coastal areas are important, serving as a critical pathway for the introduction and spread of NIS and IAS across the Mediterranean region. This region is known for its incidence of invasions caused by the ongoing influx of species via the Suez Canal (known as Lessepsian migration), which has led to significant ecological and economic consequences for the area (Çinar *et al*., 2021; Vagenas *et al*., 2024).

Species of the genus *Pterois* can have a detrimental impact on the ecosystems they invade (Del Río *et al*., 2023). For instance, the red lionfish *Pterois volitans* was imported to the United States via the ornamental fish trade, accidentally reached the sea, and began to invade the Caribbean and the Gulf of Mexico in 1985 (Trégarot *et al*., 2015; South *et al*., 2017). *P. volitans* rapidly spread to large areas, and its invasion resulted in a high consumption rate of the juveniles of commercially important and reef-associated species, devastating indigenous reef communities due to predation (Albins, 2013; Albins & Hixon, 2013). In the Mediterranean, the devil firefish, *Pterois miles* has been recognized as an IAS (Kletou *et al*., 2016). The species originates from the Indian Ocean and the Red Sea (Schultz, 1986). Since the early 2020s, *P. miles* has spread to large areas in the eastern Mediterranean (Savva *et al*., 2020; Kleitou *et al*., 2021; Ulman *et al*., 2022). While the first record of the devil firefish in the Mediterranean (Haifa Bay) dates back to 1991 (Golani & Sonin, 1992), the first individual observed in Turkish waters was reported nearly a decade later (Turan *et al*., 2014).

In recent years, *P. miles* has emerged as a target for small-scale fisheries in Türkiye. It is regularly sold at local fish markets and has become increasingly popular as a consumed seafood product (Öndes & Ünal, 2023). In October 2024, market prices fluctuated within a range of 10 to 11 euro/kg (AKD, unpublished data).

As with other IAS, *Pterois* spp. (*P. miles* and *P. volitans*) are represented by high fecundity, with these species spawning throughout the year in the Western North Atlantic, while the spawning of *P. miles* in the Mediterranean was observed in summer and autumn only (Morris, 2009; Morris & Whitfield, 2009; Savva *et al*., 2020; Mouchlianitis *et al*., 2022; Kondylatos *et al*., 2024). The estimated annual fecundity of *Pterois* spp. per female has been reported as more than 2 million eggs in the Western North Atlantic (Morris, 2009; Morris & Whitfield, 2009), while the batch fecundity of *P. miles* has been calculated at between 3225 and 63149 oocytes in the Mediterranean (Mouchlianitis *et al*., 2022). The invasion success of these species is driven by several key factors. Their high reproductive rate, early maturation, and effectiveness as predators –aided by successful feeding strategies– allow them to efficiently compete for space. Additionally, their ability to avoid predators through morphological traits (e.g., venomous spines), as well as their rapid growth rate, further enhance their capacity to establish and spread (Morris *et al*., 2009; Dimitriadis *et al*., 2020; Kondylatos *et al*., 2024). The presence of very few species that can prey on this species in the Mediterranean increases the concern of researchers and conservationists (Kleitou *et al*., 2019; Ulman *et al*., 2021; Loya-Cancino *et al*., 2023; Samourdani *et al*., 2024). Hence, they pose a serious risk in a fragile ecosystem such as the Mediterranean ecosystem, where apex predators are decreasing while epidemic diseases, mass deaths, and anthropogenic effects are increasing (Ferretti *et al*., 2008; Irmak & Engin, 2015; Garrabou *et al*., 2019; Moullec *et al*., 2019).

It is well known that scorpionfish are opportunistic carnivorous species that primarily feed on benthic invertebrates and fishes (Harmelin-Vivien *et al.*, 1989; Başçınar & Sağlam, 2009). They are also known for their characteristic ambush predation, where they move slowly, engage in "blowing" behavior to surprise their prey and use their large pectoral fins to corner their prey (Morris & Whitfield, 2012; Albins, 2013; Díaz-Ferguson & Hunter, 2019). Some weedy scorpaenids display camouflage and use this to both hunt their prey and protect against predators (Marshall *et al*., 2019). Thus, it is obvious that their foraging behaviors can show variations depending on species availability.

Although numerous studies have focused on the diets of *P. miles* and *P. volitans* in the Western Atlantic and Caribbean (e.g., Morris & Akins, 2009; Dahl & Patterson, 2014; Eddy *et al*., 2016; Harms-Tuohy *et al*., 2016; Peake *et al*., 2018; Sancho *et al*., 2018; Acero *et al*., 2019), the number of studies conducted in the Mediterranean remains limited (Zannaki *et al*., 2019; Agostino *et al*., 2020; Savva *et al*., 2020; Batjakas *et al*., 2023). As such, the impacts of this invasive species on the fragile Mediterranean ecosystem are not yet well understood (Kletou *et al*., 2016; Poursanidis *et al*., 2020; Phillips *et al*., 2024).

Regarding the feeding habits of other scorpaenids, such as the black scorpionfish *Scorpaena porcus*, red scorpionfish *Scorpaena scrofa*, and small red scorpionfish *Scorpaena notata*, observations have been mainly documented from the western and central Mediterranean (Harmelin-Vivien *et al*., 1989; Morte *et al*., 2001; Raffi-Nouira *et al*., 2016; Compaire *et al*., 2018; Omri *et al*., 2019), with no specific studies on the diets of these species in the eastern Mediterranean. Moreover, no studies have shown whether these species, distributed in the same or similar habitat and depth, feed on the same or different prey, or whether competition exists among them. To alleviate this deficiency to some extent, we aimed to determine and compare the diets of four scorpaenids in the eastern Mediterranean through the present study.

Materials and Methods

Specimens were obtained during the ordinary activities of commercial fishers operating in the winter (January and February) and summer (July and August) of 2021 between Fethiye-Göcek and Gökova in the eastern Mediterranean (Fig. 1). These operations were performed by

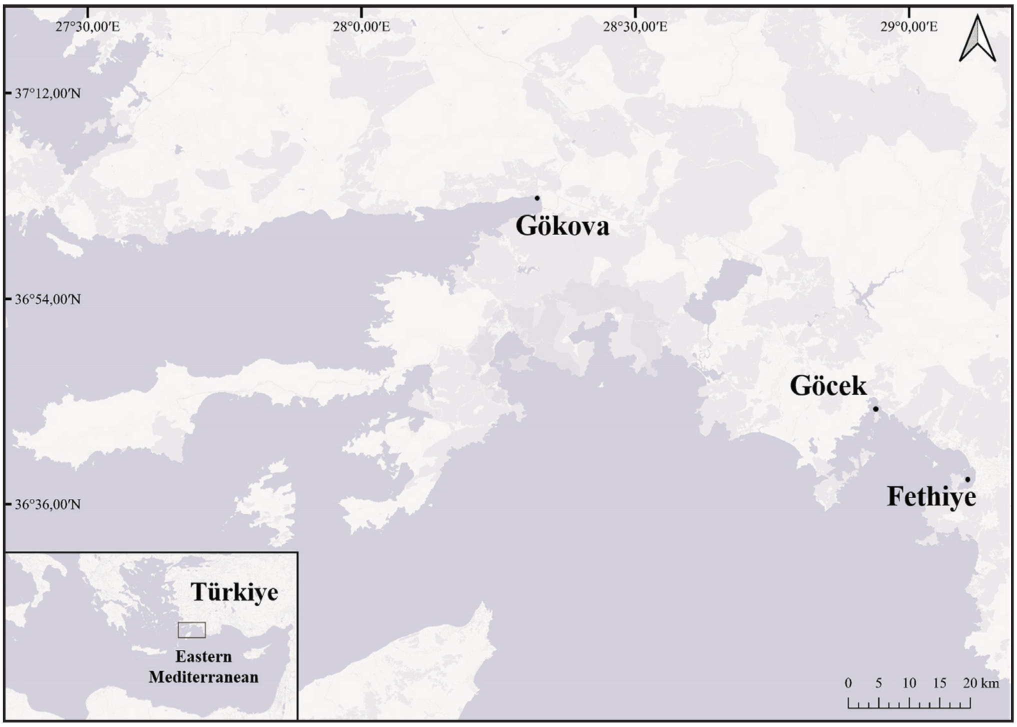

Fig. 1: Map of the study area.

several small-scale fishing boats (less than 12 m in length) using trammel nets in rocky habitats in areas shallower than 100 m. The mesh sizes of the nets varied between 40 and 60 mm, and their lengths ranged between 500 and 2000 m. The collected specimens were immediately transferred to the İzmir Katip Çelebi University Fisheries Biology Laboratory using an isothermal box with ice to avoid digestion. In the laboratory, total weight (TW) (including stomach and intestines), total length (TL), sex, and stomach fullness (empty or full) were recorded for each specimen. For TW and TL determinations, an electronic balance (accuracy 0.001g) and caliper (accuracy 0.01 mm) were used, respectively. Sex was determined by gonadal examination based on macroscopic investigation (Avşar, 2016). Stomachs were taken and weighed, with food items being separated and counted in Petri dishes containing 70% ethanol (Rajasilta *et al*., 2014). Prey items were evaluated under an Olympus SZ2-LGB stereo microscope, whereas larger ones were identified without a microscope. The weight of each prey item was measured and recorded. All prey items were identified to the lowest possible taxonomic level (Hureau & Monod, 1973; Whitehead *et al*., 1986; Galil *et al*., 2002; Bariche, 2012; Golani *et al*., 2021).

Feeding intensity was evaluated with the use of the vacuity index (VI) of the sampled stomach, which corresponds to the percentage of empty stomachs (ES) with respect to all analyzed stomachs (TS) (Ouakka *et al*., 2017).

VI= ES / TS x 100

To understand the contribution of each prey type to the diets of scorpaenids, three simple methods –numerical, gravimetric, and frequency of occurrence– were used (Hyslop, 1980). The percentages of numerical abundance (%N) were calculated using the following equation:

%N = (i/TNP) × 100

i = number of prey items, TNP = total number of prey items

Similarly, a gravimetric method was used, as follows:

%W = (i/TWAP) × 100

i = weight of prey item, TWAP = total weight of all prey items

Percentage frequency of occurrence (%F) was calculated as:

%F = (i/ TNFS) ×100

i = number of stomachs containing a specific prey item, TNFS = total number of full stomachs

(Hyslop, 1980; Rafrafi-Nouira *et al*., 2016).

The index of relative importance (IRI) identified by Pinkas *et al*. (1971), and modified by Hacunda (1981), was calculated using the following formula:

IRI = %F × (%N + %W)

This index is expressed as:

%IRI = (IRI/∑ IRI) × 100

This index was selected since it helps to avoid bias and presents a clearer picture of the relative importance of prey items in the diet.

Based on the mean TL, two size classes were determined for each species: small (TL lower than the mean value) and large (TL higher than the mean value). Sexual, seasonal, and size-related differences in the vacuity index (VI) and percentage frequency of occurrence (%F) were assessed for each species using the chi-square test (X^2) (Sokal & Rohlf, 1981) and the R software (R Core Team, 2022).

Results

In this study, a total of 608 individuals (286 *P. miles*, 112 *S. porcus*, 136 *S. scrofa*, and 74 *S. notata*) were collected. The TL of *P. miles* individuals varied from 18 to

37 cm (mean ± SD = 26 ± 4 cm). Similarly, the TL of *S. scrofa* ranged from 15 to 36 cm (mean ± SD = 23 ± 4 cm). On the other hand, *S. notata* specimens ranged from 6 to 21 cm TL (mean ± SD = 16 ± 3 cm), while *S. porcus* ranged from 11 to 24 cm TL (mean ± SD = 17 ± 3 cm).

For *P. miles*, *S. porcus*, *S. scrofa*, and *S. notata*, the VI (for the total number of each species, regardless of sex, season, and size class) was determined as 39, 58, 78, and 48%, respectively. The results indicate that VI of *P. miles* was significantly higher in winter than in summer (Table 1). Notably, there was no significant difference in the VI of other scorpaenids relating to the sampling season. On the other hand, except for *S. porcus*, the VI of scorpaenids did not show significant variations between sexes. In *S. porcus*, the VI of males was significantly higher than that of the females. Moreover, there was no significant difference in VI with regard to the size groups for any of the species (Table 1).

The overall results of the qualitative and quantitative analyses of prey ingested for each species are presented in Tables 2, 3, 4, and 5. The diet of *P. miles* was diverse when compared to those of other scorpaenids in the present study. Of the 45 total taxa identified from the stomachs, 33 were identified at the species level. While stomachs of *S. porcus* specimens included 21 taxa (14 identified at the species level), *S. notata* included 25 taxa (20 identified at the species level). The lowest diet variety was observed in *S. scrofa*, with 19 taxa (11 identified at the species level). Except for *S. scrofa*, the number of taxa in other scorpaenids was found to be higher in summer than in winter (Tables 2, 3, 4, and 5). Additionally, a total of 12 species were found to be consumed by *P. miles* and at least one of the other three scorpaenids. These species were *Gonioinfradens giardi*, *Charybdis longicollis*, *Pilumnus* sp., *Galathea* sp., *Munida* sp., *Octopus vulgaris*, *Spicara* sp., *Serranus hepatus*, *Coris julis*, *Siganus luridus*, *Odondebuenia balearica*, and *Bregmaceros nectabanus*.

Concerning the %F in *P. miles*, 84.29% of the full stomachs included Teleostei, followed by Crustacea with 36.64%, while Mollusca represented 2.09% and Annelida only 0.52%. Additionally, for *P. miles*, the %F of fish was higher in summer, while the %F of Crustacea was higher in winter (Fig. 2). The %F of Crustacea and Teleostei in *P. miles* showed significant differences depending on the sampling season (X^2 test, $P = 0.04$ for Crustacea, $P = 0.01$ for Teleostei). Moreover, the stomachs of *S. porcus* and *S. scrofa* mainly included Crustacea (%F = 82.61 and 53.33, respectively), and for both species, the %F of Crustacea was higher in winter (Fig. 2). On the contrary, the %F of both Crustacea and Teleostei was higher in summer in *S. notata*, with this species not being observed to feed on Annelida and Mollusca throughout the study (Fig. 2). On the other hand, %F was very similar in both size groups of fish species—except for *S. notata*. The %F of main prey taxa (Annelida, Crustacea, Mollusca, and Teleostei) in the other three indigenous scorpaenids did not show significant differences by sampling season (X^2 test, $P > 0.05$). Moreover, the %F of main prey taxa in four species of the Scorpaenidae family did not show significant differences between sexes (X^2 test, $P > 0.05$). Similarly, the %F of main prey taxa did not show significant differences

Table 1. Summary of X^2 test related to the sexual, seasonal and size-related differences in the vacuity index (VI) of *Pterois miles, Scorpaena porcus, Scorpaena scrofa,* and *Scorpaena notata* in winter and summer 2021 in the Mediterranean coasts of Türkiye.

Species	**Factor**	X^2	**df ***	***P*-value**
	Season			
Pterois miles		23.85	1	< 0.001
Scorpaena porcus		1.044	1	0.307
Scorpaena scrofa		0.773	1	0.379
Scorpaena notata		0.053	1	0.818
	Sex			
Pterois miles		0.12	1	0.729
Scorpaena porcus		7.063	1	0.008
Scorpaena scrofa		0.001	1	0.978
Scorpaena notata		1.145	1	0.285
	Size class			
Pterois miles		0.03	1	0.867
Scorpaena porcus		0.79	1	0.375
Scorpaena scrofa		1.43	1	0.232
Scorpaena notata		0.07	1	0.796

*df = degrees of freedom.

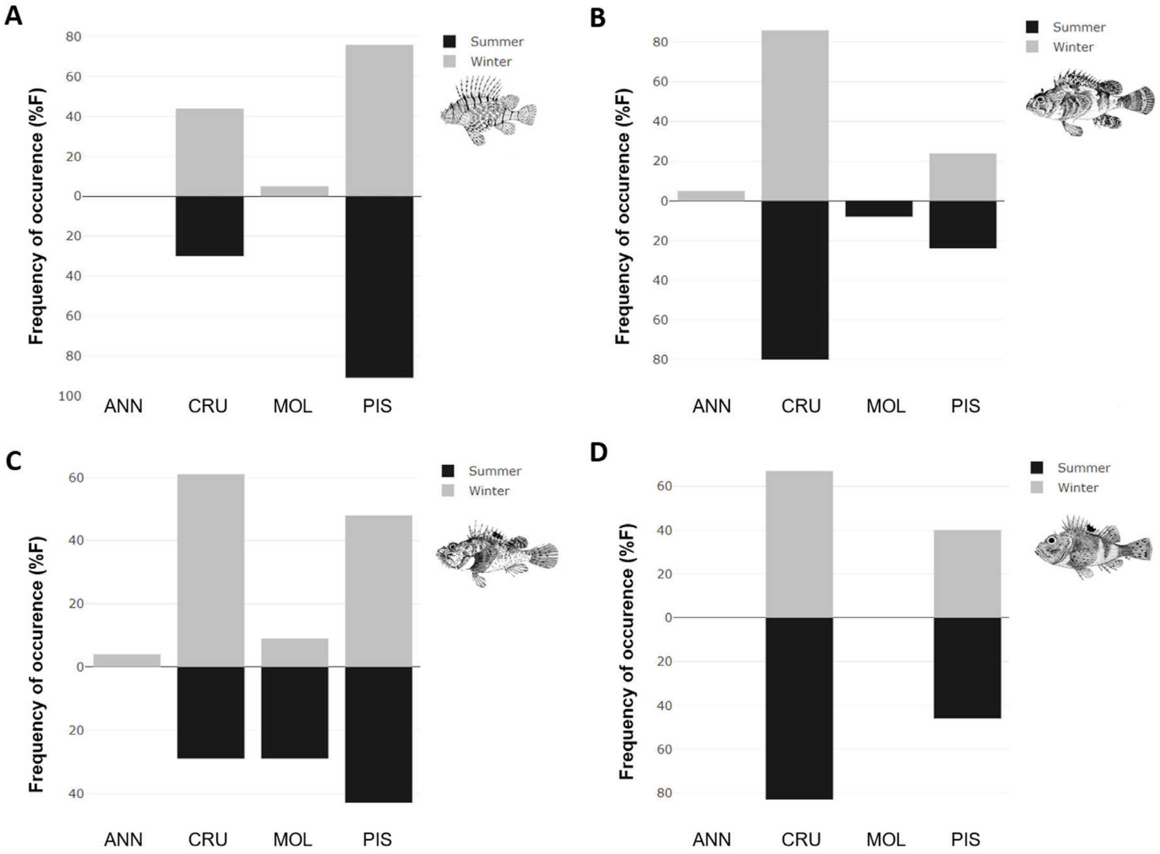

Fig. 2: Percentage frequency of occurrence (%F) of A) *Pterois miles*, B) *Scorpaena porcus*, C) *Scorpaena scrofa*, and D) *Scorpaena notata* on the southwest coast of Türkiye in the winter and summer of 2021. Meanings of abbreviations: ANN = Annelida, CRU = Crustacea, MOL = Mollusca, PIS = Pisces.

in a size classes X^2 test, $P > 0.05$)—except for the %F of Teleostei in *S. notata*. There was a significant difference in the %F of Teleostei among the size classes of *S. notata* (X^2 test, $P = 0.01$). Small specimens of the latter species preferred mainly Crustacea as prey (%F= 90), while the highest %F in large specimens was in Teleostei with 68%.

The %IRI results also demonstrated that *P. miles* fed primarily on Teleostei in both seasons, while *S. porcus* and *S. notata* preferred to consume mainly Crustacea in the winter and summer. On the other hand, the main diet of *S. scrofa* consisted of fish in the winter, shifting to cephalopods in the summer (Fig. 3). In particular, *P. miles* demonstrated high predation (%IRI=80.15) on *Chromis chromis* in the summer (Table 2). TL of *C. chromis* varied between 1.5 and 8.2 cm (mean ± SD = 4.8 ± 2.4 cm). The highest %IRI of *S. porcus* was observed for the NIS of crab *Gonioinfradens giardi* (%IRI=42.09) in the winter and unidentified crabs (%IRI=53.26) in the summer (Table 3). The highest %IRI (45.51) of *S. scrofa* was for unidentified fish species in the winter, while the highest %IRI (61.88) in the summer was determined for the common octopus *Octopus vulgaris* (Table 4). The main prey of *S. notata* consisted of Penaeidae and Brachyuran crustaceans (Table 5). Additionally, the %N and %W values for each prey item are shown in Tables 2, 3, 4, and 5.

Regarding the size classes, %IRI results indicate that marked differences were not detected between small and large individuals of *P. miles* and *S. porcus*. Unlike these species, small individuals of *S. notata* mainly fed on Crustacea, while the highest %IRI for large individuals was Teleostei. Moreover, individuals from the small size classes of *S. scrofa* and *S. porcus* did not feed on Polychaeta (Table 6).

This study also provided the northernmost record of the non-indigenous crab species *Gonioinfradens giardi* on Türkiye's coasts. A total of 13 specimens of this species were obtained from the stomachs of *P. miles* and *S. porcus*. Additionally, a specimen of the spider lobster *Dactylonida curvimana* was found in the stomach of *S. scrofa*, with this observation constituting the second record of this species in Turkish waters. Furthermore, fish species rarely reported along the Mediterranean coasts of Türkiye were found in the stomachs of *S. scrofa* (*Bellottia apoda*), and in the diets of *P. miles* and *S. notata* (*Odondebuenia balearica*) (Tables 2, 4, and 5). The results indicate that a total of 59 identified prey species were found in this study, among which 10 are NIS (*Macrophthalmus graeffei*, *Gonioinfradens giardi*, *Charybdis helleri*, *Charybdis longicollis*, *Thalamita poissonii*, *Metapenaeopsis aegyptia*, *Siganus luridus*, *Cheilodipterus novemstriatus*, *Parupeneus forsskali*, and *Bregmaceros nectabanus*).

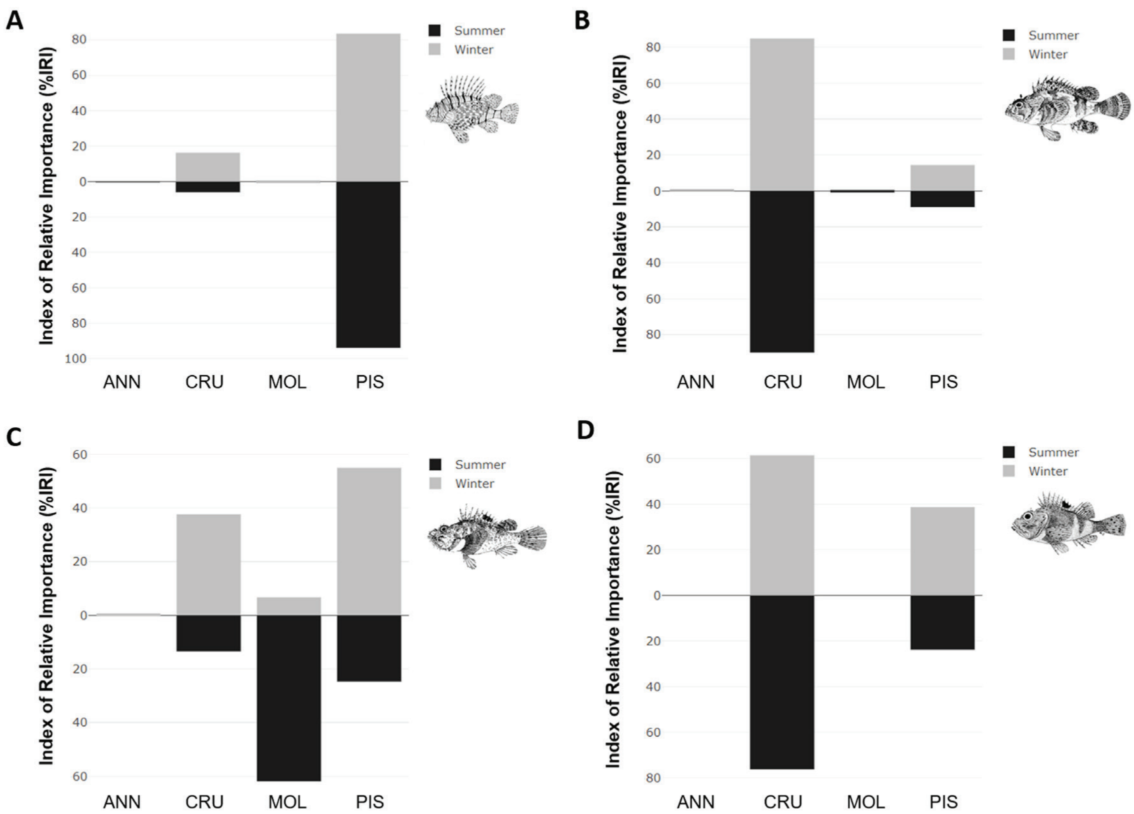

Fig. 3: The index of relative importance (%IRI) of A) *Pterois miles*, B) *Scorpaena porcus*, C) *Scorpaena scrofa*, and D) *Scorpaena notata* on the southwest coast of Türkiye in the winter and summer of 2021. Meanings of abbreviations: ANN = Annelida, CRU = Crustacea, MOL = Mollusca, PIS = Pisces.

Table 2. Overall results of the qualitative and quantitative analyses of prey ingested for *Pterois miles* in winter and summer 2021 in the southwest coast of Türkiye.

Preys of *P. miles*	**Winter**				**Summer**			
	%F	**%N**	**%W**	**%IRI**	**%F**	**%N**	**%W**	**%IRI**
POLYCHAETA	-	-	-	-	0.97	2.60	0.11	0.04
Unidentified Polychaeta	-	-	-	-	0.97	2.60	0.11	0.04
CRUSTACEA	44.32	41.4	16.07	16.27	30.10	55.41	16.07	6.01
Isopoda								
Unidentified Isopod	-	-	-	-	0.97	0.43	0.06	0.01
Mysida								
Unidentified Mysid	7.41	5.86	0.18	1.34	1.94	0.87	0.11	0.03
Stomatopoda								
Unidentified Stomatopod	1.23	0.39	0.44	0.03	0.97	1.30	0.91	0.03
Decapoda								
*[a] *Gonioinfradens giardi*	3.70	2.34	3.13	0.61	-	-	-	-
**Charybdis helleri*	-	-	-	-	0.97	0.87	1.43	0.03
**Charybdis longicollis*	1.23	0.78	0.32	0.04	-	-	-	-
Pilumnus sp.	1.23	0.39	0.19	0.02	-	-	-	-
Paguristes sp.	1.23	0.39	0.05	0.02	-	-	-	-

Continued

Table 2 continued

Preys of *P. miles*	Winter				Summer			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI
Galathea nexa	1.23	0.39	0.16	0.02	0.97	1.30	0.12	0.02
Galathea sp.	7.41	2.34	1.08	0.76	7.77	9.52	1.87	1.22
Munida rugosa	1.23	0.39	0.21	0.02	-	-	-	-
Munida sp.	2.47	2.34	0.52	0.21	2.91	6.49	1.98	0.34
Scyllarus arctus	1.23	3.91	0.70	0.17	6.80	21.65	4.16	2.41
Unidentified Brachyura	4.94	1.56	0.95	0.37	3.88	2.60	0.93	0.19
Penaeidae	16.05	16.02	6.73	10.96	5.83	5.19	2.97	0.65
**Metapenaeopsis aegyptia*	1.23	0.39	0.31	0.03	-	-	-	-
Unidentified Crustacea	11.11	3.91	1.10	1.67	11.65	5.19	1.53	1.08
MOLLUSCA	4.55	3.51	1.23	0.3	-	-	-	-
Gastropoda								
Conus ventricosus	1.23	0.39	0.01	0.01	-	-	-	-
Conomurex persicus	1.23	0.39	0.02	0.02	-	-	-	-
Unidentified Gastropod	3.70	1.56	0.03	0.18	-	-	-	-
Cephalopoda								
Octopus vulgaris	1.23	1.17	1.17	0.09	1.94	0.87	1.61	0.07
TELEOSTEI	76.14	55.06	82.68	83.44	91.26	93.07	104.08	93.82
Clupeidae	-	-	-	-	0.97	0.87	0.66	0.02
Chromis chromis	1.23	0.39	11.23	0.43	58.25	41.99	58.16	80.15
Scorpaena maderensis	11.11	19.14	5.07	8.07	1.94	0.87	10.52	0.30
Scorpeana sp.	4.94	2.73	0.43	0.47	4.85	13.42	4.58	1.20
Spicara maena	1.23	0.39	12.63	0.48	-	-	-	-
Spicara smaris	2.47	0.78	11.03	0.88	0.97	0.43	3.19	0.05
Spicara sp.	2.47	0.78	5.36	0.46	-	-	-	-
Apogon imberbis	-	-	-	-	2.91	1.73	2.57	0.17
Serranus cabrilla	1.23	0.39	5.90	0.23	-	-	-	-
Serranus hepatus	-	-	-	-	0.97	0.43	2.49	0.04
Serranus sp.	-	-	-	-	0.97	0.87	0.15	0.01
Thalassoma pavo	-	-	-	-	0.97	0.43	0.07	0.01
Coris julis	-	-	-	-	0.97	0.43	1.53	0.03
**Siganus luridus*	-	-	-	-	0.97	0.43	2.39	0.04
Blennidae	1.23	0.39	0.65	0.04	0.97	1.73	1.71	0.05
Gobiidae	9.88	8.59	3.37	3.55	6.80	9.09	1.80	1.02
Deltentosteus quadrimaculatus	2.47	0.78	0.78	0.12	-	-	-	-
γ*Odondebuenia balearica*	-	-	-	-	0.97	0.43	0.54	0.01
Gobius paganellus	-	-	-	-	1.94	0.87	1.98	0.08
Sparisoma cretense	1.23	0.39	0.20	0.02	-	-	-	-
**Bregmaceros nectabanus*	-	-	-	-	1.94	0.87	0.55	0.04
**Parupeneus forsskali*	-	-	-	-	0.97	0.43	3.42	0.05
Unidentified Fish	49.38	20.31	26.03	68.69	30.10	17.75	7.77	10.55

* non-indigenous species, α northernmost record of species, γ rare species.

Table 3. Overall results of the qualitative and quantitative analyses of prey ingested for *Scorpaena porcus* in winter and summer 2021 in the southwest coast of Türkiye.

Preys of ***S. porcus***	Winter				Summer			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI
POLYCHAETA	4.55	3.57	0.98	0.69	-	-	-	-
Unidentified Polychaeta	4.55	3.57	0.98	0.69	-	-	-	-
CRUSTACEA	85.71	78.57	78.18	84.88	80	82	60.34	90
Stomatopoda								
Rissoides desmaresti	-	-	-	-	4.0	4	2.30	0.68
Squilla mantis	-	-	-	-	4.0	2	19.42	2.30
Squilla sp.	4.55	3.57	10.76	2.18	-	-	-	-
Decapoda								
*α *Gonioinfradens giardi*	27.27	25.00	21.12	42.09	-	-	-	-
**Thalamita poissonii*	4.55	7.14	14.78	3.33	20.0	20	13.54	18.00
Xantho sp.	4.55	3.57	0.49	0.62	-	-	-	-
Portunidae	-	-	-	-	4.0	2	1.20	0.34
Galathea intermedia	-	-	-	-	4.0	2	1.01	0.32
Galathea squamifera	4.55	3.57	4.77	1.27	-	-	-	-
Galathea sp.	4.55	3.57	1.50	0.77	-	-	-	-
Unidentified Brachyura	18.18	17.86	21.17	23.75	40.0	30	19.62	53.26
Penaeidae	-	-	-	-	24.0	20	3.09	14.87
Unidentified Crustacea	18.18	14.29	3.59	10.87	4.0	2	0.16	0.23
MOLLUSCA	-	-	-	-	8.0	4	0.09	0.88
Bivalvia								
Unidentified Bivalvia	-	-	-	-	8.0	4	0.09	0.88
TELEOSTEI/FISHES	23.81	17.86	20.83	14.42	24	14	39.58	9.13
**Siganus luridus*	4.55	3.57	16.40	3.04	-	-	-	-
Sardina pilchardus	-	-	-	-	8.0	4	23.19	5.84
Lesueurigobius friesii	-	-	-	-	4.0	2	3.40	0.58
Spicara sp.	-	-	-	-	4.0	2	11.37	1.44
Symphodus sp.	-	-	-	-	4.0	2	1.40	0.37
Unidentified Fish	18.18	14.29	4.43	11.38	8.0	4	0.22	0.90

* non-indigenous species, α northernmost record of species.

Discussion

The present study presents the first comparison of the feeding habits of four scorpionfish species from the eastern Mediterranean. *Pterois miles* feeds on more species than the other three scorpaenids, including members of the family Scorpaenidae, and it presents high predation on species such as *C. chromis* during certain periods. *P. miles* is thriving in the studied areas, thereby posing a great threat to the Mediterranean ecosystem (Savva *et al*., 2020; Kleitou *et al*., 2021).

Many studies have emphasized how destructive the effects of its congener (*Pterois volitans*) are in the Atlantic and Caribbean. Based on an experimental study, a significant decline in the recruitment of indigenous fish species (average of 79% over a 5-week duration) was observed due to predation by *P. volitans* (Albins & Hixon, 2008). This species poses a major threat to coral reefs and herbivore species, feeding on more than 70 different species and causing devastating problems in food webs (Valdez-Moreno *et al.*, 2012; Albins & Hixon, 2013). Its high predation on juvenile snappers and groupers has caused marked reductions in the stocks of these economically important species in the Gulf of Mexico (Huth *et al*., 2018). The results of our study suggest that *P. miles* poses a threat to the Mediterranean ecosystem and that if its population increases excessively, it has the potential to have an impact on the Mediterranean ecosystem similar to that of the *P. volitans* in the Atlantic. The combination of increasing impacts of climate change and the mismanagement of fisheries has led to serious changes in the Mediterranean ecosystem, resulting in declines in stocks of indigenous species in the eastern Mediterranean; for example, more than 90% of the catch composition of small-scale fishers' nets now consists of NISs (Öndes & Ünal, 2023). Similarly, a recent study conducted in the

Table 4. Overall results of the qualitative and quantitative analyses of prey ingested for *Scorpaena scrofa* in winter and summer 2021 in the southwest coast of Türkiye.

Preys of *S. scrofa*	**Winter**				**Summer**			
	%F	**%N**	**%W**	**%IRI**	**%F**	**%N**	**%W**	**%IRI**
POLYCHAETA	4.35	3.23	0.22	0.68	-	-	-	-
Unidentified Polychaeta	4.35	3.23	0.22	0.68	-	-	-	-
CRUSTACEA	60.87	51.64	32.73	38.34	28.57	37.5	6.7	13.44
Mysida								
Unidentified Mysid	4.35	3.23	0.16	0.66	-	-	-	-
Decapoda								
**Charybdis longicollis*	4.35	3.23	8.47	2.29	-	-	-	-
$^{\beta}$*Dactylonida curvimana*	4.35	3.23	9.16	2.43	-	-	-	-
Munida sp.	4.35	3.23	1.90	1.00	-	-	-	-
Scyllarides latus	4.35	3.23	0.60	0.75	-	-	-	-
Unidentified Brachyura	13.04	9.68	1.97	6.84	14.29	12.5	4.11	5.05
Penaeidae	8.70	6.45	7.95	5.64	14.29	25	2.59	8.39
Unidentified Crustacea	21.74	16.13	2.30	18.05	-	-	-	-
MOLLUSCA	8.70	6.46	27.63	6.67	28.57	25	76.72	61.88
Gastropoda								
Unidentified Gastropod	4.35	3.23	9.76	2.54	-	-	-	-
Cephalopoda								
Octopus vulgaris	4.35	3.23	17.87	4.13	28.57	25	76.72	61.88
TELEOSTEI/FISHES	47.83	41.96	39.65	54.98	42.86	37.5	16.58	24.68
Engraulis encrasicolus	-	-	-	-	14.29	12.5	14.55	8.23
**Cheilodipterus novemstriatus*	4.35	3.23	6.70	1.94	-	-	-	-
Coris julis	4.35	3.23	17.87	4.13	-	-	-	-
$^{\gamma}$*Bellottia apoda*	4.35	3.23	2.46	1.11	-	-	-	-
Chlopsis bicolor	4.35	3.23	0.71	0.77	-	-	-	-
Conger conger	4.35	3.23	0.96	0.82	-	-	-	-
Congeridae	4.35	3.23	0.34	0.70	-	-	-	-
Unidentified Fish	30.43	22.58	10.61	45.51	28.57	25	2.03	16.45

* non-indigenous species, β second record of species , γ rare species.

eastern Mediterranean (Rhodes Island) highlighted the increased abundance, biomass, and occurrence frequency of IAS in gillnet and trammel net fisheries (Kondylatos *et al*., 2023). Öndes & Ünal (2023) also declared that *P. miles* was the most commonly caught species in 36 mm trammel nets on the southern coasts of Türkiye, which provides clear evidence of the increased abundance of this species in the region. Notably, only a few species –including dusky grouper (*Epinephelus marginatus*), white grouper (*Epinephelus aeneus*), common octopus (*O. vulgaris*), and silver-cheeked toadfish *Lagocephalus sceleratus*– were reported as predators of *P. miles* (Ulman *et al*., 2021) in this region. In recent years, this species has begun to be consumed by locals and has become the target species of some small-scale fishing communities. Supporting more selective fishing pressure on the species and expanding its market is of great importance in combating this IAS and minimizing the negative effects it may have on the populations of remaining native species (Ünal *et al*., 2022; Olguner *et al*., 2024).

The present study demonstrated that the main prey groups of *P. miles* were Teleostei, followed by Crustacea. Mollusca and Annelida were rarely observed in the investigated stomachs. These findings are very similar to those of other studies conducted in the eastern Mediterranean (Zannaki *et al*., 2019; Agostino *et al*., 2020; Savva *et al*., 2020; Batjakas *et al*., 2023; Koilakos *et al*., 2024). For example, a recently published study evaluated the diet of devil firefish in three sites of the Aegean Sea, Greece, and indicated that this species mainly preyed upon teleosts (4 to 83% numerical abundance) and decapods (12 to 95% numerical abundance) (Batjakas *et al*., 2023). Earlier, Zannaki *et al*. (2019) reported that the diet of *P. miles* in Rhodes, north-eastern Aegean Sea, mainly consisted of Teleostei (78.5% in number, approximately 94.7% in biomass). Similarly, the percentage of prey index of *P .miles* included 87.39% fishes and 12.61% crustaceans in Cyprus, SE Mediterranean (Savva *et al*., 2020). The

Table 5. Overall results of the qualitative and quantitative analyses of prey ingested for *Scorpaena notata* in winter and summer 2021 in the southwest coast of Türkiye.

Preys of *S. notata*	Winter				Summer			
	%F	%N	%W	%IRI	%F	%N	%W	%IRI
CRUSTACEA	66.67	80.02	23.51	61.32	83.33	76.82	25.69	76.21
Mysida								
Unidentified Mysid	6.67	34.29	5.30	12.27	-	-	-	-
Stomatopoda								
Rissoides desmaresti	6.67	2.86	6.70	2.96	-	-	-	-
Squilla sp.	6.67	2.86	1.13	1.23	-	-	-	-
Decapoda								
Pilumnus hirtellus	-	-	-	-	4.17	1.79	1.30	0.29
Pilumnus sp.	-	-	-	-	4.17	1.79	1.36	0.29
Ilia nucleus	-	-	-	-	4.17	1.79	2.89	0.44
**Thalamita poissonii*	6.67	2.86	1.26	1.28	-	-	-	-
Xantho poressa	-	-	-	-	4.17	1.79	1.59	0.32
Xantho sp.	6.67	2.86	0.24	0.96	-	-	-	-
Pisa tetraodon	-	-	-	-	4.17	1.79	0.32	0.20
Ethusa mascarone	-	-	-	-	4.17	1.79	0.27	0.19
Goneplax rhomboides	-	-	-	-	4.17	1.79	2.07	0.36
**Macrophthalmus graeffei*	-	-	-	-	4.17	1.79	2.07	0.36
Galathea sp.	6.67	2.86	0.65	1.09	4.17	1.79	1.39	0.30
Penaeidae	20.00	11.43	4.34	14.66	50.00	48.21	9.33	64.69
Unidentified Brachyura	26.67	17.14	3.79	25.95	25.00	12.50	3.10	8.77
Unidentified Crustacea	6.67	2.86	0.10	0.92	-	-	-	-
TELEOSTEI/FISHES	40	20.01	76.49	38.69	45.83	23.24	74.32	23.78
Serranus hepatus	6.67	2.86	30.50	10.34	4.17	1.79	3.57	0.50
Sardina pilchardus	6.67	2.86	24.34	8.43	4.17	1.79	14.17	1.49
Engraulis encrasicolus	6.67	2.86	12.89	4.88	16.67	8.93	39.12	18.00
Lesueurigobius friesii	-	-	-	-	8.33	5.36	7.00	2.31
Lesueurigobius suerii	-	-	-	-	4.17	1.79	2.07	0.36
**Bregmaceros nectabanus*	-	-	-	-	4.17	1.79	8.36	0.95
$^{\gamma}$*Odondebuenia balearica*	6.67	2.86	3.15	1.86	-	-	-	-
Unidentified Fish	20.00	8.57	5.61	13.18	4.17	1.79	0.03	0.17

* non-indigenous species, γ rare species.

Table 6. The size related differences in the percentage index of relative importance (%IRI) of *Pterois miles*, *Scorpaena porcus*, *Scorpaena scrofa*, and *Scorpaena notata* in winter and summer 2021 in the Mediterranean coasts of Türkiye.

		Main Prey Taxa			
Species	Size Class	Polychaeta	Crustacea	Mollusca	Teleostei
P. miles	Class 1 (≤ 26 cm)	0.046	10.06	0.104	89.78
	Class 2 (> 26 cm)	0	6.38	0.1	93.51
S. porcus	Class 1 (≤ 17 cm)	0	89.03	1.17	9.79
	Class 2 (> 17 cm)	2.42	86.62	0	10.96
S. scrofa	Class 1 (≤ 23 cm)	0	23.03	27.02	49.95
	Class 2 (> 23 cm)	1.58	36.54	15.74	46.14
S. notata	Class 1 (≤ 16 cm)	0	88.39	0	11.60
	Class 2 (> 16 cm)	0	44.81	0	55.19

latter authors also noted that the frequency of occurrence of accidental prey, such as fishing lines, plastics, and dry leaves of *Posidonia oceanica* was 11.11%, while that of parasites (Nematoda and Trematoda) was 29.63%.

P. miles prey heavily on certain key species within the Mediterranean ecosystem. For instance, our results indicate that *P. miles* fed mainly on damselfish *Chromis chromis* in summer. Likewise, Savva *et al*. (2020) highlighted that *C. chromis* was one of the most frequent prey items (F = 27.16%) of *P. miles* in Cyprus. Similar results were reported in another study conducted in Cyprus (Agostino *et al*., 2020). In Rhodes, *C. chromis* was identified as one of the primary fish species consumed by *P. miles* (Zannaki *et al.*, 2019). Since this species is the most abundant fish in rocky areas of the Mediterranean, it has a key role in transferring carbon, nitrogen, and phosphorus directly from the pelagic system to the littoral, while also serving as an important predator of zooplankton and prey item of larger fishes and seabirds (Pinnegar, 2018). In line with this assumption –and based on the findings related to the predation of *P. miles*– the decline in this species' population may also be attributed to the devil firefish invasion. Nevertheless, feeding pressure from *P. miles* on this key species can show seasonal variations. For instance, our results highlighted that predation on the species reduced drastically in the winter season.

Moreover, in the present study, 12 of the species detected in the stomach of *P. miles* were also found in the diet of at least one of the other scorpaenids. For example, in the winter, *P. miles* placed relatively high pressure on Penaeidae, while in the summer, *S. notata* exhibited the highest level of predation on the latter. Nevertheless, *P. miles* not only compete for food with other scorpaenids but also feed on them (Table 2).

Seasonal variations in the diet of *S. scrofa* were observed in the present study. This species mainly preferred Mollusca in the summer, while Crustacea and Teleostei were common prey groups in the winter. Notably, this species demonstrated high predation on *O. vulgaris* in the summer. However, the level of predation was significantly lower in the winter. This may be related to the octopus' migration to shallow areas during the spring and summer months due to its reproductive cycle; thus, these areas also included small-sized octopus specimens during that period (Hernández-Garcia *et al*., 2002; Katsanevakis & Verriopoulos, 2004). The extant literature provides little information on the feeding biology of *S. scrofa*, and there are not many studies with which we can compare our findings. One available study performed in western Libya reported that the most important prey groups of *S. scrofa* were the bony fish and crustaceans, contributing by 48.02 and 44.19% respectively (Shahrani & Shakman, 2015). Similarly, Bradai & Bouain (1990) investigated the feeding habits of *S. scrofa* from the Gulf of Gabes, Tunisia, and reported that bony fish were the most abundant prey.

The present study noted that *S. notata* fed mainly on crustaceans and less commonly on fish. In particular, Penaeidae was represented with high %IRI values in the summer, while brachyuran crustaceans were preferred by a significant number of specimens in both seasons. Similarly, a previous study performed in the seagrass beds near Marseilles, France noted that this species mostly fed on Caridae (Harmelin-Vivien *et al.*, 1989). Another study notified that the main prey items observed in the stomachs of *S. notata* in the western Mediterranean were decapod crustaceans (e.g., *Pisidia longimana*, *Pilumnus hirtellus*, *Processa mediterranea*, and *Alpheus glaber)* (Morte *et al*., 2001). Additionally, Mokrane *et al*. (2015) reported very similar results for the Algerian coast, where the diet of *S. notata* mainly consisted of Brachyura and Natantia. Furthermore, the main prey groups of *S. notata* in the eastern Adriatic Sea were reported as Crustacea, Mollusca, Polychaeta, and Teleostei; among them, decapod crustaceans (e.g., of the genera *Alpheus*, *Galathea*, *Liocarcinus*, and *Pilumnus*) were dominant (Šantić *et al*., 2021).

Our study showed that like *S. notata*, the highest %F and %IRI values for *S. porcus* were found for crustaceans, followed by fish species. The same situation was reported in the SW Mediterranean (Algeria and Tunisia) (Rafrafi-Nouira *et al.*, 2016; Omri *et al*., 2019). It was reported that the diet composition of *S. porcus* showed variations depending on the season, size, and sex, as well as Palaemonidae, which was the most common prey group in the NE Atlantic (Compaire *et al*., 2018). Unlike findings from the Mediterranean Sea, this species also had relatively high predation with %IRI = 35 for one of the economically important species in the Black Sea: red mullet (*Mullus barbatus*) (Başçınar & Sağlam, 2009).

In the present study, the performed transportation and handling procedures, as well as storage conditions and time between collection and dissection, aimed to minimize any further digestion in the collected specimens. Thus, the relatively high vacuity index values found in other species when compared to *P. miles* in both seasons depict the true status of our specimens in their environment at the moment of capture. Studies conducted on the feeding of *S. porcus* in various regions of the Mediterranean have reported that the highest VI varied between 42 and 57% (Morte *et al*., 2001; Castriota *et al*., 2012; Rafrafi-Nouiraa *et al.*, 2016; Omri *et al.*, 2019), while that for *S. notata* varied between 41 and 69% (Morte *et al*., 2001; Castriota *et al*., 2012). Notably, these values are similar to our findings. It should also be noted that the sampling method can influence VI because fish may also regurgitate their stomach contents due to the stress experienced during fishing operations (e.g., bottom trawling) (Compaire *et al*., 2018). Moreover, our study indicated that the empty stomach ratio in *P. miles* was significantly higher in winter, and other scorpionfish species did not show significant seasonal differences. Similarly, Compaire *et al*. (2018) did not find significant seasonal variations in the VI of *S. porcus*, whereas Morte *et al.* (2001) noted significant differences in *S. porcus* and *S. notata*, with the maximum values for both species occurring in summer.

The current study also contributed to the enrichment of our knowledge on the distribution of some NISs in Türkiye through the recording of their northernmost and second records. For example, this study reports the northernmost record of the brachyuran crab *Gonioinfradens* *giardi*, which is found to constitute a significant part of the winter diet of *P. miles* in Türkiye. Based on the use of both morphological and molecular analyses, Galil *et al.* (2018) reported that the species previously reported as *Gonioinfradens paucidentata* in the Mediterranean was incorrectly identified, noting that *G. giardi* is the correct name of the species. *G. paucidentata* was first reported from Kaş, Türkiye in 2009 (Karhan & Yokeş, 2012). Additionally, the spider lobster *D. curvimana* was first detected in Turkish waters in the Gulf of Antalya, Levantine Sea in 2007 (Irmak & Öndes, 2019). In the current study, the single *D. curvimana* individual obtained from the stomach of the *S. scrofa* in the winter of 2021 constitutes the second record for Turkish waters. This species has also been reported in Rhodes and Cyprus in the eastern Mediterranean (Corsini-Foka & Pancucci-Papadopoulou, 2012; Chartosia *et al*., 2018). Furthermore, among the fish included in scorpionfish diets, there are some species rarely reported from Türkiye. For example, previous studies have reported the presence of the species *Bellottia apoda* (Gramitto *et al*., 2011) and *Odondebuenia balearica* (Stern *et al*., 2019) in the SE Mediterranean. Notably, 17% of the species identified in the present study are alien to the Mediterranean.

In conclusion, this study provides important information on the diets of four scorpaenids in the eastern Mediterranean. *P. miles*, an IAS, exhibited higher dietary diversity when compared to other species. Notably, it even exhibited predation on other scorpaenids. Concerning diet overlap, a total of 12 species –including some economically important species such as *Octopus vulgaris* and *Siganus luridus*– were observed to be consumed by *P. miles* and at least one of the other three scorpaenids studied here. Furthermore, it is thought that competition may exist between the three native species (especially *S. notata*) and *P. miles* in terms of predation on the Penaeidae family. In future studies in the region, more detailed evaluations can be conducted by examining the diets of other predators that inhabit the same habitat as these four species. Additionally, applying trophic models should enhance the analysis.

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