

Article

Trophic Ecology of the Devil Firefish *Pterois miles* in the Eastern Mediterranean: An Integrated Study Based on Stomach Content and Stable Isotope Analyses

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Abstract

The trophic ecology of *Pterois miles* in the Mediterranean Sea was performed by integrating data from stomach contents (SCA) and stable isotopes analyses (SIA), based on samples caught off the Greek island of Rhodes, SE, Aegean Sea, for the first time. This combined approach provides information on ingested (SCA) and assimilated (SIA) food and thus allows for the depiction of predator–prey relationships. Specimens of devil firefish, including both juveniles and adults (total length of analyzed specimens spanned from 11.40 to 31.50 cm), were collected from different sites around Rhodes. Their diet consisted of bony fish, cephalopods, crustaceans, and gastropods. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values ranged from -18.0‰ to -14.4‰ and from 7.2‰ to 9.2‰ , respectively. SIA data allowed for the estimation of the trophic position of devil firefish from Rhodes Island, which showed a mean value of 3.1 ± 0.6 and confirms that the species primarily relies on a benthic baseline. Further, our isotopic values approach those obtained in North Carolina and Bermuda, confirming its role as a mesopredator in the Mediterranean benthic food webs. Although preliminary, such results can provide an important baseline for future investigations on the species and the potential impact on the Mediterranean food webs.

Keywords: biological invasions; *Pterois miles*; Bayesian mixing models; diet; Aegean Sea

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1. Introduction

Within an invaded area, alien species are considered one of the major threats to global biodiversity, having the potential to directly consume or outcompete native species, alter habitats, and affect ecosystem structure and function [1–4]. Many alien species that were introduced into the Eastern Mediterranean Sea through the Suez Canal are thermophilic [5]. The devil firefish *Pterois miles* (Bennett, 1828) was first recorded in 1991 off

the Israeli coasts [6], and two decades later it rapidly invaded the Eastern Mediterranean and spread as far as Tunisia and southern Italy (Sicily) in the central Mediterranean [7–12]. Currently, in the Southern Aegean waters, *P. miles*, the species, was frequently found in fishing nets, and sightings in shallow waters exponentially increased [13].

The biological and ecological traits of *P. miles* in the Mediterranean Sea are the focus of an increasing scientific interest ranging from surveys to field and laboratory experiments on population structure [14–16], local knowledge and awareness [17,18], distribution [7], and distribution modeling [11,19]. Among these traits, information on the trophic habits of this species is of relevance to ecological impact quantification and management support. Preliminary data suggested that the devil firefish in the new Mediterranean environment maintain the feeding habits consistent with those documented in their native range and in their established populations in the western Atlantic [20,21].

Outside the Mediterranean, the diet of the invasive *P. miles* and its congeneric *Pterois volitans* (Linnaeus, 1758) has been studied mainly in the invaded temperate and tropical western Atlantic. The stomach content analysis (SCA) suggested a generalist carnivorous diet [22]. Moreover, stable isotope analyses (SIA) were used to investigate the diet of the congeneric invasive *P. volitans* in the Southeast US Atlantic Ocean [23], the Colombian Caribbean regions [24], and the Bahamas [25,26]. The results offered additional information on its trophic status [27], corroborating the feeding behavior of a generalist carnivore, with a preference for bony fish [23].

The use of both conventional dietary analysis and SIA methods allows having a comprehensive view of a species' diet. While SCA provides only a short-term picture of the diet in a precise moment [28], SIA gives integrated information over a long period of time. Further, a main drawback of the SCA is that the recovered prey items are often partially digested and therefore difficult to identify, whereas high frequencies of empty stomachs may necessitate large sample sizes [29]. Such methodological issues can be potentially resolved by using SIA [30]. Numerous studies demonstrate how effective SIA has been applied to disentangling the food web structure in an environment and in providing information on assumed food vs. ingested, as for SCA [23,26,27,31].

The estimation of trophic position (TP) can also be measured by SIA and simulate the capture of complex trophic interactions through the reticulate pathways of ecological communities [32], therefore contributing to food-chain theory [33]. SIA has been used to assess the effects of biological invasion on the native food web structure [34], also in the Mediterranean Sea [31,35], and to estimate the trophic position of a species with difficulties in diet quantification [36].

Information on the biology and ecology of non-indigenous species is required to interpret the mechanisms by which introduced species become established and invasive [37]. Discovering strategies of such invasions comprises a crucial step for mitigating their impacts [37]. In this context, the main aim of this study was to provide new information on the trophic habits of *P. miles* in the Eastern Mediterranean basin based on both stomach contents (ingested food) and SIA (assimilated food), and to provide preliminary data on the structure of the predator–prey relationship.

2. Materials and Methods

A total of 26 individuals of *P. miles* were collected from five different locations along the coasts of Rhodes Island, Greece (Figure 1).

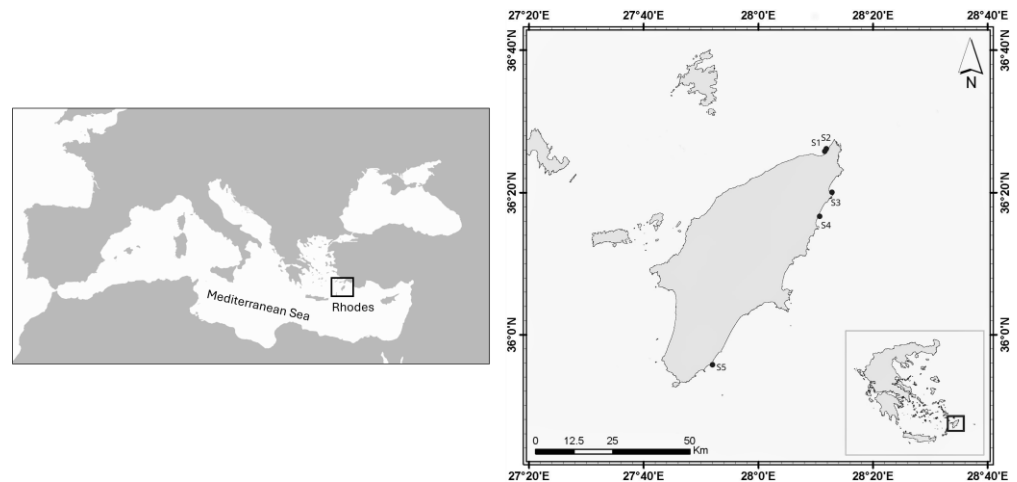


Figure 1. Map of sampling sites around the island of Rhodes in Greece. The five sampling sites are depicted with black dots (S1: Kritika; S2: Kritika; S3: Faliraki; S4: Afandou; S5: Plimmiri).

Specimens were captured by seining and static fishing nets used by local registered fishing vessels, at 2–50 m of depth from October 2019 to January 2020. All individuals were stored in the freezer ($-20\text{ }^{\circ}\text{C}$) till further analysis. For the identification of *P. miles*, the method outlined by [38] was followed. In brief, the following parameters were determined for each individual: total (TL) and standard (SL) lengths with an electronic vernier (accuracy $\pm 0.01\text{ cm}$), sex (unsexed, females, and males), total wet weight (TW), and net weight (NW) after devil firefish internal organ removal (accuracy $\pm 0.01\text{ g}$).

Each stomach, including its contents (SW), and the net stomach weight (NSW) after emptying the contents into a Petri dish, were determined with an accuracy of $\pm 0.01\text{ g}$. Based on [39], the difference between SW and NSW provides the food weight (FW): $\text{FW (g)} = \text{SW (g)} - \text{NSW (g)}$. The fullness index (FI) was expressed as a percentage of the ratio of the total fish weight (W) and ingested food weight (FW): $\text{FI} = \text{FW}/\text{W} \times 100$ [40]. The feeding intensity of devil firefish was determined by the vacuity index (VI) expressed as $\text{VI} = \text{total number of empty stomachs observed}/\text{total number of the stomachs examined} \times 100$ [41].

The contents of the gastrointestinal tracts were preserved in 70% ethanol. Prey items were identified to the lowest taxonomic level possible using a Leica S6D stereoscope, following the methods of [42,43]. When prey items were highly digested, and thus unidentified (in the case of fishes), the presence of otoliths permitted the assignment of unidentified remains to a fish species, according to the AFORO database (Anàlisi de Formes d’Otolòlits) database (i.e., <http://aforo.cmima.csic.es/>, accessed on 10 March 2020; [44]).

Prey items found in the stomach content were counted, measured, and weighed with an accuracy of $\pm 0.01\text{ cm}$ and $\pm 0.01\text{ g}$, respectively. The frequency of occurrence (% F) of the various prey items found in one or more gastrointestinal tracts (F) is expressed as a percent of the total number of devil firefish stomachs used for the diet analysis [29]. Additionally, the percentage of numerical abundance (% N) (i.e., percentage of prey in relation to the total number of prey items counted in all the stomachs containing food), the percentage of gravimetric composition (% W) (i.e., percentage of the prey weight in relation to the total weight of prey items counted in all the stomachs containing food) were calculated, and the index of relative importance (IRI) was determined as $\text{IRI} = (\% \text{ N} + \% \text{ W}) \times \% \text{ F}$.

For SIA, a portion of white muscle close to the dorsal fin from each specimen was extracted and oven-dried at $60\text{ }^{\circ}\text{C}$ for 24–48 h and then stored in the freezer at $-20\text{ }^{\circ}\text{C}$ until further processing. Subsequently, the defrosted samples were ground into a homogenous fine powder using an agate mortar and pestle. Approximately 1 mg was weighed with a

Mettler Toledo balance (accuracy to 0.001 mg) and put into tin capsules. The same process was followed by all identified prey taxa from the SCA. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in the samples were determined using a Delta V Plus Isotope Ratio Mass Spectrometer (Thermo Fisher Scientific Inc., USA), coupled in a continuous flow to a Thermo Flash EA 1112 elemental analyser (Thermo Fisher Scientific Inc., USA), for the determination of total carbon and nitrogen at the Laboratory of Stable Isotope Ecology of the University of Palermo (Italy).

Stable isotope ratio was expressed, in relation to reference international standards (atmospheric N_2 and Vienna PeeDee Belemnite for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively), as

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}}) \times 1000$$

where R is the $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$, respectively. Analytical precision based on standard deviations of internal standards (International Atomic Energy Agency IAEA-CH-6; IAEA-NO-3; IAEA-N-2) ranged from 0.10 to 0.19‰ for $\delta^{13}\text{C}$ and 0.02 to 0.08‰ for $\delta^{15}\text{N}$. Since lipids were not extracted from the samples prior to SIA, a relationship was used between C/N ratios and $\delta^{13}\text{C}$ ratios to evaluate the effect of lipids on the isotopic value. The bulk $\delta^{13}\text{C}$ values were normalized for lipid concentration according to the model proposed by [32] when C/N was >3.0 . The $\delta^{13}\text{C}$ lipid-free values obtained were compared afterwards with the $\delta^{13}\text{C}$ bulk with a paired t-test. Correlation analysis was then performed between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ vs. the total length of the fish to assess if any changes in the isotopic signatures with size occur. The differences in terms of the isotopic values between sexes were determined by one-way ANOVA with post hoc Tukey HSD test in R.

A dual Bayesian approach that included a stable isotope mixing model was used for the calculation of the trophic position (TP) of the devil firefish. Specifically, the package `tRophicPosition` in R (version 0.7.7.) was used for the estimation of TP for *P. miles* based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The model applies Markov Chain Monte Carlo Simulations for stable isotope data to estimate TP [45]. The full baseline model that incorporates the factor α [32] was selected, and the stomach content findings were used as baseline organisms. For the pelagic baseline, the isotopic values of *Apogon* sp., *Spicara smaris*, *Chromis chromis*, *Serranus hepatus*, and those from an unidentified pelagic Actinopterygii were selected to represent the pelagic resource. The benthic resources represented the second baseline, and these included *Gobius* sp., *Scorpaena* sp., the gastropod *Turritella* sp., the isopod *Nerocila orbignyi*, and the cephalopod *Sepia officinalis*. For the trophic enrichment factor (TEF) a standard values of $0.5\text{‰} \pm 0.85\text{‰}$ for $\delta^{13}\text{C}$ and $3.39\text{‰} \pm 0.98\text{‰}$ for $\delta^{15}\text{N}$ were applied from the inbuilt bibliography in `tRophicPosition` [32,45,46]. The Markov Chain Monte Carlo simulations were run through 20,000 iterations and a burn-in of 20,000 with four chains.

To discriminate between two distinct sources of C and N for pelagic vs. benthic, two equations were used:

$$\delta^{15}\text{N}_{\text{c}} = \Delta\text{N}(\text{TP} + \lambda) + \alpha (\delta^{15}\text{N}_{\text{b1}} + \delta^{15}\text{N}_{\text{b2}}) - \delta^{15}\text{N}_{\text{b2}} \quad (1)$$

$$\delta^{13}\text{C}_{\text{c}} = \delta^{13}\text{C}_{\text{b1}} + \delta^{13}\text{C}_{\text{b2}} (1 - \alpha) \quad (2)$$

where $\delta^{15}\text{N}_{\text{c}}$ is the nitrogen isotopic ratio of the predator (devil firefish), $\delta^{15}\text{N}_{\text{b1}}$ is the nitrogen isotopic ratio of the first baseline (pelagic), and $\delta^{15}\text{N}_{\text{b2}}$ is the nitrogen isotopic ratio of the second baseline (benthic). The trophic enrichment factor (TEF) is ΔN for nitrogen, TP is the trophic position of the *P. miles*, and λ is the trophic position of the baseline [47] for the first equation. Furthermore, for the second equation the model uses a secondary mixing model to calculate α , which accounts for the fraction in $\delta^{13}\text{C}$ and estimates the relative contribution of each source to the devil firefish trophic position, where additional variables $\delta^{15}\text{N}_{\text{b1}}$, $\delta^{13}\text{C}_{\text{b1}}$, $\delta^{15}\text{N}_{\text{b2}}$, and $\delta^{13}\text{C}_{\text{b2}}$ refer to the $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of baselines one and two, respectively, and α is the proportion of N derived from baseline one

[32,34,45]. The full model is based on Equation (1); however, α includes the trophic discrimination factor (TDF) for carbon based on Equation (3):

$$a = (((\delta^{13}\text{C}_{\text{b2}} - (\delta^{13}\text{C}_{\text{c}} + \Delta\text{C})))/((\delta^{13}\text{C}_{\text{b2}} + \delta^{13}\text{C}_{\text{b1}}))) \quad (3)$$

where the additional variables $\delta^{13}\text{C}_{\text{c}}$ is the $\delta^{13}\text{C}$ value of the devil firefish, and ΔC is the TDF for C [45] modified from [32]. The Bayesian approach allows the equations, which both include TP and α , to be solved iteratively, with $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and TEFs for predators and baselines modeled as random variables with vague prior normal distributions of their means [dnorm(0, τ), $\tau = 1 \times \text{SD}2(-1)$] and vague prior uniform distributions of their standard deviations [dunif(1,100)]. The C and N observations of *P. miles*, baselines, and TDFs are randomly modeled variables, and TP and α are also treated as random parameters [45].

Based on [48], the selection for the most appropriate TEFs for the predator (devil firefish) was simulated by a Monte Carlo simulation of stable isotope mixing polygons, with 1000 iterations for the Stable Isotope Mixing Model. Furthermore, any samples that fall within the polygon in <5% of iterations should be excluded from the mixing model [48].

Finally, the R package 0.5.1.217. *simmr* [49] was used to correlate the dietary proportions of devil firefish samples with various food resources, as elucidated by the qualitative SCA, using the estimated stable isotope values from the species tissue samples. Calculation included the dual stable-isotope data ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the tissues of *P. miles* specimens and the sources (*Gobius* sp., *Turritella* sp., *Sepia officinalis*, and *Spicara smaris*). For TEF measurements, the $\Delta^{13}\text{C} = 0.01\text{‰} \pm 1.01$ and $\Delta^{15}\text{N} = 3.4\text{‰} \pm 0.99$ were calculated based on the available bibliography [32,45,46].

3. Results

Out of the 26 specimens of *P. miles*, 7 were females, 11 males, and 8 juveniles. The total length varied from 11.40 cm to 31.50 cm (mean \pm SD: 22.38 \pm 6.38 cm), and the total weight ranged from 9.3 g to 625.4 g (mean \pm SD: 191.2 g \pm 154.99 g).

The fullness index (FI) for the total number of *P. miles* was 1.29%, and the vacuity index (VI) was 46.15%. According to IRI, the three most important fish families in the devil firefish diet were Gobiidae, Centracanthidae, and Pomacentridae. A high proportion of empty stomachs was observed (12 stomachs, 46%).

The majority of the 36 individual prey items were bony fish (26 items, 72%) (Table 1).

Table 1. List of the taxa identified in *Pterois miles* stomach contents, in terms of % N, % W, % F, and % IRI.

Taxon	% W	% F	% N	% IRI
Unidentified fish	2.6	7.0	6.9	10.5
<i>Apogon</i> sp.	0.7	2.8	1.4	0.5
<i>Atherina boyeri</i>	3.3	2.8	1.4	1.0
<i>Spicara smaris</i>	16.1	4.2	6.9	10.2
<i>Gobius niger</i>	14.2	4.2	2.8	7.5
<i>Gobius</i> sp.	2.4	1.4	2.8	2.3
Gobiidae unid	1.9	1.4	5.6	5.8
<i>Chromis chromis</i>	2.8	1.4	2.8	6.1
<i>Scorpaena scrofa</i>	3.1	1.4	1.4	1.0
<i>Scorpaena porcus</i>	0.8	1.4	1.4	0.5
<i>Serranus hepatus</i>	0.5	7.0	1.4	0.4
Triglidae unid.	0.0	2.8	1.4	0.6
Total fish	48.5	38.0	36.1	46.6
<i>Sepia officinalis</i>	0.2	1.4	1.4	0.3

<i>Turritella</i> sp.	0.2	1.4	6.9	1.6
Unidentified crustaceans	0.1	1.4	1.4	0.3
<i>Alpheus</i> sp.	0.3	1.4	1.4	0.4
<i>Nerocila orbignyi</i>	0.0	1.4	1.4	0.3
<i>Thalamita poissonii</i>	0.8	1.4	1.4	0.5
Total invertebrates	1.5	8.5	13.9	3.4

For Actinopterygii, the Gobiidae family contributed the most by number and by weight (% N = 22.2, % W = 37.0); the rest of the Actinopterygii families had 33.3% N and 22.5% W. Other prey items included mollusks (six items, 17% N) and crustaceans (three items, 11% N) (Table 1). Devil firefish of different sizes fed on a wide range of prey sizes (Figure 2).

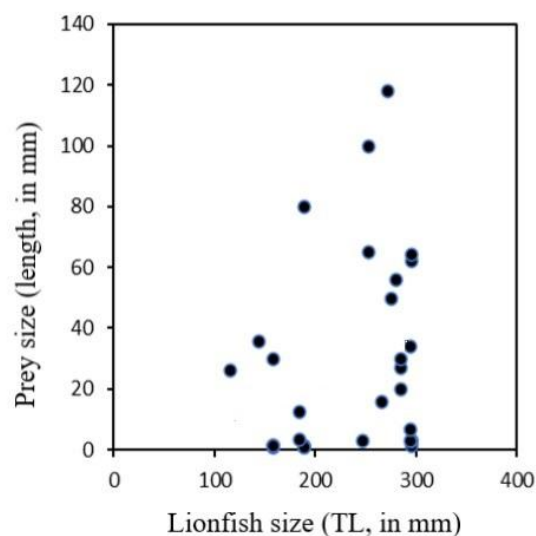


Figure 2. Prey size in respective length of the consumers (*Pterois miles*) from Rhodes Island, Greece.

Otolith identification allowed the classification of *Serranus hepatus* and *Gobius niger* as prey.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the total devil firefish samples varied from -18.0‰ to -14.4‰ and from 7.2‰ to 9.2‰ , respectively. For juveniles, the isotopic value of $\delta^{13}\text{C}$ ranged from -16.4‰ to -14.4‰ and for $\delta^{15}\text{N}$ from 7.2‰ to 9.2‰ . Female devil firefish isotopic values $\delta^{13}\text{C}$ varied from -18.3‰ to -15.8‰ , and for $\delta^{15}\text{N}$ from 7.9‰ to 8.4‰ . For male specimens, the $\delta^{13}\text{C}$ isotopic values had a range from -17.6‰ to -15.8‰ , and for $\delta^{15}\text{N}$ from 7.8‰ to 8.7‰ . The correlation analysis showed a significant increase of $\delta^{15}\text{N}$ with increasing size TL (Pearson $R = 0.44$, $p < 0.001$), while $\delta^{13}\text{C}$ significantly decreased with increasing TL ($R = -0.43$, $p < 0.001$) (Figure 3).

The $\delta^{13}\text{C}$ values revealed a significant difference between the unsexed *vs.* the females and males (ANOVA test, $p < 0.05$). However, the $\delta^{13}\text{C}$ value did not show a significant difference between males and females ($p > 0.05$). For the $\delta^{15}\text{N}$, no significant differences were detected between sexes. Prey taxa $\delta^{13}\text{C}$ values ranged from -18.8‰ (*Gobius* sp.) to -12.8‰ (*Turritella* sp.). Prey taxa $\delta^{15}\text{N}$ varied from 4.7‰ (*Gobius* sp.) to 7.7‰ (*G. niger*). The Actinopterygii class tended to have higher $\delta^{15}\text{N}$ values than crustaceans and mollusks.

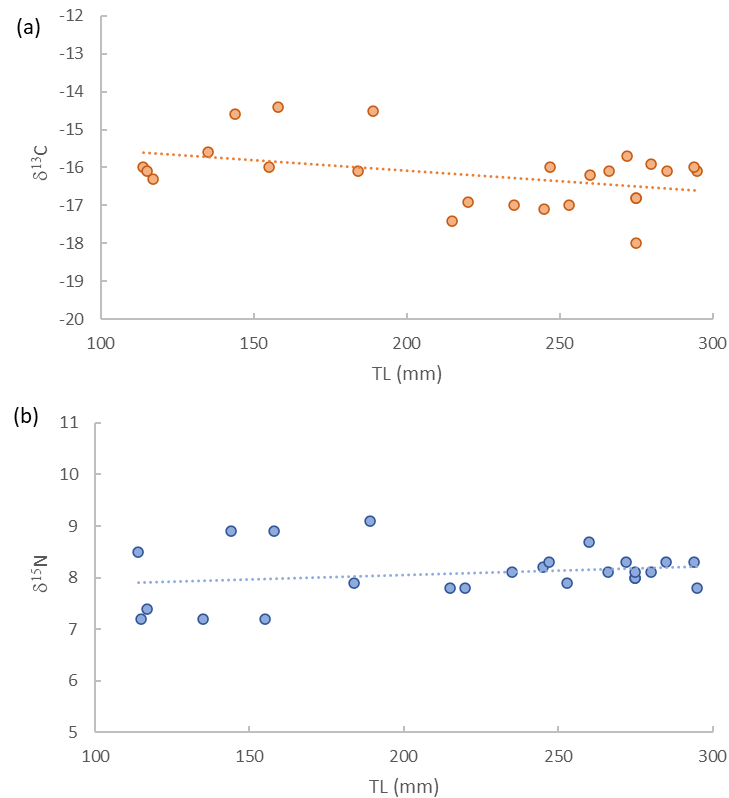
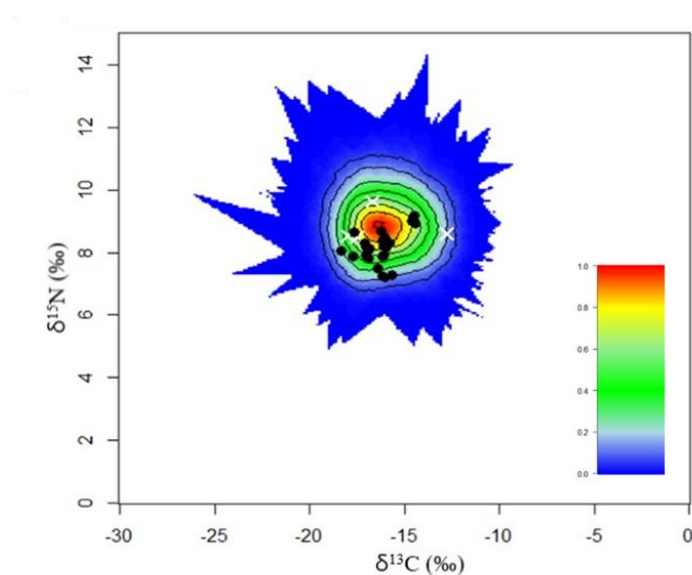
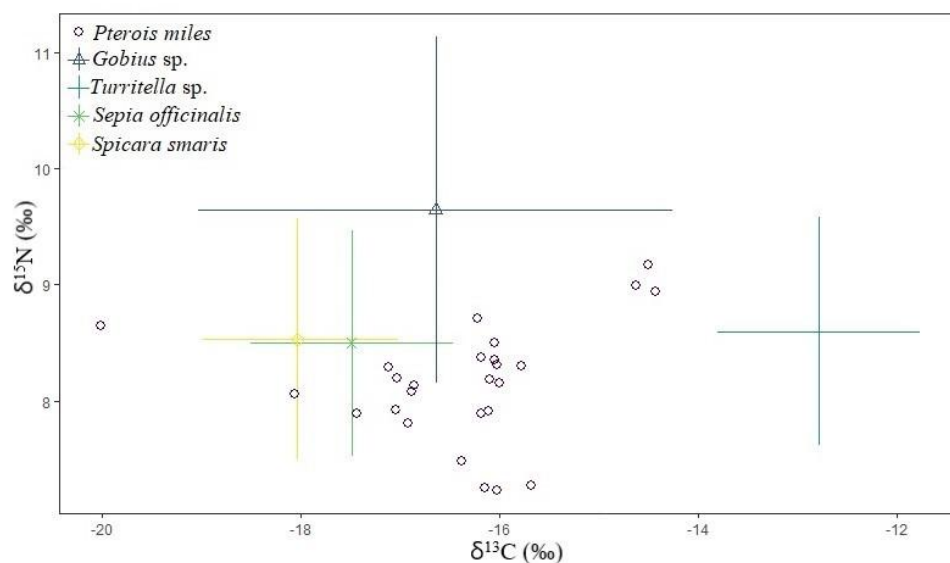


Figure 3. Isotopic values $\delta^{15}\text{N}$ (a) and $\delta^{13}\text{C}$ (b) vs. total length (TL) for *Pterois miles*.

According to the mixing polygon (Figure 4a), all the specimens were within the 95% mixing region (the outermost contour). Conversely, the lowest $\delta^{13}\text{C}$ isotopic value (-18.3‰) belonged to a female devil firefish (TL = 275 mm and TW = 269 g), whereas the highest $\delta^{13}\text{C}$ value (-14.4‰) belonged to an unsexed devil firefish (TL = 158 mm and TW = 33.61 g). For the $\delta^{15}\text{N}$ isotopic value, the lowest (7.2‰) belonged to an unsexed devil firefish (TL = 155 mm and TW = 32.7 g). The highest $\delta^{15}\text{N}$ value (9.2‰) was also detected on an unsexed devil firefish (TL = 189 mm and TW = 73.9 g). The *simmr* confirmed *P. miles* relies mostly on teleosts rather than invertebrates (Figure 4b).



(a)



(b)

Figure 4. (a) The simulated mixing region for the biplot shown in (b), the positions of the devil firefish (black dots) and the average source signatures (white crosses) are shown. Black dots represent individual predator values, and white crosses indicate mean source signatures. (b) A biplot of stable isotopic signatures for the predator *Pterois miles* and resources (*Gobius sp.*, *Sepia officinalis*, *Turritella sp.*, *Spicara smaris*). This biplot was created using the Bayesian mixing model *simmr*. Error bars represent 95% confidence intervals and incorporate errors in the source isotopic signatures and in trophic enrichment factors.

Devil firefish occupied an extended position in the marine food web (Figure 5). Additionally, it is 2.1‰ above the benthic resource and 2.6‰ above the pelagic ones in terms of $\delta^{15}\text{N}$. The results from the two-baseline full model revealed a mean TP of 3.1, with a minimum of 2.6 and a maximum of 3.8. An alpha value of 0.06 occurred for the full baseline model, which means that each baseline provides 6% of the energy inputs to the *P. miles*.

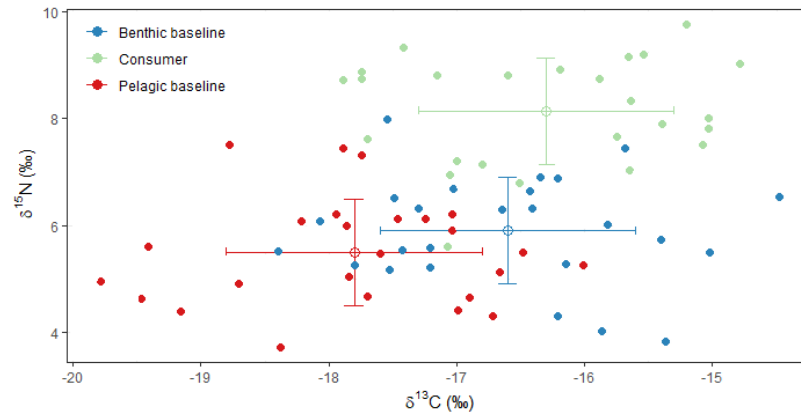


Figure 5. Trophic position of devil firefish (consumer) vs. the benthic and pelagic baselines.

4. Discussion

The current study offers an insight into the feeding ecology and the trophic position for the Lessepsian invader *P. miles* in the Eastern Mediterranean, based on stable isotope analysis integrated with stomach content data. Although few specimens were analyzed for stomach contents, most of the *P. miles* were found to feed on fish, followed by mollusks and crustaceans, as observed in [21,50]. On the contrary, the number of specimens analyzed for SIA fully adhered to the work carried out by [35]. The isotopic composition of *P. miles*, with a mean $\delta^{13}\text{C}$ of -16.3‰ and a mean $\delta^{15}\text{N}$ of 8.1‰ , notwithstanding differences due to spatial variations (i.e., depth, longitude, latitude), was consistent with the isotopic values obtained for *Pterois* spp. in North Carolina [23] and Bermuda [51]. A natural geospatial tag potentially can be provided by stable-isotope ratios for fish migration [52] and invasion into new marine environments. Additionally, these values overlap for piscivore (-16.3‰ to -17.6‰) and opportunistic generalist fishes (-15.8‰ to -18.0‰) [53], providing additional support that lionfish are generalist predators [23].

Ontogenetic shifts in devil firefish diet were confirmed by the significant increase of $\delta^{15}\text{N}$ vs. total length, while $\delta^{13}\text{C}$ significantly decreased with increasing size. High site fidelity has been recorded in small *Pterois* spp. [54], while larger individuals are able to migrate from their shelter to surrounding habitats [55]. This could suggest that larger-sized specimens fed mainly on higher trophic level species (i.e., medium-sized fish or large crustaceans), while the smaller-sized specimens possibly prey on a lower trophic level, such as foraging fishes. Additionally, the TP of devil firefish from this study is consistent with findings from other areas (i.e., Bermuda [22,51]).

Lionfish are considered opportunistic generalist carnivores with a broad dietary niche that includes fish and invertebrates in the western Atlantic [22,56]. This can also be highlighted by similar studies using SIA, providing additional support that lionfish indeed act as a generalist predator [22,23,51,57].

Additional studies conducted in the Eastern Mediterranean have shown that in Cyprus, *P. miles* consume a range of teleost and crustacean prey, including *S. smaris* and *Sparisoma cretense* [58]. These are highly economically valuable fish and may be substantially impacted by the feeding habits of *P. miles* [58]. Moreover, observations from other areas of the Mediterranean—such as the Ionian and the southern Adriatic—indicate that local fishers frequently report declines in small coastal fish that overlap with lionfish diet preferences (authors' unpubl. data). Although these trends may also be influenced by additional stressors (e.g., overfishing, habitat degradation, climate-driven changes), the expanding diet of *P. miles* suggests a potential cumulative impact on a wider suite of commercially important species, including small pelagics, juvenile sparids, and labrids. Such predation pressure could reduce the abundance of key target species at local scales,

potentially altering catch composition and affecting artisanal fisheries that rely heavily on nearshore fish communities. Further research is therefore needed to quantify predation rates, assess spatial variability in impacts, and understand how lionfish expansion may interact with other anthropogenic drivers to influence regional fishery yields. This agrees with the lionfish behavior observed in the Bahamas, where a reduction of 79% towards the native fish caused by the broad diet of this invasive predator was observed [59]. In Cyprus, the main target of the species is the damselfish *C. chromis*, which acts as a foraging fish for the native (e.g., *Thalassoma pavo* and *Apogon imberbis*) and non-indigenous mesopredators (e.g., *Parupeneus forsskali*) [20,58]. Off the coast of Turkey, devil firefish prey on *Mullus surmuletus*, another economically important species [15]. Outside of the Mediterranean Sea, lionfish (*P. miles* and *P. volitans*) fed mainly on Gobiidae, Pomacentridae, Mullidae, Labridae, amongst other teleost families [60], while in Bermuda, both crustaceans and teleosts make a substantial contribution to the lionfish diet than elsewhere in the world [57]. The SCA described in the present work was comparable to the feeding habits observed both within their native and invaded ranges (see [21]). Indigenous fish in the Eastern Mediterranean will have to compete with the invasive *P. miles* for prey items, such as Gobiidae and Pomacentridae, and the dusky grouper *Epinephelus marginatus* will have to compete with the devil firefish as both predators share the same resources [58,61].

This study reveals clear ecological patterns in the trophic behavior of the devil firefish in the Eastern Mediterranean, including an ontogenetic dietary shift that reflects changes in habitat use and predatory impact across life stages. These findings provide important insights into how this invasive predator integrates into local food webs and the potential pressures it may exert on native communities. The trophic baseline generated here offers a valuable foundation for future research aimed at assessing long-term ecological impacts and informing management strategies in the region.

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