

Article

The Devil Firefish *Pterois miles* (Bennett, 1828): Life History Traits of a Potential Fishing Resource in Rhodes (Eastern Mediterranean)

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Abstract: The devil firefish *Pterois miles* (Bennett 1828) is recognized as one of the 100 worst invasive alien species (IAS) in the Mediterranean Sea with significant socioeconomic and ecological implications. A total of 363 individuals were collected between April 2021 and March 2022 from the Levantine Sea (the Eastern Mediterranean), aiming to assess the current progression of the population. The male to female ratio (1:1.03) did not significantly depart from 1:1, with length–weight relationships exhibiting positive allometric growth. Five age groups were identified, with the third and fourth age groups being the predominant (74% of the population). The highest reproductive intensity was observed during summer followed by autumn. The onset of sexual maturity (L_{50}) for the total population was estimated at 22.44 cm in total length (2.1 years). The asymptotic length was estimated at 45.35 cm for the total population, with males growing larger than females. Longevity was estimated at 14.4 years for the total population. The inflection point was estimated at 4.31 years for the total population. Length with a 50% probability of capture (LC_{50}) was estimated at 23.03 cm, with the respective age (t_{50}) of 2.2 years. The exploitation rate ($E = 0.48$) indicated that the population is underexploited. The optimum (F_{opt}) and target (F_{lim}) fishing mortality were higher in comparison with the present fishing mortality ($F = 0.41$), indicating a potential for commercial exploitation of the species.

Keywords: invasive species; Levantine Sea; mortality; von Bertalanffy; Southern Aegean Sea



Citation: Kondylatos, G.; Theocharis, A.; Mandalakis, M.; Avgoustinaki, M.; Karagyaurova, T.; Koulocheri, Z.; Vardali, S.; Klaoudatos, D. The Devil Firefish *Pterois miles* (Bennett, 1828): Life History Traits of a Potential Fishing Resource in Rhodes (Eastern Mediterranean). *Hydrobiology* **2024**, *3*, 31–50. <https://doi.org/10.3390/hydrobiology3010003>

Academic Editor: Gioele Capillo

Received: 30 January 2024

Revised: 23 February 2024

Accepted: 26 February 2024

Published: 28 February 2024



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1. Introduction

Eastern Mediterranean coastal ecosystems are subjected to ongoing shifts in species abundance and community composition [1–5]. To date, in the Mediterranean Sea, almost 1000 non-indigenous taxa have been identified as established and casual [6,7], with fishes occupying the second highest diversity among them. Their numbers continue to rise, presenting increased establishment success [7–9]. The Suez Canal is the most significant entry and ever since the opening in 1869, this human-made passageway has allowed hundreds of species from the Red Sea to cross into the Mediterranean [6,10,11]. A considerable number of these species are migrating westward and establish sizable, reproduceable populations in the eastern Mediterranean.

According to several studies, it is rather clear that the introduction of marine invasive alien species (IAS) to an ecosystem poses a serious threat to the biodiversity, structure and function [12–18]. *Caulerpa taxifolia* (M.Vahl) C.Agardh, 1817, first discovered in the basin in 1984 [19,20], and *Caulerpa cylindracea* Sonder, 1845, first documented in the Mediterranean

in 1990 [21], are two of the first invasive species that raised significant concerns about becoming major threats to the Mediterranean ecosystem. In the late 2010s, the two introduced invasive marine Indo-Pacific lionfishes, the devil firefish *Pterois miles* (Bennett 1828) and the red lionfish *Pterois volitans* (Linnaeus, 1758), were recognized as the first truly invasive marine fishes and a major ecosystemic threat [22,23].

Pterois miles is one of the most recent Lessepsian fish invaders in the Mediterranean Sea. Kletou et al. (2016) and Dimitriou et al. (2019) [24,25] verified the genetic similarity of the *P. miles* populations in the Mediterranean Sea and a pattern of repeated introductions of the species in the basin into the Mediterranean originating from the northern Red Sea. It is an Indian Ocean species with a natural geographic range that includes the marine area spreading from the Red Sea to eastern South Africa, the Arabian Sea and the Persian Gulf, the Gulf of Oman, the Laccadive Sea, the Bay of Bengal, the Andaman Sea and Indonesia [26,27]. Although it was firstly recorded in the Mediterranean Sea in 1991, off the coast of Israel [28], several years passed after the second record, when two individuals were discovered in 2012 off the coast of Lebanon, breaking a 20-year silence [29]. Shortly after, in 2014 and 2015, two individuals were discovered in Turkish and Cyprian coastal waters, respectively, whereas in Rhodian waters, Greece, it was first recorded on 15th July 2015 [24,30–33]. Many more records followed and 31 years after its first record, *P. miles* is known to be present in Israel, Cyprus, Greece, Italy, Lebanon, Libya, Tunisia and Turkey [22,29–38]. The species demonstrates one of the most rapid invasions and expansions in the basin [5,39]. It has developed large populations in the eastern basin but it is not enough clear which invasion stage the species attains in each Mediterranean subregion [40,41], or whether the numbers of the species are peaking or levelling off or decrease, as in the case of the lionfish invasion in the western Atlantic [42].

The devil firefish can be encountered in a wide range of depths [43–45] and is found mainly associated with hard substrates, hiding in cavities of, crevices or caves but also on Neptune grass *Posidonia oceanica* (Linnaeus) Delile, 1813 beds [46]. Given the fact that other invasive species such as the porcupine sea urchin *Diadema setosum* Leske, 1778) and indigenous species such as the common spiny lobster *Palinurus elephas* (Fabricius, 1787) share the same refuges, non-consumptive effects of these species with *P. miles* may occur [47]. Of the most commonly applied fishing gear of the coastal small-scale fisheries of Greece, the most promising for the collection of *P. miles* are the static nets [48]. Nevertheless, in the western Atlantic, Morris (2012) [49] and Farquhar (2017) [50] reviewed that the most popular removal method was spearing followed by handnets, reflecting the differentiation between geographic regions in the use of the most appropriate fishing gear targeting lionfishes.

A number of characteristics, including early maturation and reproduction, anti-predatory venomous defenses, and ecological adaptability of the devil firefish, combined with the absence of adaptive responses on behalf of the prey that encounters a new predator and the overfishing of regional predators, contribute to the spectacular success of its establishment in the invaded areas [51–57]. Undoubtedly, the species is a unique opportunistic predator and a generalist carnivore that may consume a wide range of fish and crustaceans, in consumption rates that can substantially surpass the rates of prey production [17,49,53,58–62]. On the other hand, rather few predators of the devil firefish have been recorded within the Mediterranean Sea. These include the dusky grouper *Epinephelus marginatus*, the white grouper *Epinephelus aeneus*, the common octopus *Octopus vulgaris* and the silver-checked toad fish *Lagocephalus sceleratus* [37,63,64] with the first three under fishing or preying pressure [65–67]. For the time being, the water temperature seems to be the only effective constraint in the ongoing dispersal of *P. miles* within the basin [38,68,69]. In fact, the minimum temperature the species can survive in is 10 °C [56,68,70], whereas Dimitriadis et al. (2020) [38] plotted on a map the possible expansion region of the species within the Mediterranean, based on the isotherm of 15.3 °C, which is also the distribution limit for *P. volitans* in North Carolina, USA [69].

Throughout the literature, it is clear enough that the eradication of the species from the invaded areas is unlikely [22,41,58,71,72]. Additionally, there are many suggestions

for the population control of the devil firefish in the invaded areas of the Atlantic and the Mediterranean [4,41,49,56,73–80]. However, managerial tactics, if any applied, aiming at minimizing the negative effect and the population control of *P. miles*, can be viable but they do not always bring out the desired results [58,73,74,76,78]; and in several other cases, they proved discouraging for various reasons [12]. Irreversibly, *P. miles* has conquered many regions of the basin and unless retreated or overlapped by starvation, some pathogen or an efficient competitor [42,49,58,81], local communities depended on coastal fisheries will have to admit the species as a potential food source and income resource and practice targeted removals [17,48,49,73,78,79,82–84]. The idea of turning an invasive species to food source is not a modernism [83–85].

In the western Atlantic, culling is the most successful measure to control the lionfish culling [80,86,87]. For the Mediterranean, we believe that management actions towards minimizing negative effects to the ecosystem of *P. miles*, should focus in the development of a targeted lionfish fisheries [58], along with establishing it as a new product in the commerce of fresh and processed fish [56]. Tailored management removal efforts of *P. miles* will be improved by knowing and understanding life history information of the species within each of the invaded areas [55,57,88–91]. While several of the prominent traits of the species were documented in Cyprus [46], no research on the growth and mortality has been published in Greek waters. The objectives of this study were to investigate the population structure, sex ratio, growth, age composition, mortality, reproduction, and level of exploitation of this species, hence providing vital information that is currently lacking in a region affected by this Lessepsian invader. These data are essential for the development of strategic plans to control the invasive lionfish population and specifically in the estimation of the sustainability of this new fisheries resource.

2. Materials and Methods

2.1. Study Area and Sampling Methodology

Three areas of the eastern Rhodian coastal marine waters were selected (Figure 1). From April 2021 to March 2022, monthly experimental fishing trials were applied in each area, within the depth zone of 8–35 m. Two fishing vessels of the Rhodian small-scale coastal fleet were employed (total length of 13.3 m and engine power of 106.5 KW, and total length of 9.0 m and engine power of 7.35 KW, respectively). The fishing gear employed was gill nets (GNSs) and trammel nets (GTRs) as illustrated in Frid and Belmaker (2019) [92] and described analytically in a recent work [93], were applied as typically performed by local fishers of the island. The deployment of GNSs and GTRs was conducted in the early night hours. The former were retrieved two hours after deployment and the latter during sunrise. In total, 36 hauls were performed with each type of fishing gear.

Total length (TL) and total weight (TW) of the collected individuals were measured to the nearest 0.1 cm and 0.01 g, respectively. Rhodes has some qualities that make the surrounding marine waters highly suitable for the study of non-indigenous species (NIS), as reported previously [48]. The region is on the natural pathway of the dispersion of NIS entering the Mediterranean Sea via the Suez Canal and constitutes the main secondary pathway of their further westward or northward expansion. Furthermore, Rhodian coastal waters present a high abundance of *P. miles*.

2.2. Statistical Analysis

Data for statistical analysis were evaluated for normal distribution with the Shapiro–Wilk test for normality and homogeneity of variance by employing variance ratio and Levene’s tests. Welch’s test was employed for sex comparisons when data were normally distributed but violated the assumption of homogeneity of variance [94]. Mood’s median test was used for comparisons where data failed both assumptions of normality and homogeneity [95].



Figure 1. Map of the study area (red outline) and location of sampling areas (color-shaded areas).

The chi-square goodness-of-fit test [96] was employed to assess the null hypothesis of equal proportions between male and female ratio and compare our findings with published literature. Statistical analysis was performed with Jamovi (Ver. 2.4.6) [97], at an alpha level of 0.05. According to Munro and Pauly (1983) [98], the length–weight relationship was calculated separately for females, males, and combined sex by fitting the exponential curve to the data, where TL is the total length (cm), TW is the total weight (g), “a” (growth factor) is the intercept of the curve, and “b” is the slope (allometry coefficient) (Equation (1)). The standard Student *t*-test was employed to assess allometric relationships, isometry ($b = 3$) or allometry ($b \neq 3$). The two-samples *t*-test was used to compare the equations between the sexes.

$$TW = a \times TL^b \quad (1)$$

Length frequency distributions calculated per 1 mm size class were divided into age groups using Bhattacharya’s approach [99] to identify the mean of length for each cohort [100,101], with the use of the FiSAT II program (FAO, Rome, Italy) (version 1.2.2), as in a previous work [46].

A catch curve based on net selectivity was constructed by applying linear regression fitted to ascending line of input points generated from a plot of the capture probability against length group to calculate the length at first capture (L_c) (50% capture probability) and values of the lengths at 25% (L_{25}) and 75% (L_{75}) capture probabilities.

2.3. Growth

Growth parameters were calculated using the Von Bertalanffy (1938) [102] growth equation (Equation (2))

$$L_t = L_\infty \times \left(1 - e^{-k \times (t-t_0)}\right) \quad (2)$$

where k (growth coefficient) is the rate at which the asymptotic length, L_∞ , is approached, t is the age in years and t_0 is the hypothetical age at which the fish has zero length.

The index of growth (in length) performance [98] was derived using the von Bertalanffy parameters (Equation (3))

$$\varphi' = \log K + 2 \times \log L_\infty \quad (3)$$

The maximum lifespan was estimated according to Froese and Binohlan (2000) [103] (Equation (4)).

$$t_{\max} = \frac{2.9957}{k} + t_0 \quad (4)$$

The inflection point (time when growth rate starts to decrease) was estimated according to Ricker (1979) [104] (Equation (5)).

$$\text{Inflection point} = t_0 + \frac{\ln 3}{K} \quad (5)$$

2.4. Mortality and the Exploitation Rate

Natural mortality was calculated using the updated Hoenig_{nls} estimator according to Then et al. (2015) [105] (Equation (6)).

$$M = 4.899 \times t_{\max}^{-0.916} \quad (6)$$

Total mortality (Z) was calculated using Beverton and Holt's (2012) [106] empirical equation (Equation (7)).

$$Z = K \times (L_\infty - L_{\text{mean}}) / (L_{\text{mean}} - L') \quad (7)$$

where L_{mean} is the mean length of all fish in a sample representing a steady-state population and L' is the cut-off length or the lower limit of the smallest length class included in the computation.

The length-converted catch curve [107] was further employed to estimate the total mortality rate (Z).

The annual fishing mortality rate (F) was obtained by subtracting natural from total mortality according to Sparre and Venema (1998) [101] (Equation (8)).

$$F = Z - M \quad (8)$$

The exploitation rate (a measure of the number of fish that are caught from a population each year) was calculated as the ratio of fishing mortality to the total mortality [107] (Equation (9)).

$$E = F/Z \quad (9)$$

The length class with the highest biomass (L_{opt}) (optimum length) was calculated according to (Beverton, 1995) [108] (Equation (10)).

$$L_{\text{opt}} = \frac{3 \times L_{\text{inf}}}{3 + \frac{M}{K}} \quad (10)$$

2.5. Reproduction

The length at which 50% of individuals in a population have reached sexual maturity is known as the onset of sexual maturity (L_{50}). Sex and maturity stage were determined

macroscopically for each specimen. Fish were deemed mature if they had developing, ripe, or spent ovaries. Immature/resting fish, considered non-reproductive, were assigned a 0 while mature fish were assigned a value of 1. To model the link between fish length and the likelihood of sexual maturity, a binary logistic regression was fitted to the data [109]. The latter is a method used to model the relationship between one or more independent variables and a binary dependent variable, which is transformed using the logit transformation into a probability ranging from 0 to 1.

Each gonad was removed and was weighed after removal of excess water. The reproductive cycle was assessed seasonally with the use of the gonad-somatic index (GSI) calculated according to Ulman et al. (2021) [110] (Equation (11)).

By examining the seasonality of the gonadosomatic (GSI) (Equation (11)) for each sex, the spawning cycle of the species was analyzed in the study area.

$$\text{GSI (\%)} = \frac{\text{GW}}{\text{TW}} \times 100 \quad (11)$$

where GW is the gonad weight, LW is the liver weight and TW is the total weight.

The annual recruitment pulses and their relative strength were determined from a routine implemented in FiSAT II software using the time series length–frequency data and growth parameters (L_{inf} , K and t_0), which involves the backward projection of length frequencies onto time axis based on growth parameters [111].

Fulton's condition factor (K) was further employed as an estimate of body condition in fish (Equation (12)) according to Fulton (1904) [112].

$$K = 100 \times \frac{\text{Weight (in g)}}{\text{Length (in cm)}^3} \quad (12)$$

2.6. Relative Y/R and B/R Analysis: Knife-Edge Selection

The relative yield per recruit (Y'/R) was estimated using the knife-edge method of Beverton and Holt's model (1957) [113], by which the optimum exploitation rate (E_{opt}) and the maximum exploitation rate (E_{max}) were obtained. Further biological reference points including optimum length (L_{opt}), optimum fishing mortality (F_{opt}), fishing mortality limit (F_{lim}) and the optimum exploitation rate (E_{opt}) were estimated according to previous research [108,114,115].

3. Results

3.1. The Sex Ratio

A total of 363 individuals (184 females and 179 males) were caught with a M:F sex ratio of 1:1.03 in favor of females. The sex ratio did not significantly depart from 1:1 ($\chi^2 = 0.10$, $p > 0.05$), but a significant departure from reported male to female ratio of 0.649:1 [46] in the island Cyprus ($\chi^2 = 13.95$, $p < 0.001$) was identified.

3.2. Population Structure

Significantly greater total length (Welch's test $p < 0.001$) and weight (Mood's Median test, $p < 0.05$) were indicated for males.

The range of total length among sexes (Figure 2) was higher for males (37.8 mm) compared to females (34.3 mm), with a similar trend indicated for total weight (787.8 gr and 636.0 gr) for males and females, respectively (Figure 3).

3.3. Length–Weight Relationship

A highly significant positive allometry was indicated for the total and male population ($p < 0.001$) and a significant positive allometry was indicated for the female population ($p < 0.05$) (Figure 3). No significant difference was observed between the male and female length–weight relationship.

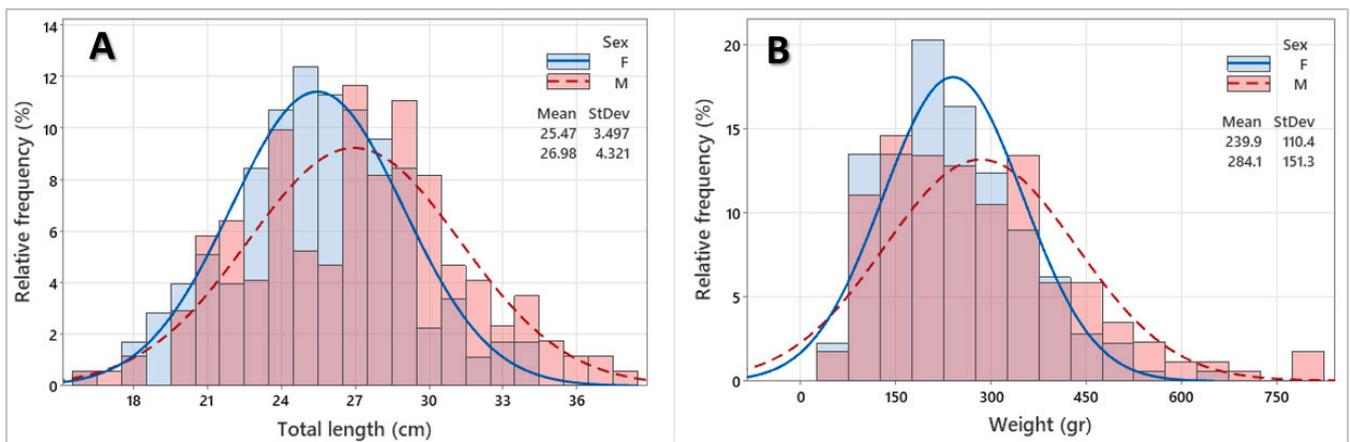


Figure 2. Total length–frequency (A) and weight–frequency (B) distribution of *P. miles* population with overlaid fitted normal distribution for both sexes.

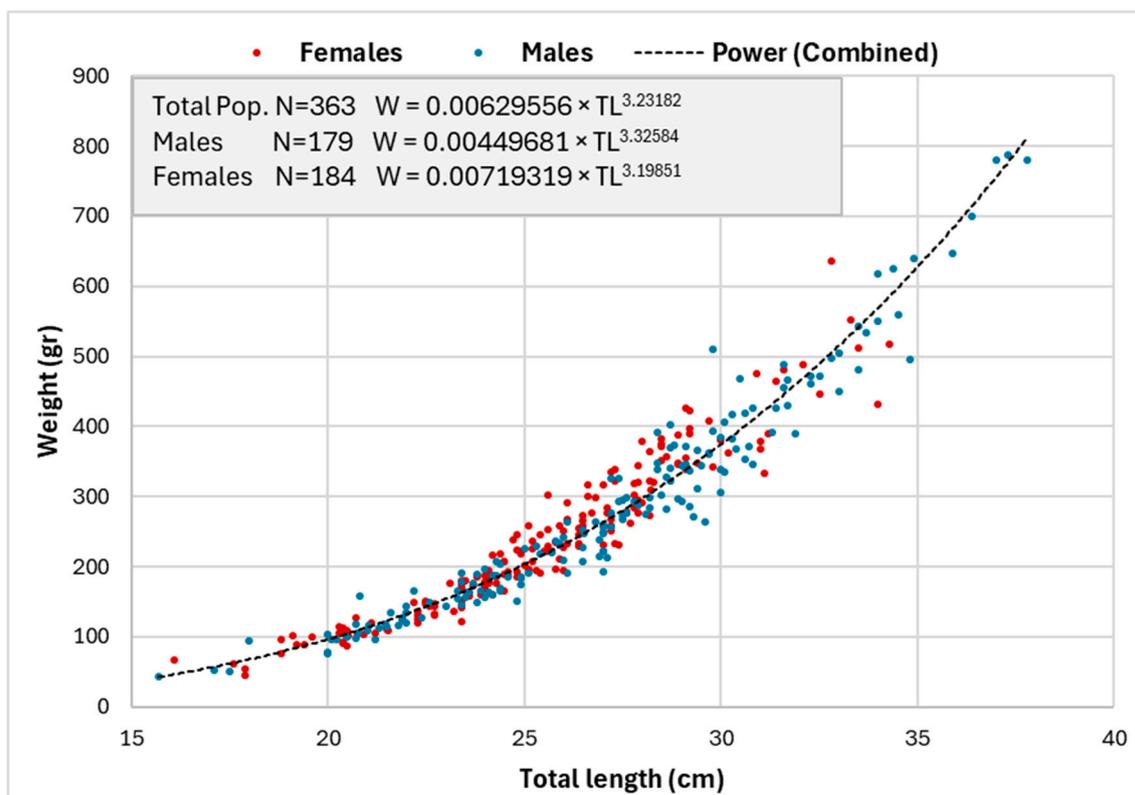


Figure 3. Length–weight relationship of the 363 *Pterois miles* individuals of the present study.

3.4. Age Composition

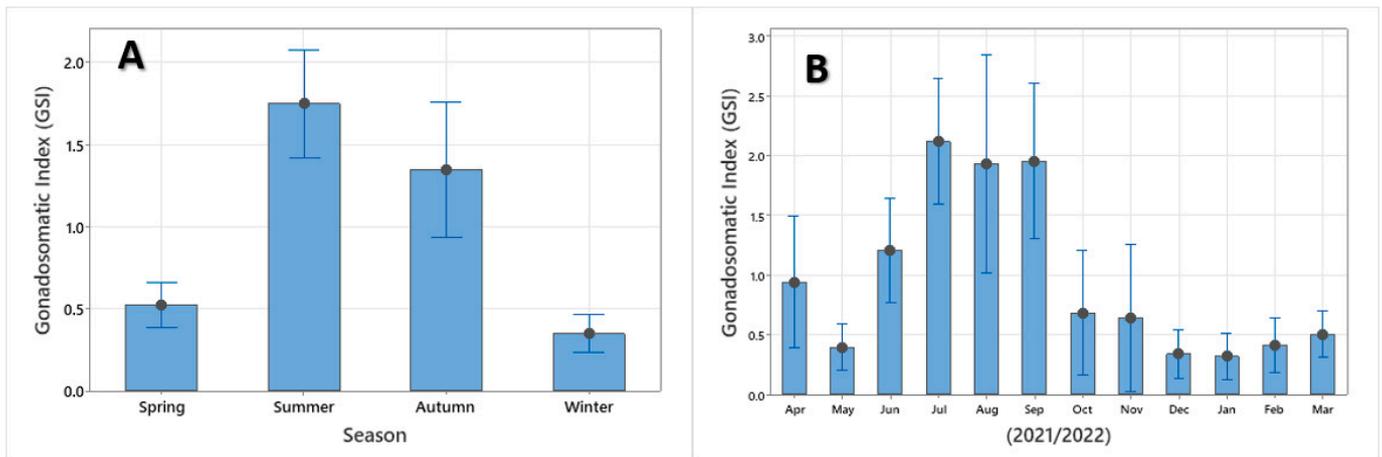
The dominant cohort was the three-year class, comprising 41.5% of the population, out of the five age classes identified (Table 1).

3.5. Reproduction

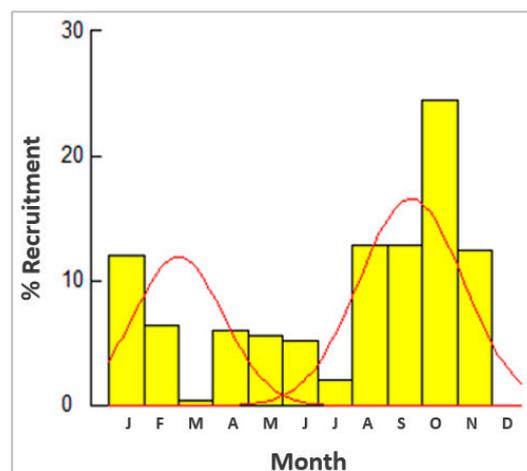
The highest reproductive intensity was exhibited during summer followed by autumn (Figure 4A) with significant differences observed between spring–summer and spring–autumn and similarly between winter–summer and winter–autumn.

Table 1. Population characteristics of the identified age groups for the total *P. miles* population.

Age Group	Mean Total Length (cm)	Standard Deviation	Population %
1	18.12	0.59	2.79
2	21.32	0.84	14.90
3	25.01	1.39	41.49
4	28.35	1.20	32.40
5	33.52	1.16	8.42

**Figure 4.** Mean seasonal (A) and monthly (B) GSI (bars indicate 95% confidence interval) of the total *P. miles* population.

The annual recruitment pattern of *P. miles* (Figure 5) indicated that recruitment occurred throughout the year with two prominent peaks of different magnitudes. The minor one occurred from January to June with a peak in January (12.12%), while the major one happened from August to November with a peak in October (24.29%)

**Figure 5.** Recruitment pattern of *P. miles*.

The onset of sexual maturity (L_{50}) for the total population was estimated at 22.44 cm in total length (2.1 years) and 21.92 (1.9 years) and 22.90 (2.2 years) for males and females, respectively (Figure 6). The inflection point was estimated at 4.31 years for the total population.

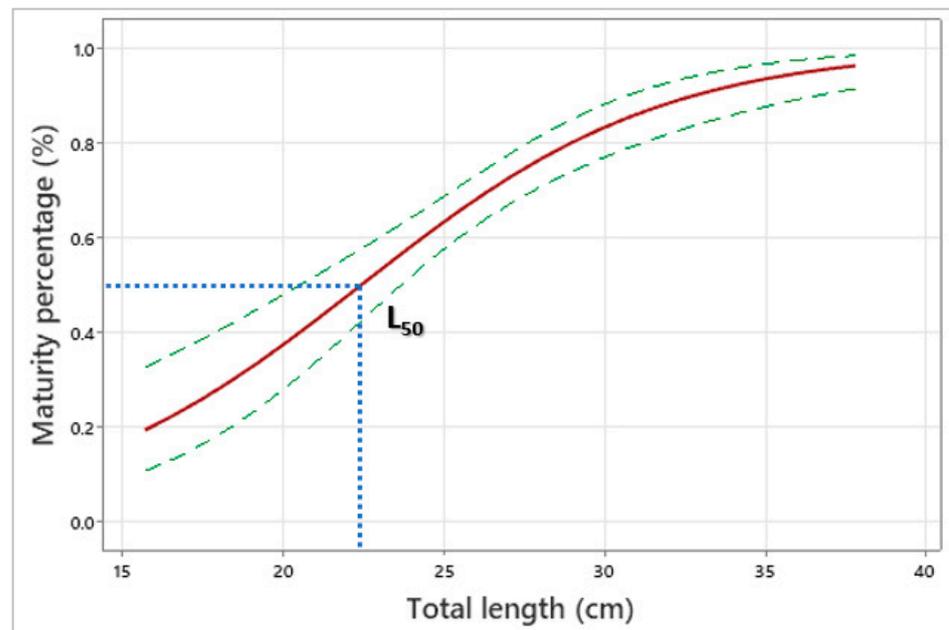


Figure 6. Binary logistic regression for the proportion of mature *P. miles* in relation to its total length (red line indicates model fit, green dashed line indicates 95% C.I., blue dashed line indicates L_{50}).

3.6. Condition Factor

The Fulton condition factor did not exhibit large fluctuation throughout the study period (1.33 ± 0.17) with the highest values exhibited during summer and autumn (Figure 7) and the lowest in spring and winter.

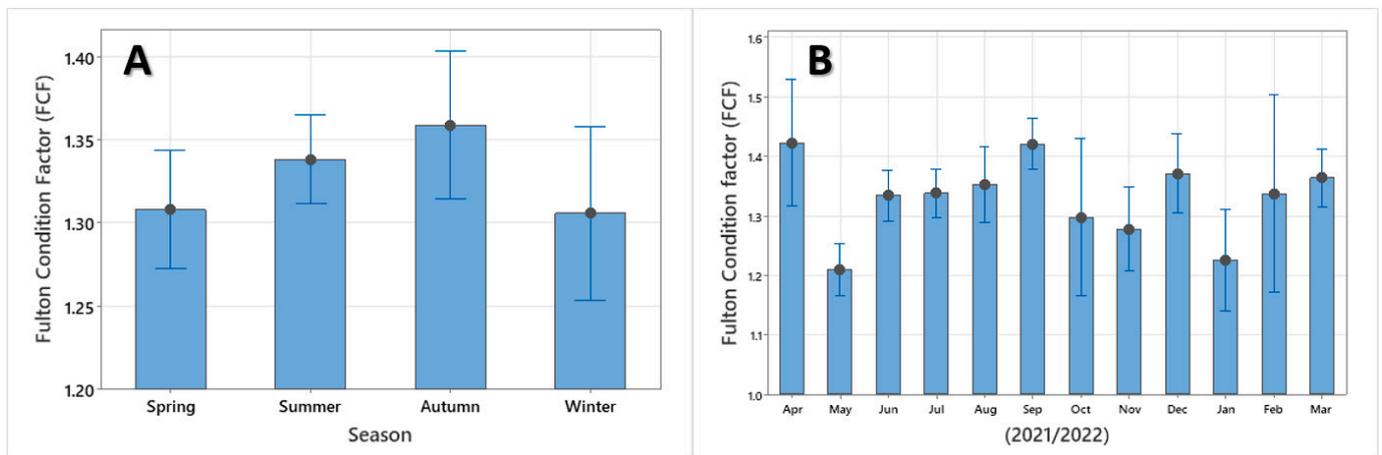


Figure 7. Mean seasonal (A) and monthly (B) FCF (bars indicate 95% confidence interval) of the total *P. miles* population.

3.7. Growth and Mortality

The Von Bertalanffy growth equation for the total population, was estimated as:

$$\text{Total length (cm)} = 45.35 \times \left(1 - e^{-0.1875(\text{age}+1.5506)}\right)$$

The growth index (Φ') was estimated as 2.59, longevity at 14.4 years and inflection point at 4.31 for the total population.

Natural mortality (M) was estimated as 0.43, total mortality (Z) as 0.83 and fishing mortality (F) as 0.41. The exploitation ratio (E) was estimated at 0.48, indicating an underexploited population.

3.8. The Probability of Capture

The probability of capture was estimated at 25% (LC_{25}), 50% (LC_{50}), and 75% (LC_{75}) levels as 22.05, 23.03, and 23.98 cm, respectively (Figure 8), with age at a 50% probability of capture (t_{50}) being estimated at 2.2 years.

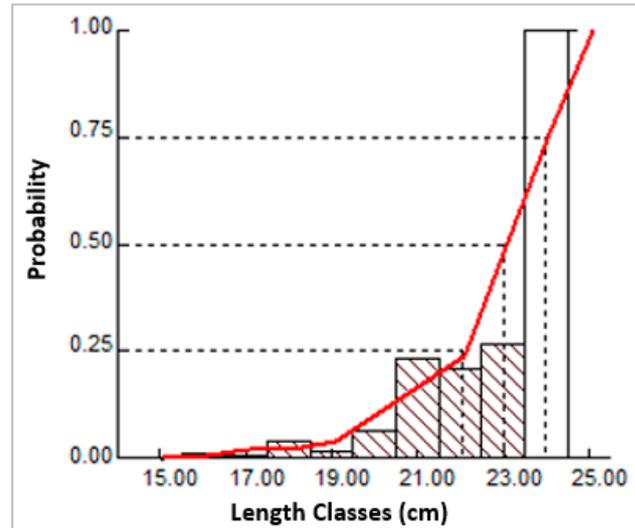


Figure 8. Probability of capture for different length classes (LC_{25} , LC_{50} , LC_{75}).

3.9. Relative Y/R and B/R Analysis: Knife-Edge Selection

The yield per recruit (Y/R) against the fishing mortality and the exploitation rate are shown in Figures 9 and 10, respectively. Results of the yield-per-recruit analysis and biological reference points are shown in Table 2.

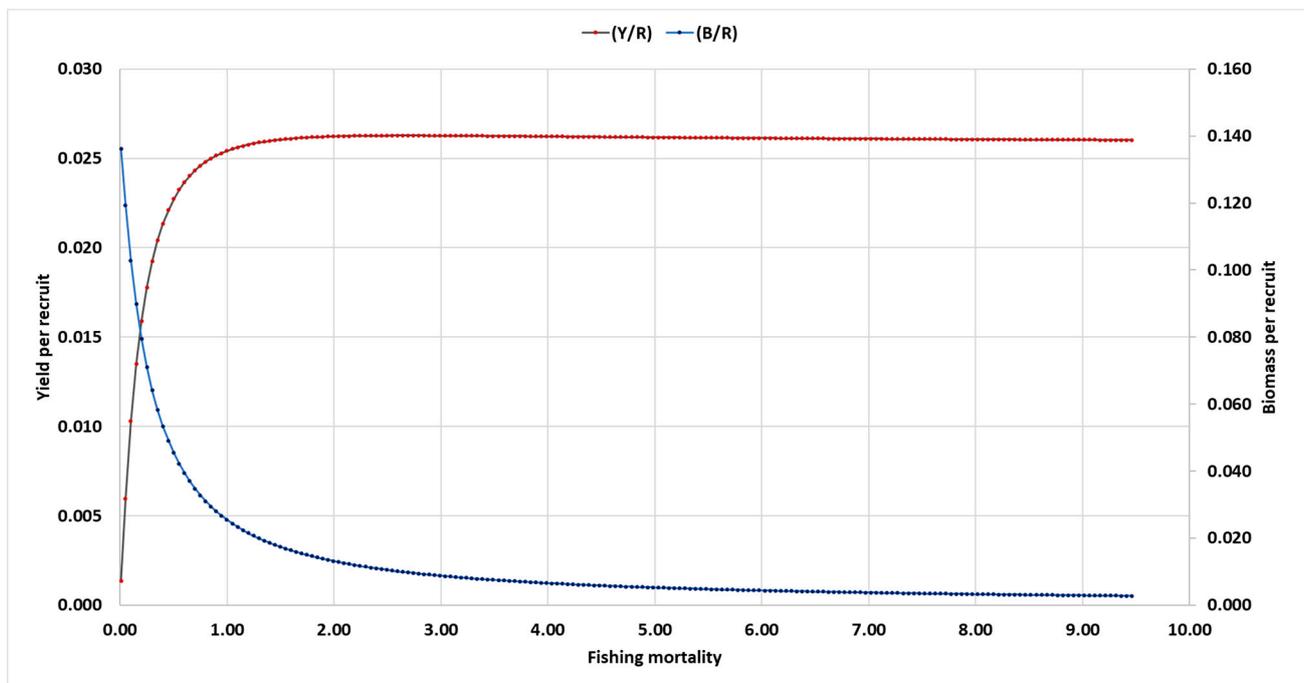


Figure 9. Yield per recruit (Y/R) and biomass per recruit (B/R) of *P. miles* for different fishing mortalities.

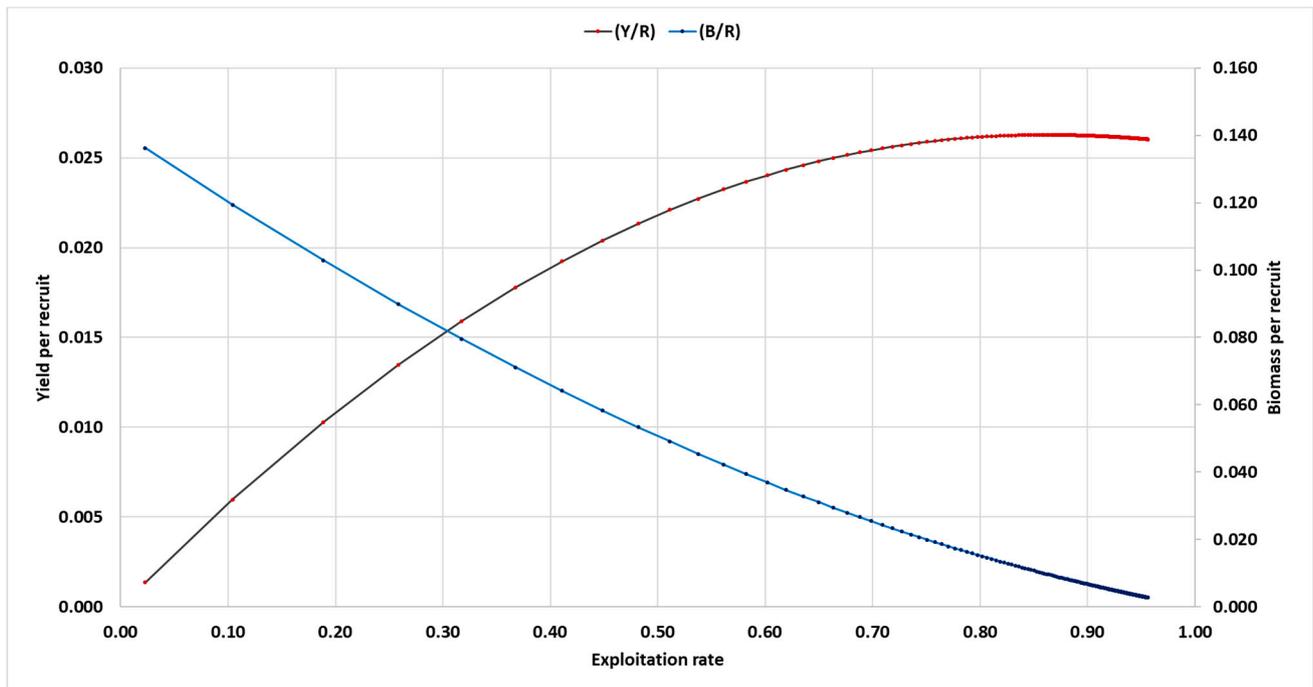


Figure 10. Yield per recruit (Y/R) and biomass per recruit (B/R) of *P. miles* for different fishing exploitation rates.

Table 2. Relative yield/recruit analysis (knife edge) and biological reference points of the population.

	E	Y/R	B/R
	0.01	0.006	0.852
	0.20	0.011	0.714
	0.30	0.015	0.585
	0.40	0.019	0.467
	0.50	0.022	0.360
	0.60	0.024	0.264
	0.70	0.025	0.180
	0.80	0.026	0.108
	0.90	0.026	0.048
	0.99	0.026	0.004
Biological reference points		Y/R	B/R
E_{\max}	0.862	0.023	0.009
$E_{0.1}$	0.707	0.025	0.024
$E_{0.5}$	0.371	0.017	0.017
F_{opt}	0.424	0.021	0.051
F_{lim}	0.553	0.023	0.042
E_{opt}	0.500	0.022	0.045

E, the exploitation rate; Y/R, yield per recruit; B/R, biomass per recruit; E_{\max} , the exploitation rate which produces the maximum yield; $E_{0.1}$, the exploitation rate at which the marginal increase in relative yield per recruit is 1/10th of its value at $E = 0$; $E_{0.5}$, value of E under which the stock has been reduced to 50% of its unexploited biomass; F_{opt} , the optimum fishing mortality; F_{lim} , the fishing mortality limit; E_{opt} , the optimum exploitation rate.

4. Discussion

Biological invasions constitute one of the major negative impacts of human interventions in ecosystems [116] and that of the Mediterranean Sea is one of the most invaded areas with alien species [117], which influenced biodiversity, ecosystem services and human health [15,17,118]. In regard to economy, it was estimated that within the last 30 years the aquatic invasive species induced a total cost of USD 27.3 billion [119]. A wide range of

variables, such as temperature, salinity, habitat variation, food availability, maturity stage, fishing season, high fishing mortality, and genetic factors, affect a teleost's sex ratio, GSI and spawning period [120].

In the present study, the sex ratio was estimated at 1:1.03 (M:F). In a study from Cyprus [4] on 268 lionfish individuals (sexed: 82 males, 127 females), caught in the period September 2017–August 2018, the sex ratio was 1:1.55. A ratio of 1:1.54 was reported in another study [46] from the same area, where 206 individuals of *P. miles* were sexed as 81 males and 125 females. Both are significantly different than the sex ratio in the present study. Similar studies from the Atlantic reported a M:F ratio of 1:1 [88,121]. The significance of the sex ratio to the population size of the species was pointed out by Edwards et al. (2014) [88], who emphasized the need to remove a sufficient number of females in order to make lionfish removal efforts effective in terms of suppressing the populations of the species.

The devil firefish individual weight can be differentiated because of (a) the increased predation and the gonad development, combined with the reduced energy consumption for the search for prey, (b) the selectivity of the fishing gear, (c) the topography (substrate) of the fishing area and (d) the collection depth. In Cyprus, out of the 268 *P. miles* individuals studied, the largest in length was a male with TL 37.1 cm and TW 755.0 g [4]. The heaviest individual was a male with TW 850.0 g and TL 36.8 cm. In another study from Cyprus, the TL range of the *P. miles* individuals was 8 to 37 cm with a frequency peak in the 20–25 cm length class [46].

The establishment of management measures for a species presupposes knowledge on the structure of its populations. Through the determination of the distribution of sizes and ages it comes handy the determination of the rate at which a species grows, so that size is studied as a function of age. Based on otolith examination, Kleitou et al. (2019) [4] reported that *P. miles* grows rapidly and can reach 20 cm within the first year of life, a finding that is almost in agreement with the results of the present study, where the species reaches 18 cm in total length. Savva et al. (2020) [46] distinguished four age classes, with onset of sexual maturity reached at 16.3 cm at the first age class, whereas, in the present work, five age classes were identified with the onset of sexual maturity (L_{50}) for the total population estimated at 22.44 cm in total length at the second age class. The maximum age identified in the present study was five years old. In the Atlantic, Gardner (2012) [122], in reference to a study from the Cayman Islands, reported that individuals of TL 19 cm aged between zero to two years. In the present study, the two-year-old individuals attain a TL of 21–22 cm. Further research is necessary for the Rhodian and Mediterranean waters with the use of otoliths compared with the present data to establish potential difference between the two methods. In the Mediterranean, otoliths were used for age estimation only from one study [4]. In the Atlantic, there are considerable literature data involving lionfish otoliths [57,91,123].

A significant life history trait is knowledge of the reproductive period. Analyzing changes in body weight, and gonadal development can help to understand energy trade-offs in the development of reproductive strategies, particularly in the inverse relationship between the hepato-somatic index (HSI) and the gonadosomatic index (GSI), while condition factor (CF) indicates the fish's relative condition [110]. In the present study, the highest overall reproductive intensity of *P. miles* was exhibited during summer. The highest value of GSI was obtained in July followed by August and September, a straight-forward proof that *P. miles* in Rhodes is sexually mature during the summer months. The prominent drop in the GSI during May (Figure 4B) can be attributed either to a large variability within the population (sampling bias) or a primary spawning occurrence in the end of spring. The second hypothesis is further supported by the slight drop in FCF, which was observed during May (Figure 7). The large confidence intervals that were observed on Figure 4 (and Figure 7) could be attributed to the presence of large variability within the population and/or temporal or spatial variation.

According to a recent study [46], reproduction in Cyprus occurs in the summer. Mouchlianitis et al. (2021) [124] are the only researchers that examined all aspects of *P. miles* reproductive biology in the eastern Mediterranean. These authors reported that the species exhibited active spawning only in June and July, but females capable of spawning were present throughout autumn.

In the western Atlantic, a few years earlier, Gardner (2012) [122], in 1872 lionfish individuals, found that GSI presented a significant monthly variation with two peaks during the year, that coincided with maximum and minimum values of sea temperature. The highest GSI value they recorded for females was 6.19. Furthermore, the same authors report that after reproductive maturity, lionfish appeared to spawn year-round, a conclusion supported by the high GSI values found in Morris (2009) [125], with a spawning frequency of 2.42 days. From the same area, there are reports of lionfish breeding throughout the year, based on the presence of females in the fifth stage of maturity [54,55,125]. In Bermuda, actively spawning fish were identified only between certain summer and autumn months, even though females of the *P. miles* and *P. volitans* were capable of spawning year-round [91]. However, the findings from our study are not in accordance with those from the tropical Caribbean, where lionfish reproduction is characterized by two major spawning peaks that occur during intervals of stable cool seawater temperatures (27 °C, December–February) and stable warm seawater temperatures (30 °C, July–August). Temperature has been shown to be a moderating factor in the peak spawning period of the species in the Mediterranean as well as in the Atlantic [91,122]. It is estimated that climate change and the resulting further temperature increase in the Mediterranean will lead to prolongation of the spawning period of lionfish. Food availability also seems to play an important role, with photoperiod and the moon phases expressed through tidal cycle needing further investigation [122].

According to Stergiou and Moutopoulos (2001) [126], the length–weight relationship is crucial to fisheries biology and is very helpful in research that evaluate fisheries. It is important to record the length–weight relationships for established invasive species because they reveal how the population has changed through time and space in the invaded habitat [127]. In contrast to a previous study [60] on Rhodian devil firefish individuals that reported a “b” value of 2.896, positive allometry was identified in our study. The “b” values reported in Iskenderun Bay [128] and in Cyprus [46] did not significantly differ from our findings. The L–W allometric relationship demonstrated a very rapid rise in weight with length, suggesting that the lionfish gains weight as it ages and may perhaps become substantially stouter or have a deeper body. The findings of the current study were consistent with those of studies conducted in the western Atlantic invasive range [127], and the minor differences between studies are typically attributed to sample size, season, feeding habits, stage of maturity, environmental factors, and the rapid growth in early life stages [129,130].

The estimation of growth parameters (L_{∞} , K , t_0), age, mortality, and exploitation rates, are considered fundamental and constitute the first step in fishery stock assessment. Asymptotic length (L_{∞}) was similar in comparison to Daghan and Demirhan (2020) [128], but higher than the one reported from Cyprus [46]. K was similar to that described in the former study [128] and lower than in the latter [46]. The t_0 value in the present study is higher than in the aforementioned studies. As widely recognized, a number of factors, including environmental conditions (such as temperature and salinity), habitat variability, the latitude effect, food availability, maturity stages, fishing season, sampling methodology, the selectivity of fishing gear, and genetic variations, may be contributing to observed differences in L–W relation, age, growth, and mortality values [131–136].

Mortality estimates associated to growth parameters are important to understand population dynamics [137]. The current results suggest that fishing mortality and natural mortality of *P. miles* in the study area was equal to 0.41 and 0.43, respectively, suggesting an exploitation rate lower than 0.5 ($E = 0.48$), which is an indication of an underexploited population. The estimated optimum fishing mortality and fishing mortality limit as 0.42 and 0.5, respectively, indicated that there is potential for further fishing mortality increase

if the aim was to commercially exploit the population. This indication is further supported by the difference between the optimum exploitation rate and the current exploitation rate, which were estimated as 0.5 and 0.48, respectively. Given the edible flesh of *P. miles*, it is thus clear that the species has the potential of becoming a marketable fish.

Currently, in Rhodes, the number of fish markets the species is already sold in is limited (EUR 10 per kilo), [48]. Nevertheless, the fact that the devil firefish is already marketed is an encouraging practice and it should be adopted in more areas and in a more intense pace. The slow rates of its incorporation in the live fish commerce can be majorly attributed to the bad reputation *P. miles* received [80,138,139], which resulted in inhibiting its demand among potential consumers throughout Greece and possibly other Mediterranean countries. The bad reputation is attributed to the venomous spines (12–13 dorsal, 3 anal and 2 pelvic spines), which contain apocrine-type venomous glands [125].

To restore the negative image of the species and place it among other commercially important fishery products, a lot of work must be carried out. Lionfish gastronomy and tasting events held in multiple cities and places, such as cities with high tourist traffic, hotels, restaurants, the street and more, will majorly assist in that direction. Simultaneously, we see as an important element in the promotion of the devil firefish as a food source, the consumer's, and retailer's information that the goal is a population size decrease in the species and not the discovery of a new addition to the menus. According to the second management measure of the Article 19 of the EU Regulation No 1143/2014 [140] "The commercial use of already established invasive alien species may be temporarily allowed as part of the management measures aimed at their eradication, population control or containment, under strict justification and provided that all appropriate controls are in place to avoid any further spread".

This new fishing resource could have the potential of substantially contribute to the economy of the coastal small-scale fisheries of the eastern Mediterranean, where the populations of the lionfish are thriving [48,79,84]. However, caution is needed because a new fisheries resource involves risks. According to Nuñez (2012) [84] a new fisheries resource needs adequate orthological management in order to be sustainable. Creating a market for a certain species can produce uncontrollable pressure to maintain it and if this species turns out to be an economic resource there is a possibility of intentional introduction of the species to other, uninvaded areas [84]. Additionally, a continuous monitoring plan of the catches is crucial for the sustainability of the *P. miles* fisheries exploitation [79]. Morris (2012) [49] summarized all strategies and issues referring to motivation of lionfish capture. Among them is to clarify the negative perceptions about the dangers of lionfish, educate the public on seeing it as a food source and as a "green alternative" in relevance to other fish species, develop marketing strategies and many more. At the same time, measures and regulations aiming to benefit the ecosystem have to be adopted [5,41,49,79] so that the combination of the lionfish fisheries and the holistic protection of certain coastal areas (e.g., fishing restrictions, creation of marine protected areas, invasive species targeted fisheries within protected sites, licensing to fish for lionfish with specially designed spearguns and bottom traps even within marine protected areas), may contribute efficiently towards the recovery of the marine ecosystem [41,79]. We believe that these solutions are the most realistic and direct for Rhodian and by extension the Greek waters.

5. Conclusions

In the coastal waters of Rhodes, the creation of large populations of the devil firefish seems to be facilitated. Five age classes were identified and the onset of sexual maturity (L_{50}) of the population was estimated at 22.44 cm in total length (second age class), and the maximum age was estimated at five years old. The reproductive intensity of *Pterois miles* was highest during summer followed by autumn. According to the L–W allometric relationship, the species gains weight as it ages and may perhaps become substantially stouter or have a deeper body. The estimated optimum fishing mortality and fishing mortality

limit indicate that *P. miles* is hardly exploited in Rhodian waters and if the aim was to commercially exploit this local population there is substantial potential for further increase in the catches. The current study provides new information on the population structure and life history characteristics of the invasive *P. miles* in Rhodian coastal waters, which is essential for developing and implementing management strategies. In order to avoid any adverse impacts on the ecosystem, the exploitation of the species as a new fishery resource in the Mediterranean has to take under consideration all the important parameters, including growth, the sex ratio, length–weight relationship, age, reproductive strategies, mortality and the exploitation rate. This is the first study presenting the mortality rates of the species, hence assisting in the awareness of the status of natural stocks in eastern basin. Nevertheless, more research is required to cover dynamic parameters concerning the devil firefish.

Author Contributions: Conceptualization: G.K.; methodology: G.K.; software: G.K. and D.K.; validation: G.K. and D.K.; formal analysis: G.K., A.T. and D.K.; investigation: G.K., A.T., M.M., M.A., T.K., Z.K. and S.V.; resources: G.K. and A.T.; data curation: G.K., A.T., M.M., T.K., Z.K. and D.K.; writing—original draft preparation: G.K., A.T., T.K., Z.K., S.V. and D.K.; writing—review and editing: G.K., A.T., M.M., M.A., T.K., Z.K., S.V. and D.K.; visualization: G.K., A.T. and D.K.; supervision, D.K.; project administration: G.K.; funding acquisition: G.K. All authors have read and agreed to the published version of the manuscript.

Funding: Fishing trials for present work were undertaken within the framework of the project EXPLIAS (“Design and piloting methods of commercial exploitation of invasive alien species with a view to contributing to their population control”; <https://explias.gr/>, accessed on 10 December 2023), which was coordinated by the National Technical University of Athens (NTUA) with the collaboration of the Hellenic Centre for Marine Research (HCMR) and the University of the Aegean (UoA) and funded by the Fisheries and Maritime Operational Program 2014–2020 of the Greek Ministry of Agricultural Development and Food, and the European Maritime and Fisheries Fund (MIS No: 5049912).

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: The datasets analyzed from the current study are available from the corresponding author upon reasonable request.

Acknowledgments: The authors would like to thank Savvas Vagianos (fishing vessel Saratoga) and Osman Karaosman (fishing vessel Nikolaos).

Conflicts of Interest: The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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