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Research Article

Comparative Reproduction Aspects of the Deep-water Shrimps *Aristaeomorpha foliacea* and *Aristeus antennatus* (Decapoda, Aristeidae) in the Greek Ionian Sea (Eastern Mediterranean)

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In the eastern Ionian Sea, the deep-water shrimps *Aristaeomorpha foliacea* and *Aristeus antennatus* constitute a virgin fishing resource, since their maximum abundance depth exceeds commercial exploitation depths. The two sympatric species share a number of common reproductive features, such as summer reproduction. A slight temporal shift in mating activity, ovarian maturation, and spawning period was observed between species. The most notable difference was the more pronounced seasonality in reproductive activity of *Aristeus antennatus* compared to that of *A. foliacea* as evidenced by the frequency of inseminated females and functionally mature males, as well as by the shorter ovarian maturation period. Nevertheless, regarding the whole life span, both sexes of *Aristeus antennatus* exhibit a more extended reproductive activity in comparison to *A. foliacea*. No notable differentiation of both species existed in comparison to other Mediterranean regions.

1. Introduction

The two red shrimps, *Aristaeomorpha foliacea* (Risso, 1827) and *Aristeus antennatus* (Risso, 1816) (Decapoda, Aristeidae), constitute the main target species for the demersal deep-water fishery in the Western and Central Mediterranean, captured exclusively by trawlers on muddy bottoms, especially near submarine trenches and canyons. Recently, new evidence from Greek waters suggested that both resources are adequate for exploitation at depths greater than 400 m, where at present almost no traditional commercial trawling exists [1–3].

A. foliacea is a cosmopolitan species while the geographical distributionof *Aristeus antennatus* is confined in the Mediterranean and the eastern-central Atlantic. Nevertheless, *Aristeus antennatus* is eurybathic with a documented depth of occurrence ranging from 80 to 3300 m ([4] and references therein), while *A. foliacea* has been recorded until now at depths from 123 to 1100 m ([5] and references therein). Another important feature is the longitudinal differentiation of the two species along the Mediterranean: *A. foliacea* increases in abundance from the western to the eastern Mediterranean, while the opposite is true for *Aristeus antennatus*.

For both species, an actual or potential commercial interest has resulted in studies on their fisheries biology and ecology, mostly concentrated in the western and central Mediterranean (see references in [4, 5]). Relatively less information exists on their reproductive biology (e.g., [6–11]), while larval life and recruitment are still obscure.

As opposed to the western Mediterranean, the two red shrimps coexist in the eastern Ionian both horizontally and vertically in an almost virgin condition. This was considered as an excellent opportunity for obtaining comparable data on their reproduction. In addition, such data, obtained for the first time for the eastern Mediterranean, could serve in the comparison of life history traits along the Mediterranean.

2. Materials and Methods

Shrimps were collected on a monthly basis (December 1996 to November 1997) in the Greek Ionian Sea between Peloponnisos and Zakynthos Island (depth range: 446–728 m) (Figure 1), using a commercial trawl (18 mm at the cod end). In totally, 90 hauls were carried out, in which 37301 *A. foliacea* specimens (17148 females, 20153 males) and 8574 *A. antennatus* individuals (7272 females, 1302 males) were caught. They were sexed and measured for carapace length (CL, mm) to the nearest 0.01 mm. The wet body weight (BW, g) was also measured with 0.001 g accuracy.

Ovarian maturity stages and spermatophore presence in the thelycum (inseminated specimens) were recorded from fresh specimens by macroscopic observation using the empirical scales of [12] for *A. foliacea* ($N = 1202$) and [13] for *Aristeus antennatus* ($N = 1487$). Four stages of development were established based on the ovarian color and size: stage I: undeveloped; stage II: developing; stage III: mature; stage IV: spawning. In the present study, recently spent individuals (SPs) were separated from those belonging to stage I. For the sake of comparison with other studies, three size groups have been defined for females: CL < 30 mm (small), 30 < CL < 40 mm (medium), and CL > 40 mm (large).

The gonad wet weight (GWW, g) and the gonad dry weight (GDW, g) (the gonads were dried in a Mement Rost Frei oven at 80° for 1 hour) were measured to the nearest 0.0001 g from 214 and 83, randomly chosen, individuals of *A. foliacea* and *Aristeus antennatus*, respectively. The relationship between gonad wet weight and gonad dry weight for each species was expressed in terms of linear regressions $F = a + bx$, where F = dry weight and X = wet weight, a = constant and b = slope. The difference between the dry and wet gonad weights is the estimated water content. Gonadosomatic index (GSI) was estimated from, randomly chosen, 502 females of *A. foliacea* and 384 females of *Aristeus antennatus* as $100 * (\mathrm{GWW}/\mathrm{BW})$, where BW = body weight.

Data from the spawning season (June-August) were used for the determination of $\mathrm{CL}_{50\mathrm{mf}}$ (the size at which 50% of females have reached maturity, stage IV) by applying a typical sigmoid symmetrical curve (logistic regression method in statgraphics 5.1 plus) $P = 1/[1+e^{(ax+b\mathrm{CL})}]$, where P is the percentage of sexually mature individuals by size class (CL), and a, b are constants [14]. The same equation was used for the estimation of $\mathrm{CL}_{50\mathrm{sf}}$ (size at which 50% of females bore spermatophore on their thelycum).

Male maturity was checked, in a great subsample, by the presence of the spermatophores in the terminal ampoullae of vasa deferentia [13] in 1525 and 503 males of *A. foliacea* and *Aristeus antennatus*, respectively. $\mathrm{CL}_{50\mathrm{sm}}$ (size at which 50% of males are reproductive) was determined as above.

Statistical differences between the two species were tested by the nonparametric Mann-Whitney, Kruskall-Whallis, and Kolmogorov-Smirnov tests [15]. We deemed only those independent variables with $P < .05$ to be significant.

3. Results

3.1. Spermatophore Presence. Mating activity of both species, as depicted by the frequency of females bearing spermatophores on their thelycum (Figure 2), was found to be consistently high (>75%) for a long period (from spring to the beginning of autumn). It seemed, however, that, although *A. foliacea*'s mating activity decreased, it did not cease totally in late autumn-early winter as in *Aristeus antennatus*, and was already pronounced earlier (February). The occurrence of the inseminated individuals among the months was not statistically different between the two species (Kolmogorov-Smirnov, $P > .05$). In both species, there was a statistically significant difference between female median CL with and without spermatophores (Mann-Whitney test, $P < .05$). Thus inseminated females were on average larger than noninseminated (CL ±SD): mated 44.92 ± 1.43 mm CL versus noninseminated 36.69 ± 6.48 mm CL in *A. foliacea*, and inseminated 41.65 ± 2.28 mm CL versus noninseminated 36.59±3.11 mm CL in *Aristeus antennatus*, in the whole study period. The smallest mated female was 25 mm and 18 mm CL, for *A. foliacea* and *Aristeus antennatus*, respectively.

During the study period, a size segregation was obvious in both species regarding the start of mating after oviposition (Table 1): only the largest females were found mated just after the reproductive season (see below) in November (*A. foliacea*) or January (*Aristeus antennatus*), followed progressively thereafter by medium sized females. It is worth noting that few mated small individuals (CL < 30 mm) of *A. foliacea* occurred only in July, whereas those of *Aristeus antennatus* were present from May to October in comparable frequencies to other size groups. As a result, larger females of both species exhibited a longer mating period than smaller ones. During the reproductive period (April–September), all females of *A. foliacea* sized between 34 and 53 mm CL were carrying spermatophores on their thelycum. Similarly, in the period May–September, all *Aristeus antennatus* females between 37 and 55 mm CL were inseminated.

3.2. Ovary Maturation. Although females with immature ovaries of both aristeids were present throughout the year, all females caught from October to March in *A. foliacea* and from October to April in *Aristeus antennatus* exhibited immature ovaries (Figure 3). In both species, the ovarian maturation process (appearance of stages III and IV) seemed to be rapid, lasting one to two months. The first mature females of *A. foliacea* were observed (both stages III and IV = 2.6%) in spring and summer, especially in April and peaking in June (both stages III and IV = 88%) and decreasing progressively during the rest of summer (July, August). In *Aristeus antennatus*, the first females with mature ovaries (stages III, IV) were found one month later (May, both stages III and IV = 11.3%), increasing in June (both stages III and IV = 52%), and reaching a maximum in July (both stages III and IV = 92%). Spent individuals appeared in July (16%) for *A. foliacea* and already in June (27%) for *Aristeus antennatus*. It seems, therefore, that although both sympatric species are summer breeders, *A. foliacea* has a rather earlier and more

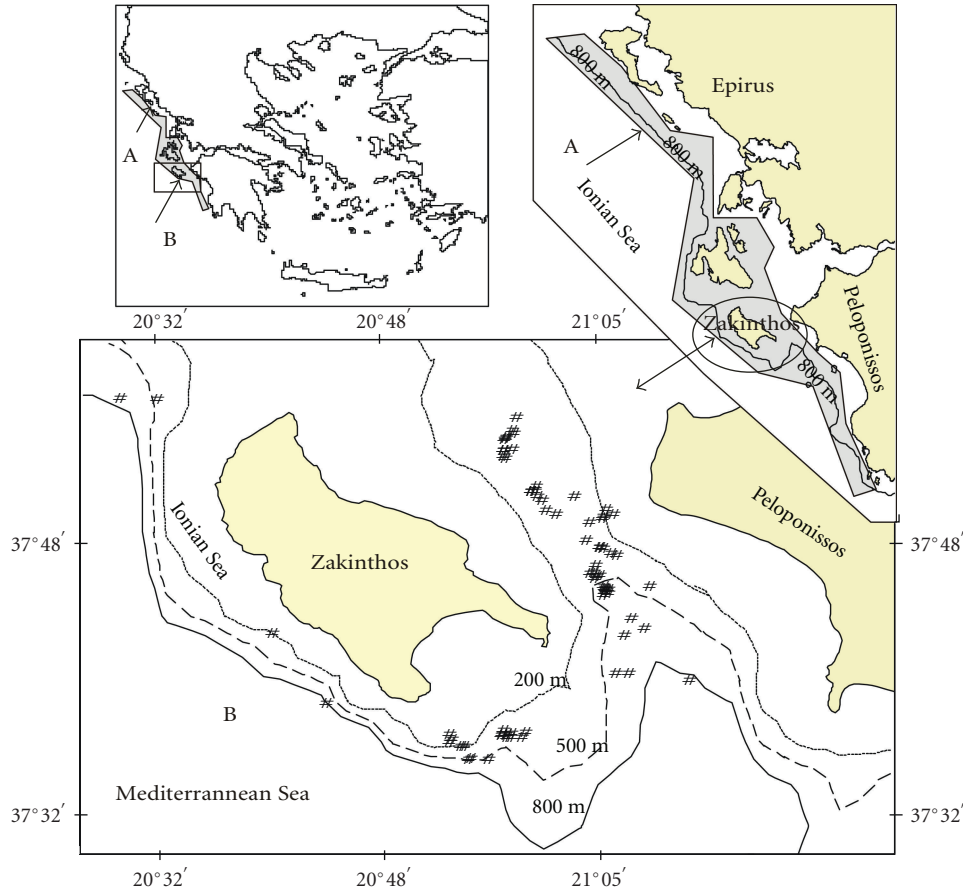

Figure 1: Map of the research area (A = deep waters of the North Ionian Sea, B = sampling area with sampling stations (#)).

Table 1: Monthly spermatophore and mature ovaries occurrence (%) per size group for *A. foliacea* and *Aristeus antennatus*.

Size (mm)	J	F	M	A	M	J	J	A	S	O	N	D
Presence of spermatophore												
A. foliacea												
CL < 30	0	0	0	0	0	0	12	0	0	0	0	0
30 < CL < 40	46	39	25	44	48	50	41	50	510	81	0	44
CL > 40	54	61	75	56	52	50	47	50	49	19	100	56
Aristeus antennatus												
CL < 30	0	0	33	28	32	32	32	0	30	22	0	0
30 < CL < 40	0	55	33	29	35	34	35	53	35	52	0	0
CL > 40	100	45	33	45	33	34	33	47	35	26	0	0
Females with mature ovaries (stages III and IV)												
A. foliacea												
CL < 30	0	0	0	0	0	0	0	0	0	0	0	0
30 < CL < 40	0	0	0	0	0	36	28	52	0	0	0	0
CL > 40	0	0	0	100	100	64	72	48	100	0	0	0
Aristeus antennatus												
CL < 30	0	0	0	0	0	0	31	0	0	0	0	0
30 < CL < 40	0	0	0	0	48	41	36	29	0	0	0	0
CL > 40	100	0	0	0	52	59	33	71	0	0	0	0

Table 2: Mean wet gonad weight, dry gonad weight (g), water content (% of wet gonad weight) and standard deviation (±SD) prematurity stage in *A. foliacea* and *Aristeus antennatus* females.

A. foliacea			
	Wet weight	Dry weight	Water content
Maturity stage	Mean weight ± SD	Mean weight ± SD	% of wet weight
I	0.181 ± 0.09	0.031 ± 0.01	77.04
II	0.366 ± 0.21	0.074 ± 0.06	78.40
III	1.385 ± 0.48	0.402 ± 0.23	68.57
IV	2.314 ± 1.06	0.661 ± 0.24	65.36
SP	0.269 ± 0.25	0.048 ± 0.01	78.45
Aristeus antennatus			
	Wet weight	Dry weight	Water content
Maturity stage	Mean weight ± SD	Mean weight ± SD	% of wet weight
I	0.159 ± 0.10	0.055 ± 0.04	73.6
II	0.507 ± 0.35	0.150 ± 0.07	54.09
III	1.576 ± 0.75	0.388 ± 0.05	54.25
IV	2.234 ± 1.51	0.604 ± 0.24	59.19
SP	0.292 ± 0.39	0.052 ± 0.07	70.91

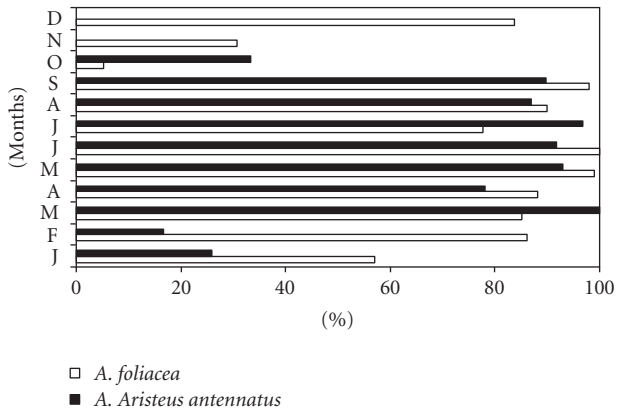

Figure 2: Monthly spermatophore occurrence in *Aristaeomorpha foliacea* and *Aristeus antennatus* females from the eastern Ionian Sea.

extended spawning period than *Aristeus antennatus*, in which reproduction processes seem to be more accelerated.

The smallest female of *A. foliacea* with developed ovaries (stage III) measured 36 mm CL and that of *Aristeus antennatus* 26 mm CL.

In accordance with the observation concerning the relationship between female size and mating period, medium and larger females of both species showed earlier ovarian maturation than smaller ones (Table 1). In spring, especially April and May, only large *A. foliacea* exhibited developed ovaries (CL range: 52–66 mm), while in summer, medium sized females entered mature condition (CL range: 32–56 mm). Finally, at the end of the reproduction period in September, only large females were still reproductive (CL range: 5056 mm). It is worth mentioning that smaller *A. foliacea* females did not contribute to the reproductive pool. In *Aristeus antennatus*, on the other hand, large- and medium-sized females showed comparable percentages in ovary maturation during end of spring-early summer (May and June) (CL range: 32–56 m), whereas smaller individuals, CL range: 26–64 mm, became mature in July. Thus *A. foliacea* large females have a more extended reproductive period (6 months) than medium sized (3 months), while small ones are not reproductive. In *Aristeus antennatus*, on the other hand, large and medium females with mature ovaries occur for a four-month period, while smaller ones appear only during the peak of the reproductive season.

Regarding female functional maturity (i.e., the cooccurrence of inseminated and individuals with mature ovaries), more than 60% of females with resting ovaries (stage I) in both species had already mated. This percentage increased to more than 90% in females with a more advanced ovarian stage. A considerable number of inseminated females were found after oviposition (38% in *A. foliacea* and 44% in *Aristeus antennatus*).

3.3. Gonad Weight and Gonadosomatic Index. The mean gonad wet and dry weight per maturity stage are given in Table 2 for both species. There is a statistically significant difference among the medians of both gonad weights per stage in both aristeids (Kruskall-Wallis test, $P = .011$). Both gonads weights increased from immature to mature specimens and the obtained values of the spent individuals were between the stages I and II for both species. The included water in the gonads decreased from the first to fourth stage due to the yolk storage.

Females *A. foliacea* presented statistically higher mean values of gonad wet weight in stages 1, IV and gonad dry weight in stages I, II, SP than those of *Aristeus antennatus* (Mann-Whitney test, $P < .05$). Females *Aristeus antennatus* presented a statistically higher mean value of gonad wet weight in stage II (Mann-Whitney test, $P < .05$). Almost

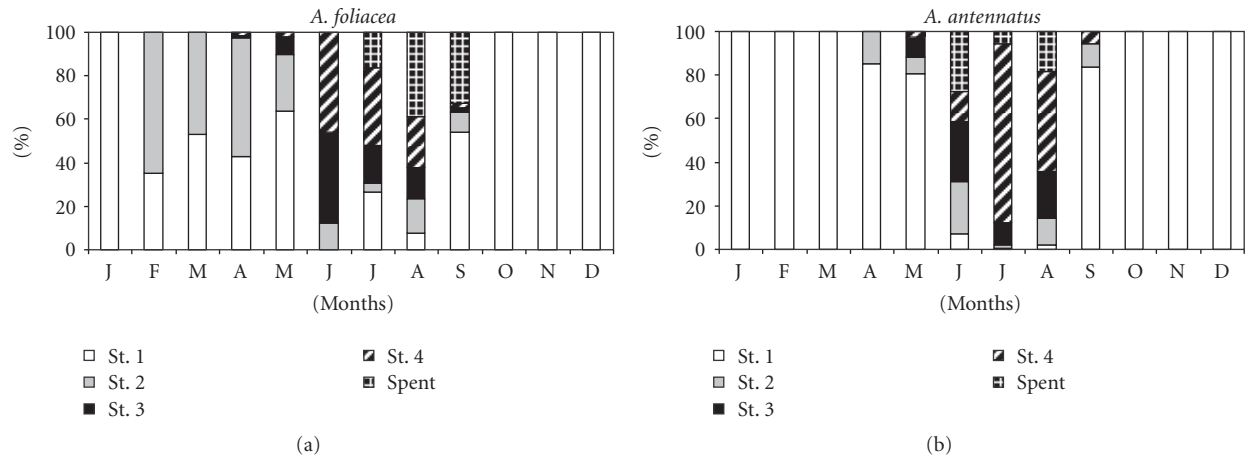

Figure 3: Monthly occurrence of ovarian maturity stages of *Aristaeomorpha foliacea* and *Aristeus antennatus* females from the eastern Ionian Sea.

all the values of water content in the gonads of *A. foliacea* per stage were statistically significantly higher than those of *Aristeus antennatus* (Mann-Whitney test, $P < .05$). The relationship between the gonad wet weight (GWW) and gonad dry weight (GDW) for each species was expressed by the equations

$$\begin{gathered} \textit{A. foliacea}\ \text{GDW} = (\text{GWW} * 0.35) - 0.02, \\ r = 0.99, \\ \text{standard error of } b = 0.003, \\ \textit{Aristeus antennatus}\ \text{GDW} = (\text{GWW} * 0.37) - 0.004, \\ r = 0.97, \\ \text{standard error of } b = 0.01. \end{gathered} \quad (1)$$

For both species, average GSI increased with ovarian maturity (Table 3), spent ovary GSI being between that of stage II and I. Monthly average GSI varied seasonally (Figure 4) reaching a maximum in summer (June, July) (7.1%) for *A. foliacea* and in the same season (July, August) (7.2%) for *Aristeus antennatus*. The average GSI did not statistically differ among the months between the two decapods (Kolmogorov-Smirnov, $P > .05$).

3.4. Size at First Female Maturity. Based on the percentages of fully mature ovaries and the presence of spermatophore by size class, the 50% size at first maturity (CL_{50mf} and CL_{50sf}, resp.) was determined (Table 4). In both species, CL_{50sf} (36.84 mm CL for *A. foliacea*, 26.03 mm CL for *A. antennatus*) was lower than CL_{50mf}, (38.84 mm CL for *A. foliacea*, 29.45 mm CL for *A. antennatus*) indicating that gonad maturity follows insemination. Both estimates of size at first maturity showed that *Aristeus antennatus* females attain maturity at a smaller size than *A. foliacea*.

3.5. Maturity of Males. The presence of the spermatophores in the terminal ampoullae in males among the months did not differ statistically between the two sexes (Kolmogorov-Smirnov, $P > .05$). Although, in *A. foliacea*, the occurrence of reproductive males was consistently very high during the whole study period (87–100%), it varied widely in *Aristeus antennatus* (Figure 5). In the latter species, spermatophore-bearing males existed in high percentages before and at the beginning of female reproductive period (January to May), while only spermatophore-deprived males existed in the middle of the reproductive period (June), increasing thereafter until its end. In accordance with the absence of *Aristeus antennatus*-inseminated females during November and December; no male was found reproductive at that period. The smallest reproductive male measured 26 mm and 20 mm CL, in *A. foliacea* and *Aristeus antennatus*, respectively. As in females, *Aristeus antennatus* males seemed to mature at a significantly smaller size than those of *A. foliacea* ($P = .001$) (Table 4).

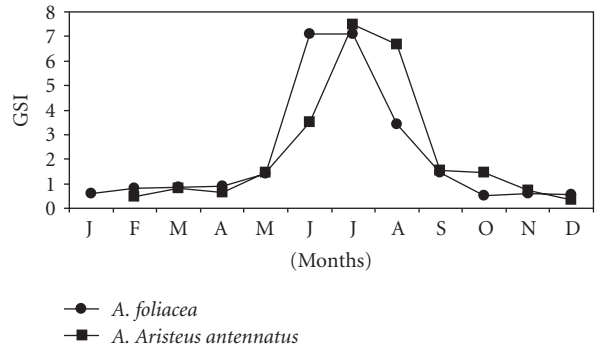

Figure 4: Temporal variation of gonadosomatic index (GSI), of *Aristaeomorpha foliacea* and *Aristeus antennatus* from the eastern Ionian Sea.

4. Discussion

In the Greek Ionian Sea, fishing pressure in depths beyond 500 m is almost absent. As a result, both aristeids constitute

Table 3: Female average gonadosomatic index (±SD) of *A. foliacea* and *Aristeus antennatus* according to the ovarian maturity stage.

Maturity stage	Gonadosomatic index			
	A. foliacea		*Aristeus antennatus*	
	Average ± SD	*N*	Average ± SD	*N*
I	0.66 ± 0.21	142	0.69 ± 0.62	123
II	1.08 ± 0.92	142	1.73 ± 0.92	23
III	6.96 ± 2.14	50	5.03 ± 2.16	29
IV	8.08 ± 2.98	124	7.86 ± 2.98	187
SP	0.91 ± 0.78	44	1.00 ± 0.78	22

Table 4: Elements of the logistic model ($P = 1/[1+e^{(ax+bCL)}]$) for the mature (CL_{mf}), mated (CL_{sf}) females and mature males (CL_{sm}) of *A. foliacea* and *Aristeus antennatus*.

CL_{50}	*a*	SE	*b*	SE
		FEMALES		
		A. foliacea		
		Ovarian maturity		
38.84 (CL_{mf})	−10.69	1.38	0.300	0.035
		Spermatophore occurrence		
36.84 (CL_{sf})	−4.85	0.59	0.131	0.013
		Aristeus antennatus		
		Ovarian maturity		
29.45 (CL_{mf})	−5.65	1.65	0.192	0.039
		Spermatophore occurrence		
26.03 (CL_{sf})	−2.49	0.606	0.095	0.010
		MALES		
		A. foliacea		
26.65 (CL_{sm})	−11.66	2.66	0.68	0.078
		Aristeus antennatus		
19.36 (CL_{sm})	−5.68	1.32	0.293	0.053

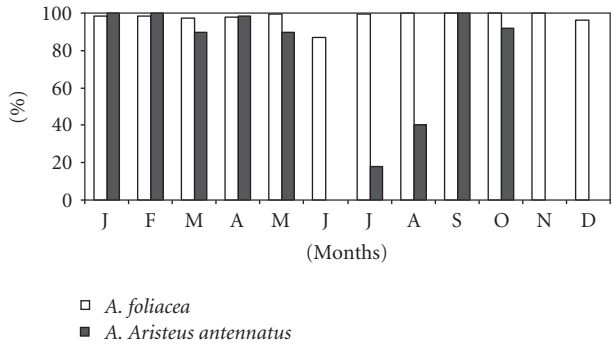

Figure 5: Monthly occurrence of reproductive males of *Aristaeomorpha foliacea* and *Aristeus antennatus* from the eastern Ionian Sea.

an unexploited resource for this area, with a potential to support a viable fishery [2, 3]. The unexploited status of both red shrimps is reflected in the presence of relatively higher percentage of large shrimp in comparison to other Mediterranean regions [16]. The relative abundance of the two species in the study area [3] conforms to the general longitudinal differentiation of the two species along the Mediterranean: *A. foliacea* shows greater abundances in the central-eastern part, while *Aristeus antennatus* in the western part.

The results of the present study demonstrated the high-reproductive capacity of both red shrimps in the study area. A remarkable succession concerning maturing, mating, oocytes' release of both species, and sexes was shown. This seasonality is a common phenomenon within the Dendrobranchiata [17]. According to [18, 19], the most feasible pattern of these processes during a month, at least in *Aristeus antennatus*, is the following: initial ovary development, molting, mating, vitellogenesis, and spawning.

Nevertheless, in the study area *A. foliacea* presented weaker seasonality in mating than *Aristeus antennatus* in

which a remarkable synchronism in fertilization exists as depicted by the sharp increase of inseminated females just before and during the reproductive season. The main mating period (>50% mated females) lasts longer in the eastern Ionian (10 months for *A. foliacea* and 7 months for *Aristeus antennatus*) than in Sardinian waters (8 months for *A. foliacea* and 6 months for *Aristeus antennatus*) [7] or the Balearic Islands (4 months for *Aristeus antennatus*) [18, 19].

The longer mating and reproductive period of larger individuals in both species from the eastern Ionian has been also pointed out from other localities (e.g., *A. foliacea*: [20] in the western Ionian Sea; *Aristeus antennatus*: [21, 22]). In *Aristeus antennatus*, this longer period of spermatophore carrying in the thelycum could be related to possible recoupling of these individuals during the same reproductive period resulting in more than one spawning [18, 19]. Nevertheless, based on the mature follicle presence and the duration of ovarian maturation, [23] it is concluded that a single batch of oocytes should develop at each reproductive period. It is worth mentioning that in the eastern Ionian, in spite the fact that males in general and especially those capable of mating are drastically decreased in the middle of the reproductive season (June to August), spermatophore presence in females remains at the same levels. This discrepancy can be possibly explained the ability of males to mate with multiple females: as it is already known from studies in the western Mediterranean, the species forms aggregations of reproductive females in a similar to the present study depth range and copulation takes place with males represented in low percentages in the beginning of the shoal formation (see [4] for references). Multiple spawnings could more likely occur in *A. foliacea*, since in the latest ovarian stage only half of the oocytes are fully mature, the rest being in previous stages [12, 24], and, according to the present study, mature males exist throughout the reproductive period in high percentages.

Regarding the relationship between mating and gonad maturity, the highest proportion of the noninseminated females of both species belonged to stage I (immature). Main mating activity precedes the appearance of gonad maturation by four months in *A. foliacea* (January–April) and by only two months in *Aristeus antennatus* (March-April). This difference could be attributed to the fact that *Aristeus antennatus* males are mainly distributed in deeper waters and enter the female shoal for copulation in late spring, while in the depth range sampled, *A. foliacea* males and females coexist, with sex ratio exhibiting a slight predominance of males [3]. For both species, it can be suggested that ovary development is induced by copulation [23, 24]. Greek stock of both species seems to agree, in general, with the maturation behavior of other Mediterranean populations: from the western Ionian Sea [20, 25, 26] and Sicily [8] for *A. foliacea*, and from the Ligurian Sea [13, 21, 22], Ibiza Channel [18, 19], Portugal [25, 26], Spain [18, 19, 23], and Algerian waters [27] for *Aristeus antennatus*. Although some unessential differences have been reported among the several areas of the Mediterranean.

Nevertheless, *A. foliacea* precedes *Aristeus antennatus* for about a month with respect to mating, ovary maturation, and spawning. This shift in timing of the reproductive components of the two aristeids has been also recorded in Sicilian waters, where also the two species coexist [7].

The fully mature female minimum size of *A. foliacea* in the present study (36 mm CL) seems to be in the upper part of the range recorded from the Mediterranean (23–40 mm CL) (see [5]) and belongs to 1+ age group, while that of *Aristeus antennatus* seems to be the smallest so far recorded and belongs to 0+ age group. Thus in the Greek Ionian Sea, *Aristeus antennatus* is already sexually active from its first year of life, having a greater ovogenetic activity than *A. foliacea*. This more extensive activity of *Aristeus antennatus* is documented by the minimum CL for mature individuals as well as and the smaller size at first maturity for both sexes, in relation to *A. foliacea*.

Reference [28] hypothesized that the younger individuals of *Aristeus antennatus* mature for the first time in June because of the puberty moult that delays deposition time and have fewer spawnings. Since this species has an open thelycum, mating and fertilization are completely external processes and the spermatophore is shed off at each molting [29]. Thus at least in the larger specimens, the processes of molting activity, the refertilization, and the multiple spawning in the same reproductive period could be explained.

Regarding GSI monthly values and prematurity stage, the obtained values in this study were in the value range from other studies. Thus for *A. foliacea* the estimated GSI values were slightly lower than those from Sicily [12] and Taiwan [24] but higher than those from the western Ionian Sea [30]. Similarly, the GSI values for *Aristeus antennatus* were higher than those from the Balearic Islands [18, 19] and similar to those from Sicily [31] and the Catalan Sea [18, 19]. In the present study, the two species seem to have comparable reproductive effort, which is directed toward fewer but larger ova in *A. foliacea* or numerous smaller ones in *Aristeus antennatus* [11].

CL_{50sf} and CL_{50mf} from the eastern Ionian Sea seem to be close to the lower values reported in the literature for both species. Thus CL_{50sf} ranges from 34 mm CL (north-eastern Tyrrhenian Sea; [32] 0 to 46.6 mm CL (central Tyrrhenian; [33] for *A. foliacea*, and from 24–28 mm CL (Spanish waters; [34]) to 28.8 mm CL (French coast; [35]) in *Aristeus antennatus*. Also, CL_{50mf} ranges from 36 mm CL (Sardinian waters; [7]) to 43 mm CL (western Ionian Sea; [20]) in *A. foliacea*, and from 18 mm CL (Sardinian waters; [7]) to 35 mm CL (western Ionian Sea; [25, 26]) in *Aristeus antennatus*.

In the study area, *A. foliacea* males were ready to copulate throughout the year, while in *Aristeus antennatus* male reproductive activity was pronounced during late winter-late spring (January-May). The fact that males of both red shrimps have a more extensive reproductive activity than females is related to the observation that immature females receive the spermatophores from the mature males and conserve them till their sexual maturation. This prolonged reproductive activity of both red shrimp males has been also reported from other authors. For *Aristeus antennatus*, [13, 18–20, 34] pointed out that mature males appear all year round, but, unlike the present results, their highest

reproductive activity is observed between late spring-late summer (from May to August). In comparison to other Mediterranean regions, a general tendency for an earlier attainment of male maturity was evident in the present study. The smallest mature male of *A. foliacea* (26 mm CL), for example, is almost the smallest ever reported (from 25 mm CL in western Ionian Sea [20] to 30 mm CL in Sardinia [36]), while that of *Aristeus antennatus* (20 mm CL) lies toward the lower limit of the value range (15.9–26 mm CL in the Catalan Sea) [18, 19, 25, 26]. In addition, the present value for CL_{50sm} for *Aristeus antennatus* (19.36 mm CL) is lower than any value in literature (range from 20 mm CL, Catalan Sea—Demestre, 1990—to 25 mm CL, western Ionian; [25, 26]). Like females, the males of the later species were sexually active within the first year of their life.

In conclusion, the study of the main aspects of reproduction of *A. foliacea* and *Aristeus antennatus* in the eastern Ionian Sea revealed that both species seem to conform to the other Mediterranean regions with regard to their major reproductive traits (i.e., reproductive period, presence of mature males throughout the year, and longer mating and reproductive period in *A. foliacea* than in *Aristeus antennatus*, etc.). The only life-history trait that seems to slightly differentiate the eastern populations of both species is an earlier attainment of sexual maturity in both sexes. This differentiation could be also attributed to the considerably higher water temperature in the eastern Ionian Sea than in the western most areas [37]. Nevertheless, in order to arrive to secure conclusions, our knowledge on the eastern Mediterranean deep-sea shrimp has to be improved by further studies on these populations and also by including a broader ecosystem approach.

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