

Spatial and temporal patterns in the Mediterranean populations of *Aristaeomorpha foliacea* and *Aristeus antennatus* (Crustacea: Decapoda: Aristeidae) based on the MEDITS surveys

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Summary: The aristeids *Aristaeomorpha foliacea* and *Aristeus antennatus* are two species of great economic importance in the Mediterranean Sea, where they are exploited almost exclusively by bottom trawlers. We analysed their geographical and inter-annual patterns using data collected, following a standardized protocol, during the MEDITS international experimental bottom trawl surveys. The data used consisted of standardized abundance and biomass indices, size structure and individual biological information collected in the northern Mediterranean for more than two decades. Several univariate and multivariate methodologies were used to analyse the data. The current study confirms previous findings, such as the longitudinal gradient in the relative presence of the aristeids, but also offers additional information for a better understanding of the intrinsic variability of the data over the years and between areas. Moreover, geographical variability in the somatic condition index is discussed, taking into account the role of environmental conditions and fishing pressure. The large geographical variability found for both species in this regional approach reflects the importance of additional studies at a small-scale geographical level. Such studies could be particularly important for managing and ensuring the stability of these species, for which large regional approaches may be inadequate.

Keywords: *Aristaeomorpha foliacea*; *Aristeus antennatus*; geographical patterns; trawl surveys; abundance; length structure; condition factor; Mediterranean Sea.

Tendencias espaciales y temporales en las poblaciones mediterráneas de *Aristaeomorpha foliacea* y *Aristeus antennatus* (Crustacea: Decapoda: Aristeidae) basadas en las campañas MEDITS

Resumen: Los aristéidos *Aristaeomorpha foliacea* y *Aristeus antennatus* son dos especies de elevada importancia económica en el Mar Mediterráneo, donde se explotan casi exclusivamente con arrastreros de fondo. Se han analizado sus tendencias geográficas e interanuales utilizando datos recogidos, siguiendo un protocolo estandarizado durante las campañas con arte de arrastre de fondo experimental internacionales MEDITS. Los datos utilizados fueron índices de abundancia y biomasa, la estructura de tallas e información biológica individual, recogidos en el norte del Mediterráneo durante más de dos décadas. Los datos recogidos se han analizado mediante diferentes metodologías univariantes y multivariantes. Este estudio confirma algunos resultados previos, como el gradiente longitudinal de su presencia relativa, pero también añade información adicional que permite comprender mejor su variabilidad intrínseca a lo largo de los años y de las áreas. Además, se discute la variabilidad geográfica del índice de condición somática teniendo en cuenta el papel de las condiciones ambientales y de la presión pesquera. La gran variabilidad geográfica descrita para ambas especies en esta aproximación regional refleja la importancia de estudios adicionales a menor escala geográfica, lo que podría ser particularmente importante para la gestión de estas especies, para las que una amplia aproximación regional podría no ser adecuada para asegurar la sostenibilidad de estos importantes recursos marinos.

Palabras clave: *Aristaeomorpha foliacea*; *Aristeus antennatus*; patrones geográficos; campañas de arrastre; abundancia; estructura de tallas; factor de condición; Mar Mediterráneo.

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INTRODUCTION

The giant red shrimp, *Aristaeomorpha foliacea* (Risso, 1827), and the blue and red shrimp, *Aristeus antennatus* (Risso, 1816), are decapod crustaceans with a wide geographic distribution in deep waters that frequently share their distribution. *A. foliacea* inhabits the eastern and western Atlantic, the western Pacific, the Indian Ocean and the Mediterranean Sea (Holthuis 1980, Ragonese 2018). *A. antennatus* has a narrower distribution, throughout the Mediterranean and the eastern Atlantic, from Portugal to the Cabo Verde Islands (Arrobas and Ribeiro-Cascalho 1987). In the Mediterranean, the species show a longitudinal gradient, as *A. antennatus* is more abundant in the north-western areas and *A. foliacea* in the central and eastern ones (D’Onghia et al. 1998, Cau et al. 2002, Cardinale et al. 2017). Both species show genetic divergence between samples from the Mediterranean and other waters. In the Mediterranean, *A. foliacea* showed low genetic divergence, although the possible existence of two somewhat differentiated genetic stocks in the western and eastern Mediterranean has been suggested (Fernández et al. 2013). For *A. antennatus*, Marra et al. (2015) considered that no barriers to gene flow exist in the Mediterranean, but Fernández et al. (2011) considered the Strait of Sicily as a barrier to gene flow and identified one western Mediterranean stock with significant genetic divergence of samples from the eastern ones.

Although both species are generally considered “deep water species”, a eurybathic condition can be recognized; both species show a wide bathymetric distribution, between 60 and 1330 m depth in the case of *A. foliacea*, and between 80 down to 3300 m depth for *A. antennatus* (Politou et al. 2004, Ragonese 2018, Sardà et al. 2004). Notwithstanding this, they are mainly exploited in a narrower preferential range

in which their abundance is higher, between 500 and 800 m depth (D’Onghia et al. 1998, Sardà et al. 2003, Politou et al. 2004). Both species are economically very important but their relative importance in the fishing exploitation shows a clear geographical pattern related to their different geographical distribution. In the western Mediterranean, *A. antennatus* is the most valuable deep water resource and the target of a well-developed bottom trawl fishery (Sardà et al. 2003), while the presence of *A. foliacea* although important in the past (Oliver Massutí 1953, Massutí and Oliver 1975, Cartes et al. 2011), is currently low. The central Mediterranean shows some overlapping in their exploitation, although the species mainly exploited in the Strait of Sicily sensu lato and southern Sardinia is *A. foliacea* (Ragonese 1995). In the eastern Mediterranean, the species are not exploited by the local bottom trawl fishery, as they operate at depths down to 400 m (Mytilineou et al. 2001, Papaconstantinou and Kapiris 2003, Politou et al. 2004). Though there is evidence of exploitation of the species since 2004 in international waters, mainly by Italian fleets (Garofalo et al. 2007), the exploitation status in the area is poorly known (GFCM 2018). The most recent assessments of their state of exploitation showed a generalized situation of overexploitation in the western and central Mediterranean (GFCM 2017).

Due to their high economic importance, numerous studies have analysed the biological and ecological aspects of both species. However, few of the studies cover large spatial areas. Cau et al. (2002) investigated for the first time the space-time distribution, abundance and size structure of both species throughout most of the Mediterranean Sea, showing high variability in the geographical distribution. This study aims to continue the work done then, using the same source of data, which is obtained in a standardized way throughout the European Mediterranean waters. The objective was to analyse the density and biomass indices, size distribu-

Table 1. – Total number (N) of MEDITS surveys, period in which they were carried out and number of valid (V) hauls between 201 and 800 m for each geographical subarea (GSA) and each regional area of reference (RAR). GSA 17 (northern Adriatic Sea) is not included due to the practical absence of the species in the area.

RAR	GSA	N surveys	Period	V hauls
1	1. Northern Alboran Sea	22	1994-2015	411
	2. Alboran Island	9	2006-2009, 2011-2015	52
	5. Balearic Islands	15	2001-2015	272
	6. Northern Spain	22	1994-2015	454
	7. Gulf of Lions	22	1994-2015	231
2	8. Corsica Island (eastern side)	21	1994-2001, 2003-2015	258
	9. Ligurian and northern Tyrrhenian seas	22	1994-2015	1376
	10. Southern and central Tyrrhenian Sea	22	1994-2015	972
	11.2. Sardinia (east)	22	1994-2015	239
3	11.1. Sardinia (west)	22	1994-2015	673
4	15. Malta Island	11	2005-2015	272
	16. South of Sicily	22	1994-2015	968
5	18. Southern Adriatic Sea	22	1994-2015	636
	19. Western Ionian Sea	22	1994-2015	974
	20. Eastern Ionian Sea	14	1994-2001, 2003-2006, 2008, 2013	141
6	22. Aegean Sea	14	1994-2001, 2003-2006, 2008, 2013	693
	23. Crete Island	14	1994-2001, 2003-2006, 2008, 2013	64
	25. Cyprus Island	10	2005-2013, 2015	71

tions and somatic condition of both species, taking into account the geographical and inter-annual variability. To this end, two spatial approaches were followed. The first considered a large geographical scale in order to evaluate the main factors affecting the overall distribution of the two species at Mediterranean level. The second analysed the inter-annual temporal trends of the abovementioned parameters at a smaller subregional scale. In the case of the condition index, however, the inter-annual patterns could not be analysed due to the shortness of the time series available.

MATERIALS AND METHODS

Information concerning *A. foliacea* and *A. antennatus* was analysed. In particular, data from the Mediterranean International Bottom Trawl Surveys programme (MEDITS; Bertrand et al. 2002a, Anonymous 2017) were used. These surveys are carried out in Mediterranean waters from late spring to summer every year, according to a standardized protocol which includes gear characteristics, haul duration and sampling procedures, following a depth-stratified random design, from 10 to 800 m depth (<http://www.sibm.it/MEDITS%202011/principaledownload.htm>). The experimental net used is the high vertical-opening GOC73, which uses a 20 mm diamond stretched mesh codend (Fiorentini et al. 1999). Taking into account consolidated knowledge of the preferential bathymetric distribution of the target species (rarely occurring on the outer shelf, 100-200 m, at least in the season in which MEDITS is carried out; Cau et al. 2002) only valid hauls carried out between 201 and 800 m depth were considered in this study. According to the protocol, expected effective haul duration at these depths is 60 minutes (after a variable pre-haul time; Bertrand et al. 2002b), but if for any reason the haul has to be stopped before, it is considered valid if lasted at least 40 minutes. The sampling period analysed was 1994 to 2015, except for some specific areas, in which the period was shorter (Table 1). Since 2003 the sampling strategy in MEDITS has

used the geographical sub-areas (GSAs) of the General Fisheries Commission for the Mediterranean (GFCM, Fig. 1A). For the requirement of the present analysis, the Mediterranean area covered by the MEDITS programme was divided into six predefined basins (defined as regional areas of reference, RAR), following the approach carried out by Cau et al. (2002) with the first years of the data series (1994-1999) (Fig. 1B; see Table 1 for correspondence between RAR and GSA): RAR1, Algerian Provincial (western Mediterranean and Gulf of Lions); RAR2, Tyrrhenian (Tyrrhenian Sea, Ligurian Sea, eastern coast of Sardinia and Corsica); RAR3, Sardinian (western coast of Sardinia and Gulf of Cagliari); RAR4, Strait of Sicily *sensu lato*; RAR5, Ionian (western and eastern Ionian Sea and southern Adriatic Sea); and RAR6, Aegean (Aegean Sea including the waters around Crete and Cyprus). The northern Adriatic Sea was not considered due to the practical absence of the species in the area. According to the protocol (MEDITS Handbook Version 9, Anonymous 2017), the period of the survey should be centred in June; this period is fulfilled in most cases, with 96.3% of the analysed hauls carried out between April and August and only 3.7% between September and December. The use of this information for each type of data is explained below.

For each valid haul, data on number and weight caught for each species were collected. The swept area from each haul was estimated from the monitoring of the horizontal opening of the gear by specific devices on the head rope of the gear and the distance covered during the haul. These values were used to standardize catches to trawled area, in order to obtain indices of abundance in both number (density index, $N\ km^{-2}$) and weight (biomass index, $kg\ km^{-2}$). Size composition (oblique carapace length, CL, in mm) was computed by sex, species and haul, and numbers for each size class were also standardized by trawled area ($N\ km^{-2}$). Additional information on individual biological parameters (individual CL and weight) for the most recent years (2012-2015) was also recorded.

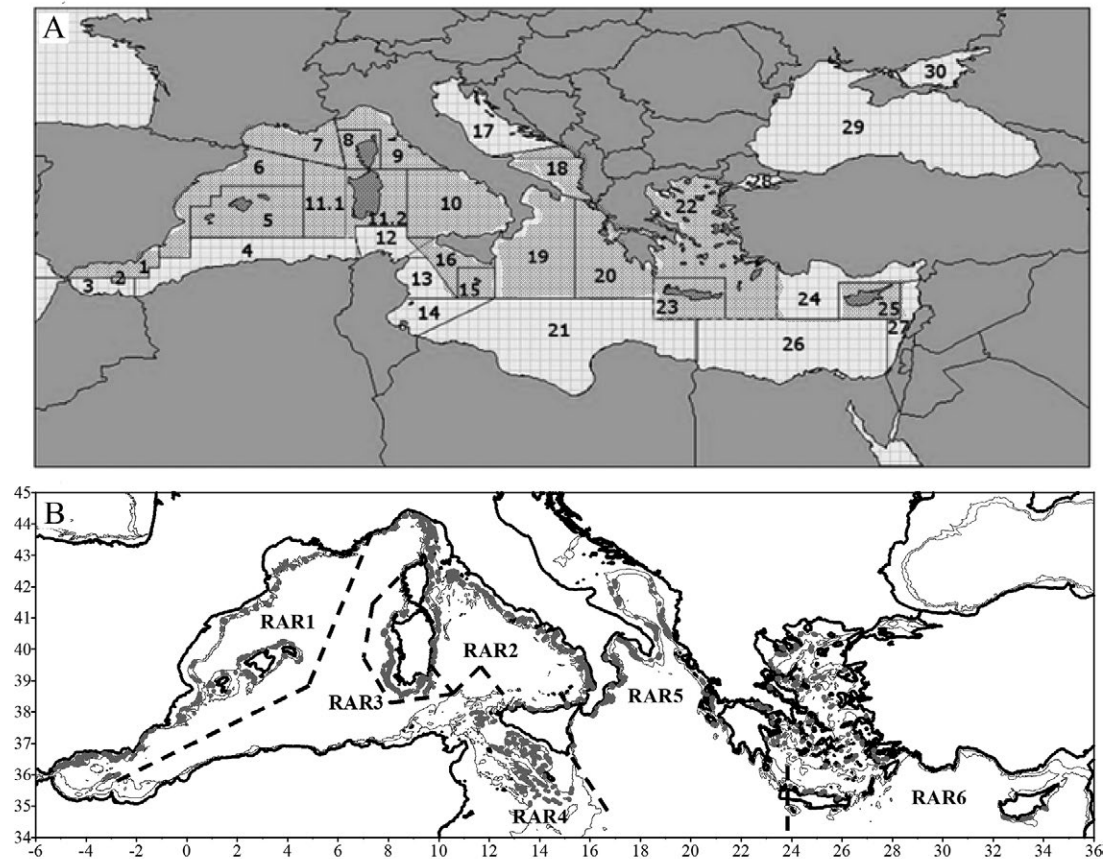


Fig. 1. – A, map of the Mediterranean and Black seas showing the 30 geographical sub-areas (GSAs) established by the General Fisheries Commission for the Mediterranean, with the GSAs included in the present study shadowed. B, map of the study area covered within the MEDITS surveys, with the sampling stations indicated in grey and the regional areas of reference (RAR) considered for the study. Isobaths 200 and 800 m are shown.

For those hauls in which at least one of the investigated species was recorded, the relative importance of *A. foliaceae* in relation to both species was calculated in numbers, as standardized abundance of *A. foliaceae* divided by total standardized abundance of both species together. Sex ratio (as percentage of females of sexed specimens, in abundance) and mean CL by sex (from the standardized size composition, $N\ km^{-2}$) were computed. For both standardized catch and size composition, the entire data set was used. Information for individual CL and weight was used to compute the individual relative condition index (Kn, Le Cren 1951) as observed weight divided by expected weight estimated from a carapace length-weight relationship by species and sex, considering information from all the RARs together. This condition index takes into account the negative allometry in the carapace length-weight relationship shown by both species. Due to the seasonal variations of somatic condition index in relation to maturity stage (Guijarro et al. 2008), this analysis was carried out considering only developing and mature specimens (i.e. stage 2, according to the MEDITS Handbook, Version 9, Anonymous 2017) caught during May and June, which corresponds to the beginning of the spawning period (Kapiris and Thessalou-Legaki 2009).

For the standardized indices, hauls with zero catches in the selected bathymetry were also included. Classic general additive models (GAM; Hastie and Tibshirani 1990) were used to analyse the spatio-temporal trends of the relative importance of *A. foliaceae*, the standardized biomass index and sex ratio for both species. GAMs were carried out with the R package, using variations of GAM formulations as implemented in the *mgcv* library (Wood 2004). A Gaussian distribution was used with log-transformed data. The model selection criterion was based on minimizing the generalized cross-validation (GCV). The lowest GCV indicates the best compromise between model complexities (e.g. number of parameters) and observed data. The covariates considered were year, latitude, longitude, depth (m) and RAR. Classical linear regressions were also used to analyse linear inter-annual trends by RAR of these abovementioned variables and also for the CL for each species. In all cases, a mean value was calculated considering all the hauls per year and RAR. An average of the length-frequency distributions was derived and graphically represented by species, sex and RAR as percentage frequency per length class. Cluster analysis was used to analyse these length-frequency distributions, after standardization, using Bray-Curtis as a similarity index, grouped in 5 mm intervals to simplify interpretation. Due to the short time series for the somatic condition index (2012-2015) and

Table 2. – Total number of valid hauls carried out between 201 and 800 m from 1994 to 2015 by regional area of reference (RAR) and depth stratum (D, 201-500 m; E, 501-800 m), number of hauls with presence of at least one of the species (Hauls one) and of each of them (Af: *A. foliaceae*; Aa: *A. antennatus*) and number of hauls with presence of both species simultaneously (Af+Aa). See Table 1 for RAR denominations.

RAR	Stratum	Total hauls	Hauls one	Hauls Af	Hauls Aa	Hauls Af+Aa
1	D	756	75	12	65	2
	E	664	487	58	467	38
2	D	1536	188	180	29	21
	E	1309	1165	1085	710	630
3	D	376	41	37	24	20
	E	297	288	275	249	236
4	D	524	80	79	2	1
	E	716	684	672	239	227
5	D	722	156	147	39	30
	E	1029	928	732	658	462
6	D	571	4	4	1	1
	E	257	99	95	27	23
Total		8757	4195	3376	2510	1691

the lack of data for some RARs, an analysis of variance was used for testing differences among RARs. A Mann-Whitney pairwise test was used to detect differences among RARs.

RESULTS

From an initial total of 9118 hauls carried out between 201 and 800 m depth between 1994 and 2015, a total of 8757 valid hauls were analysed (Table 1). From them, 47.9% (4195 hauls) had a positive presence of one of the two species (Table 2), 19.2% (1685) of only *A. foliaceae*, 9.4% (819) of only *A. antennatus*, and 19.3% (1691) of both simultaneously. Overall, *A. foliaceae* was caught in 38.5% (3376) of the hauls and *A. antennatus* in 28.6% (2510).

The relative contribution to the abundance index of *A. foliaceae* (as a percentage) showed an overall significant increasing trend in the first part of the series, with maximum values during the period 2000-2005 and a decreasing trend since then (Fig. 2, Table 3). It also decreased significantly with depth in the whole Mediterranean basin. Spatially, the clearest trend was found in longitude, with an increasing west-east trend;

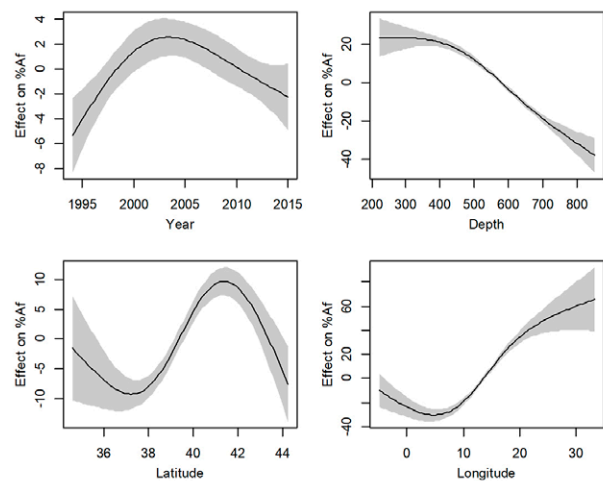


Fig. 2. – Outputs of the statistically significant generalized additive models modelling the percentage contribution (in terms of biomass index, kg km^{-2}) of *Aristaeomorpha foliaceae* (Af) in relation to both species (*Aristeus antennatus* and *A. foliaceae*) in the Mediterranean Sea, for year, depth, latitude and longitude.

Table 3. – Best general additive models obtained for the variables analysed: percentage of *A. foliaceae* in biomass (%Af); density (N km^{-2}) and biomass (kg km^{-2}) indices and sex ratio as percentage of females in abundance (%F). Af, *A. foliaceae*; Aa, *A. antennatus*. In all cases, the best model included all the analysed covariates (year, latitude, longitude and regional area of reference). Goodness of fit (generalized cross validation, GCV), adjusted R-squared (R^2), model performance (deviance explained, DE) and number of hauls analysed (N) are also shown.

Variable	GCV	R^2	DE	N
%Af	904.14	0.507	50.8	4195
N km^{-2} Af	0.762	0.52	52.1	8757
kg km^{-2} Af	1.549	0.551	55.2	8757
N km^{-2} Aa	0.715	0.459	46.0	8757
kg km^{-2} Aa	1.610	0.453	45.4	8757
%F Af	589.8	0.072	7.63	3331
%F Aa	356.21	0.149	15.4	2489

the latitudinal trend showed maximum values around 40-42°N. This was also reflected in the percentage by RAR, in which the western and eastern parts clearly showed the lowest and highest values, but at intermediate longitudes showed low and intermediate values (Table 4A). When analysed by RAR, the only significant trend found was a decreasing one in RAR3 (GSA11; Sardinian Sea, Fig. 3).

The analysis of the standardized biomass index for *A. foliaceae* showed an increase at the beginning of the series but remained stable in the last few years, with maximum values around 600 m and a decreasing trend from that depth (Fig. 4A, Table 3). Spatially, there was a clear decrease south-north and longitude showed a dome shape, with the highest values between 15 and 20°E. By area, RAR3 and 5 showed significant opposite trends, decreasing and increasing, respectively (Fig. 3); no trend was found for the other two areas in which the species was abundant, RAR2 and 4; it was practically absent in RAR1 and only abundant for some years in RAR6. The years in which the survey was not carried out in RAR6 are visible in Figure 3 as missing points (see Table 1).

The increasing inter-annual global trend found for the biomass index of *A. antennatus* (Fig. 4B, Table 3) was not clear when it was analysed by RAR, when no significant linear trend was found (Fig. 3). Each area showed maximum values in different periods, both RAR1 and RAR3 in 2002-2003 and RAR5 in 2009-2010. The highest biomass was found in the deepest

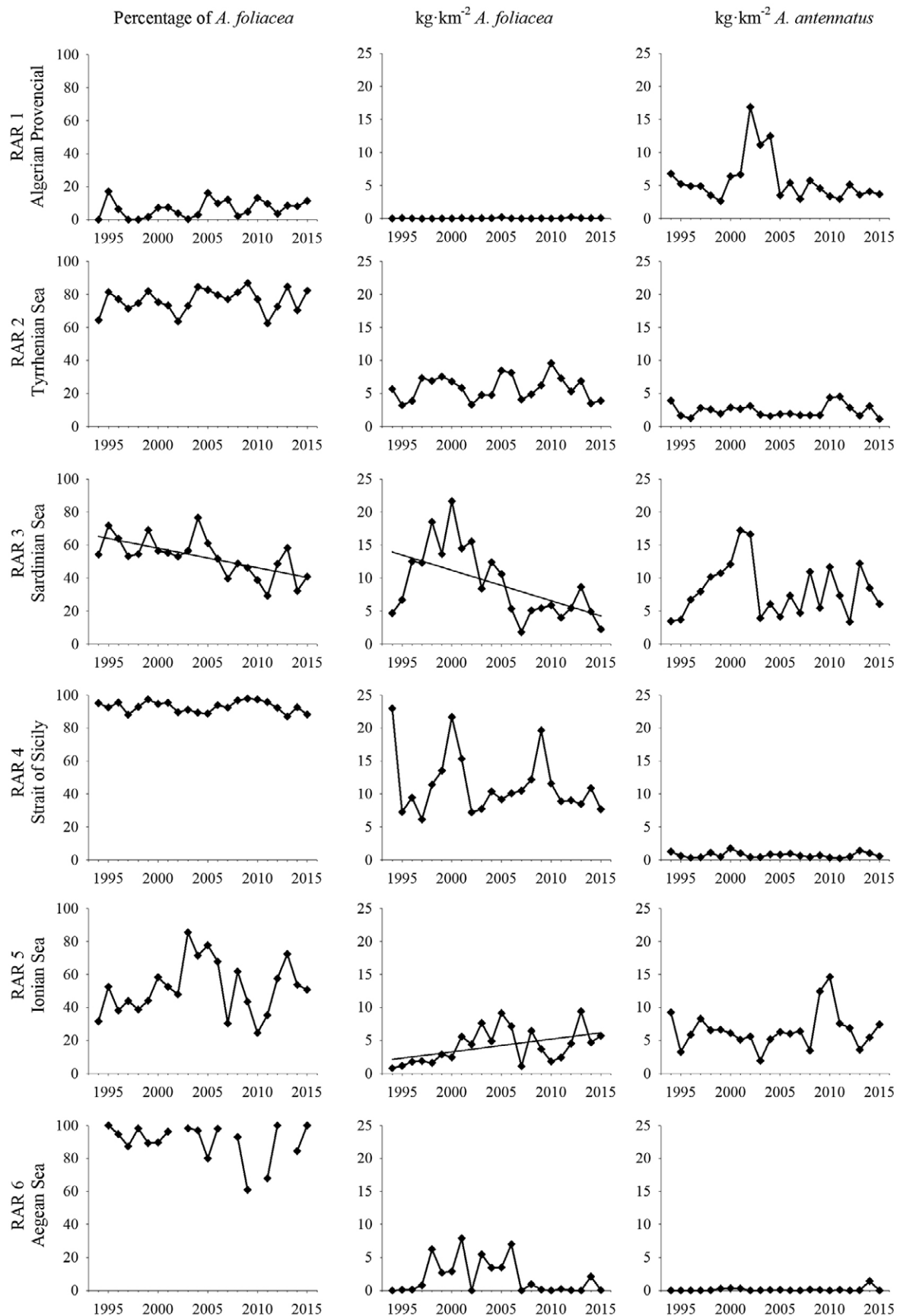


Fig. 3. – Trends in the percentage of *A. foliaceae* (left) and in the biomass index (kg km^{-2}) for *A. foliaceae* (centre) and *A. antennatus* (right) between 1994 and 2015 for each regional area of reference (RAR). The regression line is also shown when there is a significant trend.

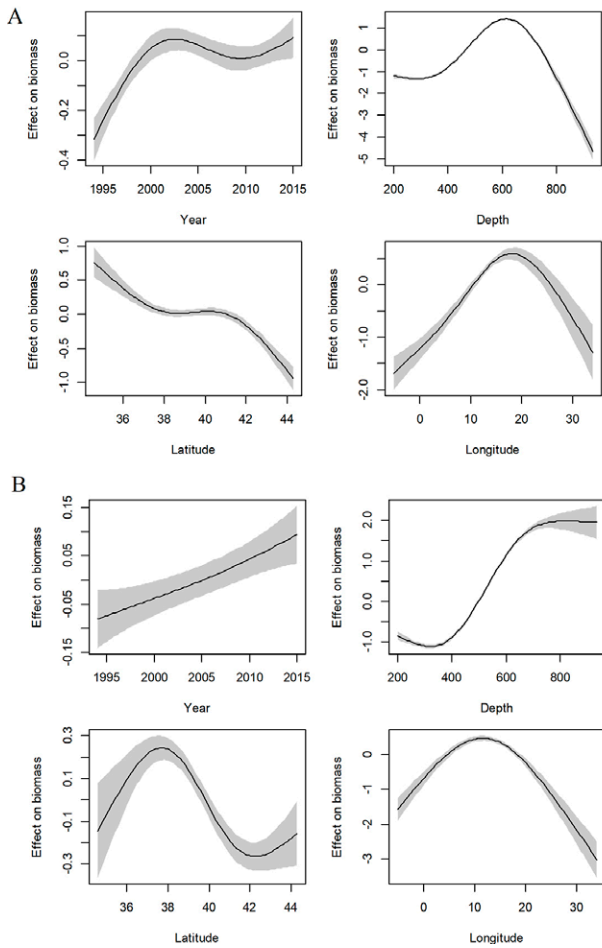


Fig. 4. – Outputs of the statistically significant generalized additive models modelling the biomass (as kg km⁻²) of *A. foliaceae* (A) and *A. antennatus* (B) by each of the four covariates in the Mediterranean.

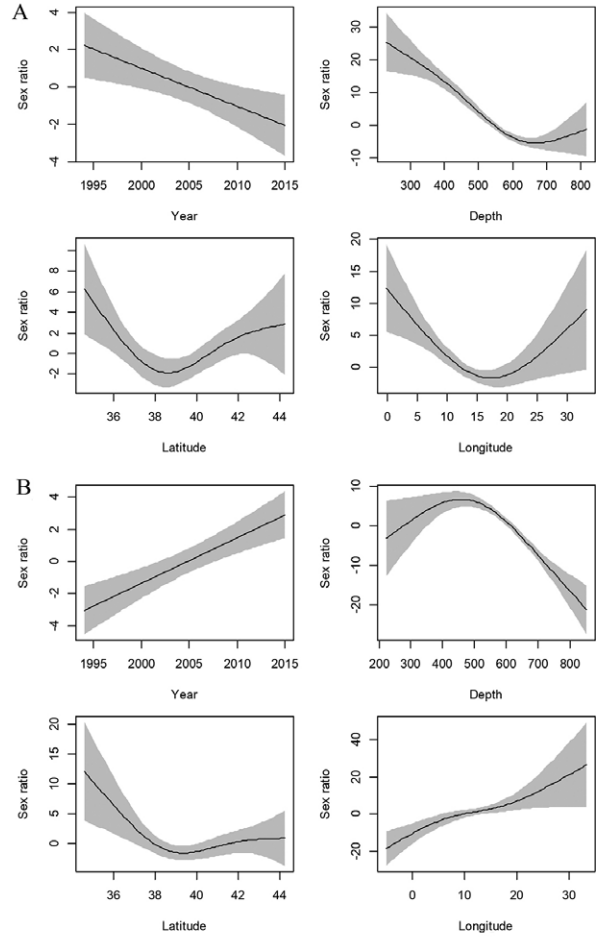


Fig. 5. – Outputs of the statistically significant generalized additive models modelling the sex ratio (as percentage of females) for *A. foliaceae* (A) and *A. antennatus* (B) by each of the four covariates in the Mediterranean.

Table 4. – Percentage contribution by species (in standardized density, N km⁻²) (A), sex ratio (as percentage of females over sexed specimens, in numbers) (B) and mean carapace length (CL, mm) and (in brackets) number of individuals measured (C), by sex (F, females; M, males) for *Aristaeomorpha foliaceae* and *Aristeus antennatus* in each regional area of reference.

		RAR 1	RAR 2	RAR 3	RAR 4	RAR 5	RAR 6
A							
<i>A. foliaceae</i>		6.6	76.3	53.6	92.8	51.8	90.6
<i>A. antennatus</i>		93.4	23.7	46.4	7.2	48.2	9.4
B							
<i>A. foliaceae</i>		63.5	57.6	56.6	52.2	55.2	57.9
<i>A. antennatus</i>		77.4	89.2	88.7	86.2	76.9	75.2
C							
<i>A. foliaceae</i>	F	39.6 (264)	40.3 (53590)	39.0 (7503)	47.8 (13007)	37.3 (22764)	40.3 (1195)
	M	34.6 (186)	32.3 (41664)	32.1 (4879)	35.0 (12380)	31.6 (17953)	33.4 (1090)
<i>A. antennatus</i>	F	36.7 (33138)	40.1 (21784)	33.9 (21784)	44.8 (1824)	39.1 (38638)	40.9 (248)
	M	25.3 (11129)	25.6 (3047)	21.9 (3047)	28.2 (303)	25.7 (13568)	29.2 (128)

grounds (700-800 m); geographically, the maximum was found around 37-38°N latitude, and longitude showed a dome form with the highest values around 10-15°E.

Sex ratio for *A. foliaceae* showed a decreasing trend over the years and with depth (Fig. 5A, Table 3). Spatially, the lowest percentages of females were found around 38-40°N and 15-20°E. By RAR, only in RAR5 was the decreasing trend significant (Fig. 6), and in all cases the average values were around 50% and 65% of females (Table 4B). For *A. antennatus*, the interan-

nual trend was opposite, increasing with time, but also decreasing by depth (Fig. 5A, Table 3). The highest percentages of females were found in the southern and eastern part of the Mediterranean. By RAR, no significant inter-annual linear trend was detected (Fig. 7), with average values between 75% and 90% of females (Table 4B).

Mean CLs for *A. foliaceae* were around 39-40 and 32-34 mm CL for females and males, respectively (Table 4C), with the highest values for both sexes in RAR4 (48 and 35 mm CL for females and males, respectively) and

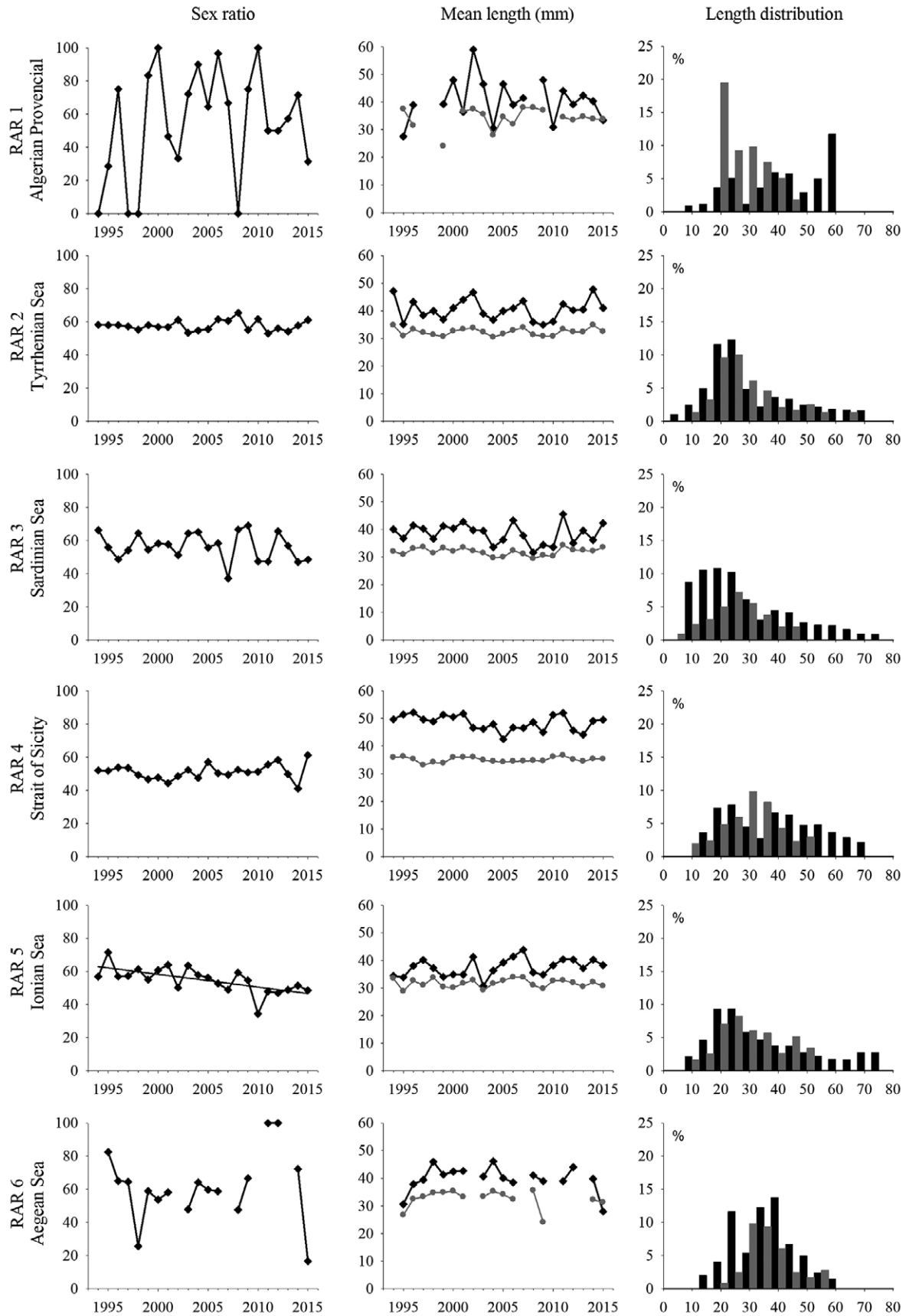


Fig. 6. – Sex ratio (as percentage of females, left) and mean length by sex (mm, carapace length, centre) between 1994 and 2015, and average length frequency distributions (right) for the same period of *A. foliaceae* for each regional area of reference. Females are shown in black and males in grey. Inter-annual linear trends are included when significant (RAR5).

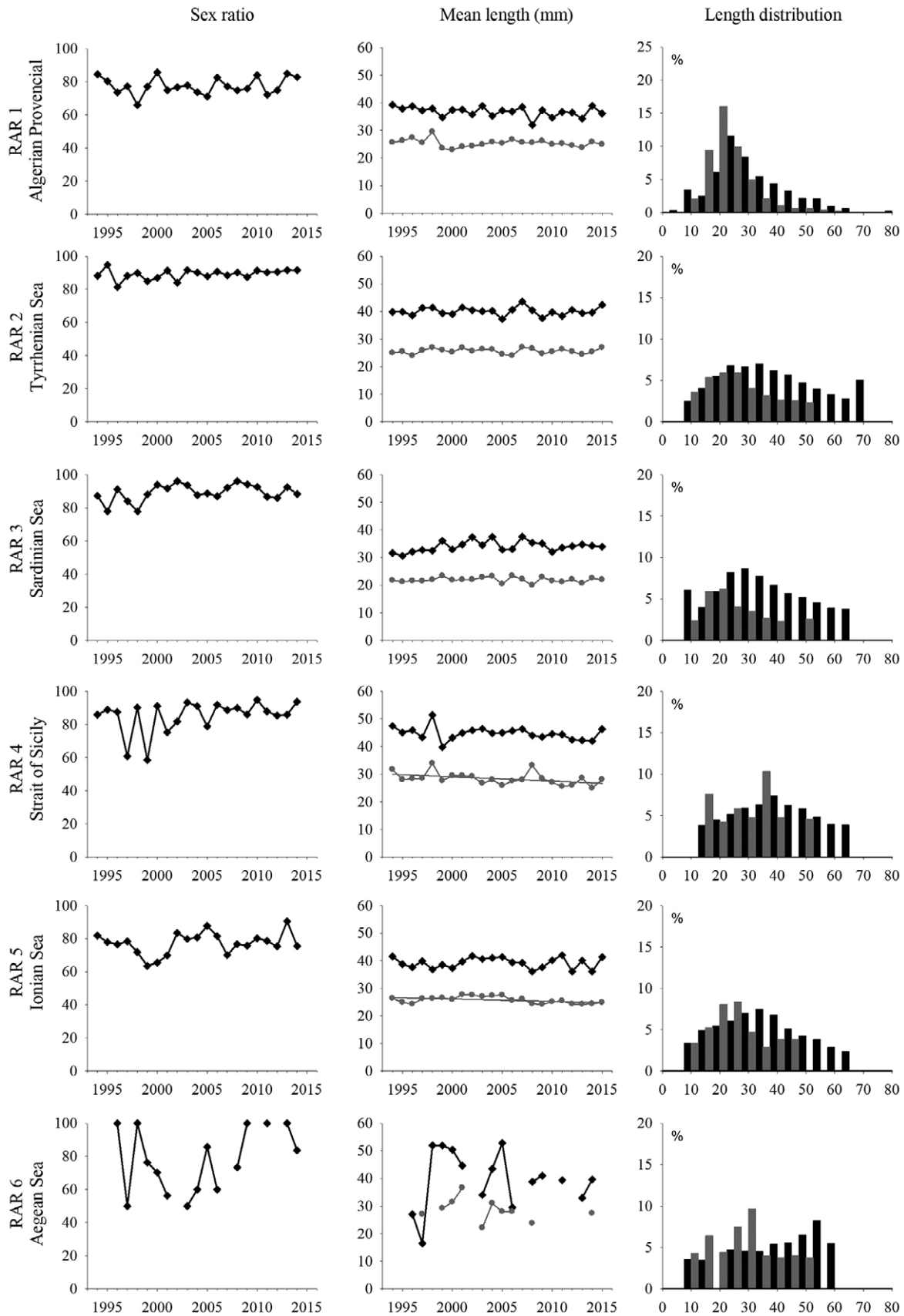


Fig. 7. – Sex ratio (as percentage of females, left) and mean length (mm, carapace length, centre) between 1994 and 2015 and average length frequency distributions (right) for the same period of *A. antennatus* for each regional area of reference. Females are shown in black and males in grey. Inter-annual linear trends are included when significant (mean length for males in RAR4 and RAR5).

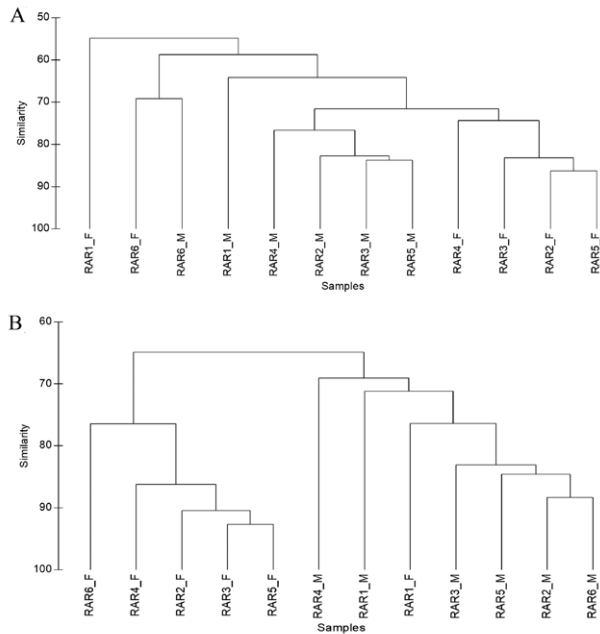


Fig. 8. – Cluster results for the length frequency distributions of *A. foliacea* (A) and *A. antennatus* (B). Codes indicate regional area of reference (RAR) and sex.

the lowest in RAR5 (37 and 32 mm CL for males and females, respectively). For *A. antennatus* (Table 4C), mean values were around 37-40 and 25 mm CL for females and males, respectively, with the highest values in RAR4 for females and in RAR6 for males (45 and 29 mm CL for females and males, respectively). The lowest values were found in RAR3 (34 and 22 mm CL for females and males, respectively). Cluster results for the analysis of the size-frequency distributions for *A. foliacea* showed two groups by sex at around 70% similarity (Fig. 8A), in which all RARs except RAR1 and RAR6 were included. The main difference between these RARs and the rest of them was the narrower length range, especially the absence of individuals larger than 60 mm CL (Fig. 6). Also, RAR1 and RAR6 showed different size distributions: in RAR1, small individuals predominated in males and medium individuals in females, but in RAR6 distributions for both sexes were more similar, with medium values. For *A. antennatus*, two main groups were observed at 70% similarity, one formed by females and one by males from all the areas, with the exception of females from RAR1, which were included in the male group (Fig. 8B). This was reflected in the size-frequency distributions (Fig. 7) in which the relative importance of females larger than 40 mm seemed to be lower in RAR1 than in the rest of the areas, which made its distribution more similar to those of males.

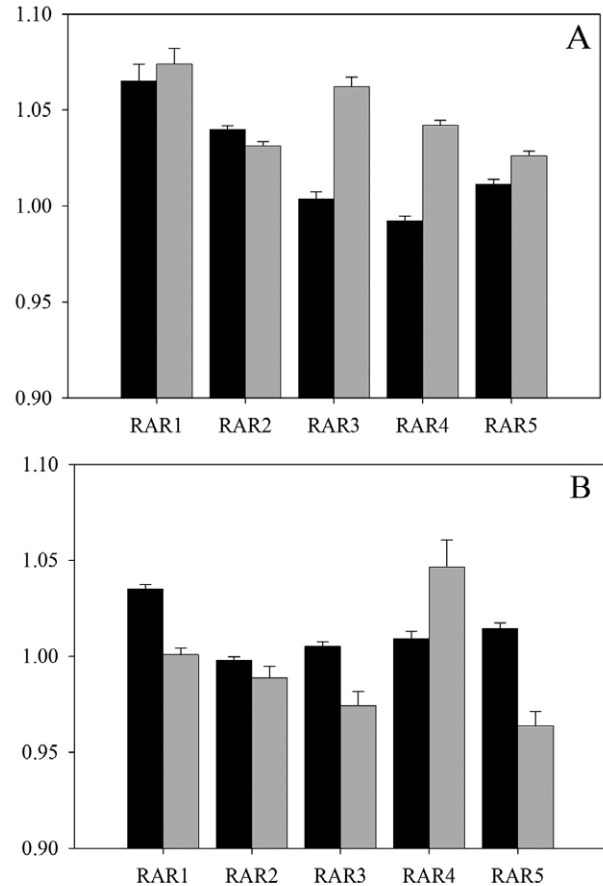


Fig. 9. – Mean condition index by RAR for *A. foliacea* (A) and *A. antennatus* (B) for each regional area of reference and sex (black: females, greys: males). Error bars are standard errors.

Somatic condition index (Kn) showed significant differences between RARs, with trends depending on the species and sex and no clear spatial pattern. For *A. foliacea*, females showed the highest values in RAR1 (Fig. 9, Table 5), followed by RAR2, RAR3 and RAR5, with RAR4 showing the lowest values. For males, the highest values were found in RAR1 and RAR3, followed by RAR4, RAR5 and RAR2. For *A. antennatus*, the highest values for females were also detected in RAR1, followed by RAR3, RAR4 and RAR5, with RAR2 showing the lowest values. For males, RAR4 showed the highest values, followed by RAR1 and RAR2, and RAR3 and RAR5 showed the lowest values.

DISCUSSION

Although the red shrimps *A. foliacea* and *A. antennatus* have a wide geographic distribution, studies

Table 5. – Summary of the results of the analysis of variance and post hoc test (PHT) for the condition index, showing the significance (*: p<0.05, **: p<0.01, ***: p<0.001) of the factor RAR.

		N	RAR	PHT
<i>A. foliacea</i>	F	4652	***	RAR1>RAR2>RAR3=RAR5>RAR4
	M	4048	***	RAR1=RAR3>RAR4>RAR5>RAR2
	F	7510	***	RAR1>RAR3=RAR4=RAR5>RAR2
<i>A. antennatus</i>	M	1954	***	RAR4>RAR1=RAR2>RAR3=RAR5

analysing large sets of data and covering a large geographical scale are rare. By using a 22-year time series of standardized data collected by the MEDITS trawl surveys, our study confirmed the longitudinal trend of the distribution of both species, with an increasing western-eastern pattern for *A. foliacea* and the opposite for *A. antennatus*, as previously reported by Cau et al. (2002). This trend was not detected by Rinelli et al. (2013), probably due to the restriction of analysis to data from the Tyrrhenian (RAR2) and Ionian seas (RAR5), without information for the westernmost (RAR1) and easternmost (RAR6) areas. However, the above authors detected a high patchiness in the distribution of abundances of both species. This high patchiness distribution might be caused by several intermingling factors, such as oceanographic features, fishing pressure, food availability and recruitment success (Rinelli et al. 2013, Orsi Relini et al. 2013, Masnadi et al. 2018), which have an effect over time. In fact, *A. foliacea* used to be very abundant in the western basin (Cartes et al. 2011, Guijarro 2012), and its disappearance has been related to changes in temperature and, especially, salinity (Cartes et al. 2011), which occurred almost at the same time in other areas of the northwestern Mediterranean Sea (Ligurian Sea: Relini and Orsi Relini 1987). According to Rinelli et al. (2013), similar events of drastic change are often not permanent and recovery may occur without any plausible or evident explanation. All of this suggests that, in the past, in agreement with historical evidence, the geographical distribution and balance between the two species was more homogeneous, at least where both species were slightly or moderate exploited.

Interannual variability of both species has been related to large-scale climatic indices, such as the North Atlantic Oscillation (Carbonell et al. 1999, Maynou 2008, D'Onghia et al. 2012) and the Mediterranean Oscillation (Massutí et al. 2008), although this variability can also show different patterns even from nearby ports (Maynou 2008, Hidalgo et al. 2015). The way these indices affect variability may be related to changes in the oceanographic features that may also be linked to more suitable conditions for the species, including temperature and salinity and an enhancement of food supply. Spatial distribution has also been related to cascading of dense shelf waters along the slope (Company et al. 2008), geomorphology (presence of canyons and seamounts; Tudela et al. 2003, Sabatini et al. 2007, 2011), type of bottom (Cartes et al. 2008) and oceanographic features (Guijarro et al. 2008).

It should also be taken into account that all these factors are associated with an intense and prolonged fisheries exploitation, resulting in a concurring effect that makes it difficult to interpret the whole picture of the distribution of the two shrimp species (Rinelli et al. 2013). It is worth nothing that fish and crustacean stocks have shown contrasting trends under similar levels of fishing pressure, which could be related to trophic cascading effects, as crustaceans generally belong to lower trophic levels than exploited fish species, so catching more fish may translate into both lower predation and higher food availability through discards

for crustaceans (Vasilakopoulos and Maravelias 2016). Additionally, crustacean assemblages have shown higher values of biomass at medium or high levels of fishing effort (Guijarro et al. 2011), and the yields of these shrimps increase at certain levels of exploitation (Dimech et al. 2012, Ragonese et al. 1994, Sardà and Maynou 1998). The existence of density-dependent phenomena, with a strong competition among specimens likely due to food limitation, might increment cannibalism incidence, so fishing might induce improvement (at least in the development phase) in the stock performance of these species (Ragonese 2018). This could be particularly true for *A. antennatus*, which seems to be more resilient than *A. foliacea* (Masnadi et al. 2018). The complexity of the dynamics of the species is clearly shown in the present study, in which inter-annual trends show high variability, with only significant linear trends for *A. foliacea* in the Sardinian Sea (RAR3, decreasing) and in the Ionian Sea (RAR5, increasing). It should be noted that the trends depend on the times series considered. For instance, in the Sardinian Sea (RAR3), previous studies with shorter data series identified increasing trends for *A. foliacea* (Cau et al. 2002, Rinelli et al. 2013), the opposite of the decreasing trend identified now. This decreasing trend could be related to the fleet modernization done in the late 1980s and the consequent transfer of fishing pressure towards deeper areas, especially on the western coast of Sardinia. On the other hand, the increasing trend described by Rinelli et al. (2013) for this species in the Ionian Sea has been confirmed here; it should be taken into account that the fishing pressure in the eastern Ionian Sea is limited. On the other hand, the steady state for both species in the Strait of Sicily contrasts with the strong reduction in the bottom trawl fleet carried out in this area in terms of capacity.

Mean length of females was around 39-40 mm CL for both species, and that of males was around 32-33 mm CL for *A. foliacea* and 25 mm CL for *A. antennatus*. Maximum values of mean length for both species and sexes were detected in the Strait of Sicily (RAR4). However, it is also worth noting that a significant decreasing trend of mean length was recorded only in males of *A. antennatus* in RAR4 and RAR5. The removal of larger and older individuals, females in this specific case, is one of the first consequences of fishing exploitation and is directly linked to the selectivity of the gears used. The comparison of size-frequency distribution patterns of *A. antennatus* between exploited and unexploited fishing grounds in the Ionian Sea showed important similarities, although the median CLs were significantly greater in the unexploited grounds (D'Onghia et al. 2005). For this species, in the highly exploited northwestern Mediterranean fishing grounds (RAR1), the relative importance of females larger than 40 mm was lower than that in the remaining areas and, in fact, their size structure was more similar to the male distribution than to the other female distributions. For *A. foliacea*, RAR1 and RAR6 were the most different from the remaining areas, probably due to the low number of individuals caught in both areas. As explained above, *A. foliacea* used to be important in

the past, but in the second half of the 1960s its abundance dropped until it became practically extinct, probably due to changes in the water masses the species occupied (Cartes et al. 2011).

Somatic condition is important not only at an individual level, as an indicator of the health of the single fish or shellfish, but also for the maintenance of the populations, because it influences essential biological processes such as growth, reproduction and survival (Lloret et al. 2002). This is also valid for decapod crustaceans and particularly for *A. antennatus*. A significant positive relationship has been detected between the somatic condition of adults during the months prior to spawning and the number of recruits in the following year, being even stronger when only males were considered (Carbonell et al. 2008). The highest values of somatic condition were observed for both sexes of *A. foliacea* and females of *A. antennatus* in the western Mediterranean (RAR1), which is the area of highest productivity in the Mediterranean as, in its general context of low-productivity, primary production exhibits a west-east decreasing trend (Siokou-Frangou et al. 2010), with the easternmost part being considered ultraoligotrophic (Stambler 2014) and even a marine desert (Azov 1991). Some of the highest values of chlorophyll concentrations in the Mediterranean are observed in this area (the Liguro-Provençal region, the Alboran Sea and the northern Catalan Coast; see Siokou-Frangou et al. 2010 and references cited therein). Individuals inhabiting high-productivity areas are in better somatic condition than those inhabiting less productive areas (Shulman and Love 1999, Lloret et al. 2002, 2005), even at small geographical scales with different levels of primary production or different habitats (Rueda et al. 2014, Ordines et al. 2015). Only for males of *A. antennatus*, the highest value of somatic condition was not found in RAR1 but in RAR4. A decreasing trend over the years of male somatic condition has been detected in the Balearic Islands (RAR1), which may raise concern about the future reproductive potential of the population (Carbonell et al. 2008). On the other hand, body condition may be enhanced under moderate exploitation due to the reduction in density-dependent phenomena (Ragonese 2018), and, in fact, the condition of hake recruits increases when recruit abundance is reduced below the carrying capacity of the ecosystem (Ordines et al. 2019). The western Mediterranean is thus an area with high productivity but also high fishing pressure for these species, so both variables should be considered in future analysis, when longer time series of somatic condition index may be available.

Although the information analysed here was collected during scientific surveys carried out in a certain period of the year, so intraannual variability is not reflected (Guijarro et al. 2008, 2011, Hidalgo et al. 2015), the usefulness of the present study lies in the comparison of a large geographical area and the long time series used. Even if only one or two genetic stocks are considered at Mediterranean level for each species (Fernández et al. 2011, 2013, Marra et al. 2015), the large geographical variability found in this regional ap-

proach reflects the importance of additional studies at a small-scale geographical level. This, together with the need to further study the unexploited part of their populations, is particularly important for the management of these species in order to ensure the sustainability of these important marine resources.

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