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Biological condition and trophic ecology of the deep-water shrimp *Aristaeomorpha foliacea* in the Levantine Sea (SW Turkey)

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Abstract

The trophic ecology (diets, stable isotope composition) and life cycle (gonado-somatic, GSI, and hepato-somatic, HSI, indices) of *Aristaeomorpha foliacea* were analysed seasonally (in May, June, and November 2012 and January 2013) off southeast Turkey (Levantine Basin), over the slope at 442-600 m depth. *Aristaeomorpha foliacea* females were mature in June, suggesting gonad maturity was somewhat delayed off southeast Turkey compared to other areas in the Eastern Mediterranean. The HSI of *A. foliacea* was highest in May and June (8.2% of body weight) for males and both immature and mature females, sharply lower in November (3.5%) and then increasing again in winter (7.1%). Stomach fullness (*F*) showed a tendency similar to HSI in both females and males, increasing from May to June. *Aristaeomorpha foliacea* had rather low δ^{15}N (6.68‰ to 8.26‰) off southeast Turkey, with females having higher δ^{15}N with increasing size. The δ^{13}C signal (-14.85 to -14.68‰) indicated that diet was mainly though not exclusively based on zooplankton (pelagic shrimps and small myctophids of 1.3-4.5 mm TL, cnidarians, hyperiids and pteropods). The increase of *A. foliacea* remains in *A. foliacea* guts and of some benthic prey (polychaetes, bivalves, gastropods) after the reproductive period would explain the moderate depletion of δ^{13}C in spring-summer. The greatest changes in the diet occurred between periods of water mass stratification (June and November) and periods of water mass homogeneity (May and January), with greater consumption of zooplankton in the latter season. *Aristaeomorpha foliacea* seems to have lower reproductive capacity (GSI 5.6%) than other deep-water species of penaeidae living in shallower (*Parapenaues longirostris*) and deeper waters (*Aristeus antennatus*). The species has a more specialized zooplankton diet, exploiting short, more efficient trophic chains, which could be an advantage explaining its dominance in oligotrophic areas of the Central-Eastern Mediterranean, including the Turkish slope.

Keywords: Biological condition, diets, deep-water, *Aristaeomorpha foliacea*, Levantine Sea.

Introduction

The giant red shrimp *Aristaeomorpha foliacea* (Risso, 1827) is distributed worldwide (Crosnier & Forest, 1973, Holthuis, 1980, Udekem d´Acoz, 1999), inhabiting intermediate and deep waters from the northeast Atlantic (western Ireland: Quigley *et al*., 1998; the Bank of Galicia: Cartes *et al*., 2014a) to the entire Mediterranean Sea (Can & Aktas, 2005), the northwest (Wenner & Boesch, 1979) and the southern (Barnard, 1950; Pezzuto *et al*., 2006) Atlantic. It has also been found in the Indo-Pacific as far east as New Zealand and Fiji (Crosnier & Forest, 1973, Udekem d´Acoz, 1999). The species has a relatively narrow depth range, living between 250 and 1300 m, though it is only abundant (at least in the Mediterranean) at mid-slope depths between 450 and 600 m (Cartes, 1995, Belcari *et al*., 2003, Can & Aktas, 2005, Cartes *et al*., 2011a). *Aristeomorpha foliacea* and some other sympatric Aristeidae (e.g. *Aristeus antennatus* in the Mediterranean; *Aristeus varidens* and *Aristeus antillensis* in the tropical and subtropical Atlantic (Crosnier & Forest, 1973; Pezzuto *et al*., 2006) are abundant in deep-sea assemblages and of considerable interest for fisheries.

Aristaeomorpha foliacea has been exploited in Mediterranean waters by trawlers for several decades (Ghidalia & Bourgois, 1961, Belcari *et al*., 2003). In some areas (e.g. the Balearic Basin), it underwent local extinction in the 1960s, which has been correlated with the increase of fishing effort (Bianchini & Ragonese, 1994) and also with other impacts (Cartes *et al*., 2011a, b): the increase of salinity and warming of the Levantine Intermediate waters (Rixen *et al*., 2005; Vargas-Yáñez *et al*., 2009) over the second half of the 20th century due to damming of major rivers. In other areas of the Mediterranean Sea, *A. foliacea* maintains stable populations to date (Papaconstinou & Kapiris, 2003; Belcari *et al*., 2003; Can & Aktas, 2005), although it has been increasingly exploited since 2004 in "virgin" areas (e.g. off Turkey and in the Levantine Sea off Libya and Egypt, Garofalo *et al*., 2007). In most cases, exploitation of such deep-water resources began before reasonably thorough knowledge of their biology and before the ecological indicators of the status of the species and its community were understood. Hence, it is generally unknown to what extent the exploited species would be vulnerable to increasing fishery pressure.

Recently, a comparative study of the trophic ecology and biology of *A. foliacea* along all Mediterranean slopes has shown differences in its ecological condition in different areas (Cartes *et al*., 2014b). However, seasonal changes in the body condition (somatic condition, hepato and gonado-somatic ratios: HSI, GSI) and trophic ecology of *A. foliacea* have not been considered in areas like the Levantine Basin, with only a few studies in other areas (Kapiris *et al*., 2009; Perdichizzi *et al*., 2012). The trophic role of *A. foliacea* has been studied in some detail in Mediterranean waters (Gristina *et al*., 1992; Cartes, 1995; Kapiris *et al*., 2010), including the eastern Basin. *Aristeomorpha foliacea* prey on a variety of benthopelagic organisms, such as the shrimp *Plesionika martia* (Lagardère, 1972; Cartes, 1995; Kapiris *et al*., 2010), small cephalopods (Bello & Pipitone, 2002) and mesopelagic zooplankton (Cartes, 1995). The influence of body size, sex and season on changes in the diet have been analysed in the eastern Ionian Sea (Kapiris *et al*., 2010).

The habitat of *A. foliacea* in the Levantine Sea includes several different water masses that fill this basin. Levantine Surface Water (LSW) is found on the surface, which in summer has the greatest salinity and warmest temperature in the entire Mediterranean Sea. Below LSW, Levantine Intermediate Water (LIW, Hecht *et al*., 1988; Yilmaz & Tuğrul, 1998) occupies the depths inhabited by *A. foliacea*. Levantine basin circulation is a series of quasi-permanent anticyclonic and cyclonic eddies (Özsoy *et al*., 1993) that condition nutrient distribution and phytoplankton production by the duration and intensity of deep winter mixing. This vertical mixing that supplies nutrients to the euphotic zone can reach as deep as 400–500 m (Hayes *et al*., 2010). This enrichment is especially important because of reduced freshwater input to the Eastern Mediterranean (EM) after construction of the Aswan High Dam on the Nile, and lower Black Sea discharge due to low precipitation in recent years (Skliris *et al*., 2007). As a consequence of low water input from land, both studies on zooplankton (based on stable isotopes: Koppelmann *et al*., 2009) and on *A. foliacea* (based on diets and stable isotopes: Cartes *et al*., 2014b) have indicated a shift of nutrient supplies for primary production towards deep-water sources in the Eastern Mediterranean. The Levantine Sea is poorly known as regards deep-sea communities (Galil & Goren, 1994). The area has been defined as the greatest marine 'hotspot' for biological invaders (Edelist *et al*., 2013), after Lessepsian migrants of Indo-Pacific origin have massively entered this basin following the opening of the Suez Canal in 1869 (Zenetos *et al*., 2012), likely changing trophic web function. This important impact has only been reported for littoral systems, though due to the importance of eddies and vertical mixing, effects could reach as deep as 500 m (Özsoy *et al*., 1993) and change the entire trophic chain, from primary producers to top predators, including *A. foliacea*. Both from the perspective of the exploitation of new resources and because the eastern Mediterranean is a vulnerable, strongly impacted marine habitat, it is crucial to have detailed ecological and biological information on *A. foliacea* in the Levantine Sea.

In our study area in the Levantine Sea (off Mersin/Antalya in southeast Turkey) *A. foliacea* is a dominant species and it has stable populations composed of large, reproductive specimens (CL to 67 mm: Can & Aktas, 2005; Garofalo *et al*., 2007). The trophic and biological dynamics of *A. foliacea* were studied based on seasonal sampling in the Levantine Basin. The main objectives of the study are: 1) to identify the seasonal patterns of variation in the diet and feeding of *A. foliacea*, establishing its trophic position in its food web; 2) to explore seasonal variations in aspects of its physiological and reproductive condition in the area; and 3) to discuss as far as possible the main environmental variables controlling those variations.

Material and Methods

Study area

Aristaeomorpha foliacea was sampled off southeast Turkey (Levantine Sea, eastern Mediterranean, Fig. 1) adjacent to Mersin Bay and the Gulf of Antalya at slope depths between 442-600 m (*ca*. at 36º 15.38 N - 34º 19.93 E and 36º 42.01 N - 31º 12.21 E) on board commercial trawlers (*Çinar Bey*, 26.2 m length, 480 HP in Mersin Bay; *Hevesim-I*, 24.0 m length, 610 HP in Gulf of Antalya). A seasonal sampling (24 h cycles with *ca*. 4-5 hauls/cycle) was performed within the same natural year including spring (20 May 2012), summer (29 June 2012), autumn (13 November 2012) and winter (24 January 2013). May, June and January samples were taken off Mersin Bay; the November sample was taken in the Gulf of Antalya, the last area with higher slope steepness than the Mersin slope (see Figure 1). Deep-living shrimp fishing began in the area, e.g. off Mersin, *ca*. 15 years ago, and currently *ca*. 15 boats (17-25 m length; generally 250-400 HP) operate, catching *A. foliacea* and other shrimps at depths of 350-550 m, especially from mid-winter to mid-summer (February-July, Bayhan, pers. obs.). Italian trawlers have also operated off Turkish coasts since 2004 (Garofalo *et al*., 2007), with a maximum of four boats operating off Mersin Bay (Bayhan, pers. obs). Thus, deep-slope communities are submitted to increasing, but still moderate, fishing pressure in the study area. The

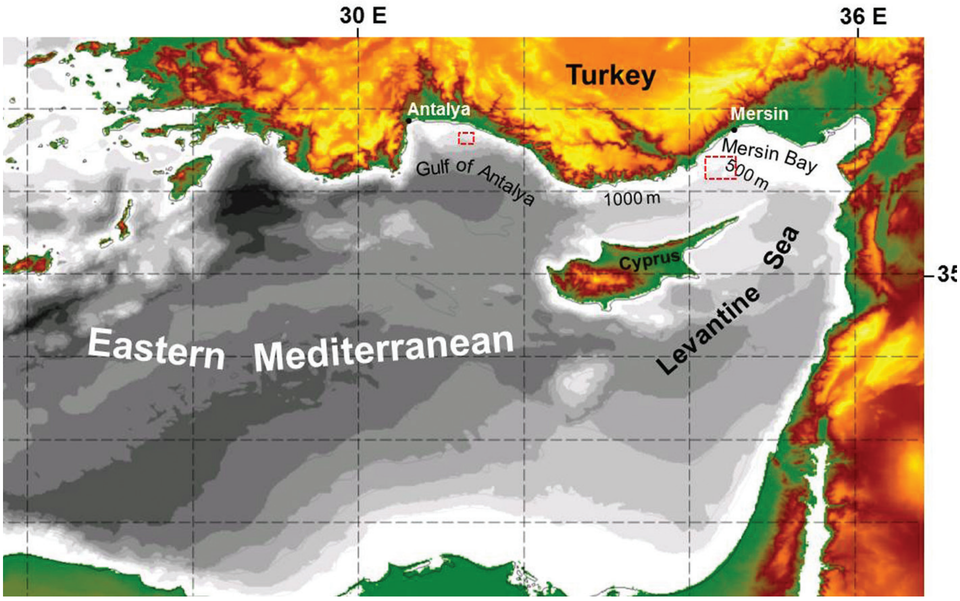

Fig. 1: Map of the study area off southeast Turkey. Squares and circles indicate the area sampled by commercial trawlers off Mersin Bay and in the Gulf of Antalya.

fishing ground off Mersin Bay is on muddy bottom, and situated to the east of a number of submarine canyons, *ca*. 27 km off the nearest coast (Figure 1). The Antalya ground is at 13.8 km off the nearest coast; it has higher slope steepness than the Mersin grounds and is also close to some small canyons, with the large Antalya Canyon at *ca*. 47 km to the W. Fishery pressure on deep resources is lower than off Mersin Bay with only 1 boat regularly operating in the area during the sampling period to catch deep-sea shrimps (Bayhan, pers. obs).

For this study, 240 specimens of *A. foliacea* were analysed: 60 (spring), 65 (summer), 54 (autumn) and 61 (winter) specimens. Specimens were collected in 4-hour hauls. Trawling speed was 2.4 knots, and the commercial gear used had 44 mm cod-end mesh. By-catch composition was established semi-quantitatively (Table 1). Some additional semi-quantitative information on by-catch (mainly decapod and fish species) was collected on 26 June 2013, onboard a commercial trawler off Mersin bay (1 haul; duration: 4 h; 400 m depth). We included this information in order to have an idea on the prey availability for *A. folicaea* with possible implications of feeding by the shrimp while being captured and inside the trawl net.

Biological and trophic analyses: gut contents and stable isotopes

The 240 specimens of *A. foliacea* from the 4 seasonal hauls were analysed to determine:

i) the weight of the hepatopancreas and gonad relative to total specimen weight in order to establish the biological condition of *A. foliacea*;

ii) stomach fullness as an estimate of feeding intensity;

iii) the diet, based on the wet weight (g) of prey identified, whenever possible to species level;

iv) the isotopic composition (δ^{15}N, δ^{13}C) of muscle in order to estimate the position of shrimps in the trophic web and the origin of their food (i.e. planktonic *vs*. benthic).

Shrimps were measured (Cephalothorax length -CL- in mm) and weighed individually to the nearest 0.001g. They were dissected, the hepatopancreas (digestive gland) and gonad was removed and weighed to the nearest 0.001g for each individual to determine the hepato-somatic (HSI) and gonado-somatic (GSI) indices. Gonad maturity was also visually estimated for females, grouping them in two basic categories (immature: transparent, slightly pink, small gonad = “state 1-2”; mature: dark, large gonad = “state 3-4”, following Kao *et al*., 1999). The following indices were used:

1) Hepato-somatic index, HSI (liver weight/specimen weight) x 100

2) Gonado-somatic index, GSI (gonad weight/specimen weight) x 100

Mean HSI and GSI were calculated by season for males and females, in the latter case calculating separately for immature and mature specimens.

Among the 240 stomachs of *A. foliacea* analysed to determine fullness (*F*), 235 contained some food that was analysed to describe the diet. From previous studies (e.g. Cartes, 1991; Cartes *et al*., 2008, 2014b), the authors established using cumulative curves of trophic diversity, that for deep-water decapod crustaceans the analysis of 10-15 specimen´ guts per haul is sufficient to reach for proper estimation of diet. Gut contents of 31, 32, 27 and 40 females were analyzed for all 4 seasons (from May to November) sampled. In parallel, 32, 33, 27 and 21 guts of males were analyzed.

Stomach fullness, *F*, is the ratio of stomach content

Table 1. By-catch composition (semi-quantitative data) in one haul performed on 26 June 2013 aboard a commercial trawler off Mersin Bay (haul duration: 4 h; 400 m depth).

	Number	***Weight*** (WW, Kg)	***Size range***	
Decapod Crustaceans				
Aristaeomorpha foliacea	very abundant	20	31-52 mm CL	
Parapenaeus longirostris	very abundant	20	-	
Aristeus antennatus	-	-	-	*distributed deeper*
Plesionika edwardsi	abundant	5	-	
Plesionika martia	-	-	-	“
Fish				
Galeus melastomus	7	-	35-50 cm TL	
Sciliorhynus canicula	45	-	20-22 cm TL	
Etmopterus spinax	3	-	20 cm TL	
Raja spp.	12	-	-	
Chlorophthalmus agassizi	very abundant	20	10-25 cm TL	
Myctophidae	1	-	-	maybe *Diaphus* sp.
Conger conger	common	-	-	
Hymenocephalus italicus	3	-	-	*small species*
Merluccius merluccius	4	5	-	
Phycis blennoides	3	-	20-30 cm TL	
Hoplostethus mediterraneus	very abundant	-	12-15 cm TL	
Trichiurus lepturus	12	-	-	*captured on surface*
Epigonus sp.	1	-	-	
Helicolenus dactylopterus	abundant	3	17-23 cm TL	
Lepidorhombus boscii	abundant	2	16-20 cm TL	
Lophius piscatorius	common	10	-	
Other invertebrates				
Gryphus vitreus	5	-	-	

weight x 100)/ specimen weight. Stomach content was weighed to the nearest 0.001g. Identification of prey was carried out to the lowest possible taxonomic level under a stereomicroscope (x10-x40). Shrimps cut and crush prey during ingestion (Cartes *et al*., 2008). As is often the case, it was not possible to obtain a direct weight for each prey item and prey type consumed; wet weight (WW, g) was estimated using the points method (Swynnerton & Worthington, 1940) that takes into account the percentage of stomach content volume occupied by each prey. To assign points, stomach content weight was partitioned into prey types by giving a number of points (i.e. 100, 50, 25) to each item of each type in the gut content volume in decreasing order. Then, the likely proportion of weight of each prey type is calculated. These indices are principally employed in biological and diet studies of fish species (Hyslop, 1980), but also deep-sea decapod crustaceans (Cartes, 1994; Cartes *et al*., 2008).

For stable isotope analyses (SIA), muscle tissue (6th abdominal segment) of 37 specimens collected in May and June 2012 was processed. Specimens for SIA included 13 males, in the size-range 31.3-36.9 mm CL and 24 females of 35.6-49.2 mm CL. Their $\delta^{13}C$ and $\delta^{15}N$ were determined. *Aristaeomorpha foliacea* specimens were immediately frozen at sea at -20 °C. In the laboratory, once muscle tissue was extracted and oven-dried to constant weight at 60 °C, and then ground to a fine powder. Following the methods of previous studies (Cartes *et al*., 2007; Fanelli *et al*., 2011*a*), samples were not defatted in order to avoid removing the natural signal of food production in the area. Aliquots of *ca.* 1 mg dry weight per sample were put into tin cups, and the $\delta^{15}N$ and $\delta^{13}C$ were determined with a ThermoFisher Flash EA 1112 elemental analyzer coupled to a Thermo Electron Delta Plus XP isotope ratio mass spectrometer (CNR-IAMC, Naples, Italy; see further details in recently published studies: Fanelli *et al*., 2011 *a*, *b*; Fanelli *et al*., 2013). Experimental precision of estimates was <0.2‰ for $\delta^{15}N$ and <0.1‰ for $\delta^{13}C$. Values for $\delta^{13}C$ and $\delta^{15}N$ were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite (vPDB) and atmospheric N_2 standards, respectively, using the following formula: $\delta\,^{13}C$ or $\delta\,^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$.

Statistical analysis of data

Changes in average diet composition of males and females (per haul) were analysed by means of non-metric Multi-Dimensional Scaling (nMDS), based on a resemblance matrix of prey weights. Multidimensional scaling (MDS) allows visualization of the level of similarity among samples of a data matrix, by displaying the information contained in a distance matrix. In this case, we analysed affinities between diets, for males/ females jointly, in each haul, displaying graphically the similarities between the diets of *A. foliacea* in different hauls in nMDS plots. Distance between hauls (diets) was inversely proportional to their relative similarity. Females of sizes classes with $CL < 35$ mm, $CL \geq 35$ mm, were analysed separately, but only in November when the hauls included females with $CL < 35$ mm.

Prey species appearing in hauls only once were removed from the data matrices. Two similarity indexes were used in nMDS ordinations: i) the Bray-Curtis similarity coefficient (after log-transformation of the data) based on prey weight and ii) Spearman-rank correlation, a measure based on the rank of abundance of prey in diets.

The PRIMER6 & PERMANOVA+ (Clarke & Warwick, 1995; Anderson *et al*., 2008) software systems were used for nMDS analyses.

The factors considered to explain the tendencies found in diets by MDS was sex (males, females) and water column (homogeneity, stratification of the water column). We did not perform any simultaneous sampling of water column T and S (e.g. CTD profiles), so this was based on the hydrographic information found in the Eastern Mediterranean. We considered January and May as periods where the water column was homogenized (similar T at surface and deep layers) while June and November (the 12th of November in this case) were periods of water stratification (Özsoy *et al*., 1993; Yilmaz & Tuğrul, 1998; satellite data). PERMANOVA were performed using one-factor designs, based on the "sex" and "water column" factors, based on Bray-Curtis distance. Significance was set at $p = 0.05$ and p-values were obtained using 999 permutations, with permutation of residuals under a reduced PERMANOVA model method. SIMPER analyses (Clarke & Warwick, 1995) were applied to identify the prey typifying the diet in *A. foliacea* for each significant factor.

Trophic diversity was calculated for diets based on species (in this case prey) richness (S), i.e. the cumulative number of prey in the diet, the Pielou evenness index J (Pielou, 1975) and the widely used Shannon-Wienner index (H). Values for S, J and H were calculated from the mean weights of the prey categories in the diet of individuals analysed in each haul as a function of season and sex.

Environmental data

Monthly surface temperature and Chlorophyll a concentration at the surface (mg Chl a/m^3) were downloaded from satellite imagery from *http://gdata1.sci.gsfc.nasa.gov*. Chl a is the best available proxy we have for surface primary production, i.e. related with possible changes in inputs to food webs. Data were downloaded from January 2012 to February 2013 for the same locations as the ones where the hauls were performed (over 350-550 m) and for a coastal area located at 36.188°N - 33.979°E inside Mersin Bay. Monthly dynamics can be extrapolated to the Gulf of Antalya where our November sample was taken.

Results

The species dominating the catches of 26 June 2013 by number (Table 1) were the decapods *A. foliacea* and *Parapenaeus longirostris* and the fish *Chlorophthalmus agassizi* and *Hoplostethus mediterraneus*.

The HSI of *A. foliacea* was highest in May and June for females of maturity level 2-3, with only small gonad development (HSI=0.082, Fig. 2), sharply decreasing in November to 0.035 (post-hoc Tukey's test, $p < 0.01$) and increasing again in winter to 0.071 ($p<0.05$). The HSI of males showed the same dynamics (Figure 2), with somewhat lower values (HSI=0.072-0.056). Mature females reached the same HSI in June 2012 as that of females with small gonads.

The GSI of females increased from May to June (Fig. 2) and then decreased. The increase was obvious (from GSI=0.007 in May to 0.056 June, post-hoc Tukey's test, $p < 0.001$) for mature females, and also among females with less well-developed gonads (to 0.011)($p < 0.05$). GSI increase was smaller among males in June (from 0.006 to 0.007), but also significant ($p < 0.05$). All females

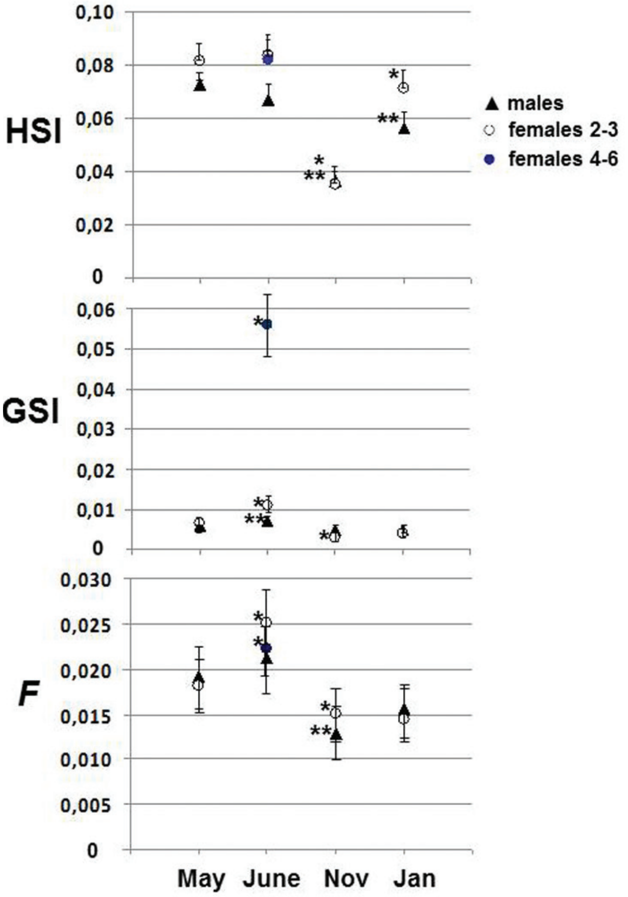

Fig. 2: HSI, GSI and stomach fullness (F) of *A. foliacea* in a natural year between May 2012 and January 2013 off Mersin Bay. (●) mature females; (○) immature females; (▲) males. Confidence intervals at 95% included. Significant changes ($p < 0.05$) comparing two contiguous periods indicated, for females (*) and for males (**).

and males underwent a decrease of gonad condition in November to the lowest GSI values recorded in our series (0.003-0.004), which was significant for females ($p<0.05$).Stomach fullness (F) showed a general tendency in both females and males similar to that described for HSI. It increased from May to June, especially among 2-3 females (from 0.018 to 0.025, post-hoc Tukey's test, $p<0.05$, Figure 2), less so among females with well-developed gonads. There was a generalized significant decrease of F in November (to 0.012-0.014) in females and males ($p<0.05$, in both cases) that was sustained during January. Reconstructing a virtual year, there must be an increase of F in May, prior to gonad maturation of females (June).

Size of *A. foliacea* in the four seasons sampled ranged between 29.3 and 52.6 mm CL in females and 27.1-38.8 mm CL in males. Mean CL ranged from 41.0 mm in May to 44.1 mm in June for females, without any significant differences among seasons. The same was found for males, with mean CL of 32.8 mm in November and 34.2 mm in June. Only in November did we sample mid-sized females of mean CL=30.9 mm that plotted separately in MDS analyses for diet.

Changes in the diet

Aristaeomorpha foliacea consumed different prey depending on season and sex. The nMDS based on Bray Curtis distances (Figure 3a) showed a significant difference in the diet between the periods of water mass stratification (June and November) *vs*. those of homogeneity (January and May) (PERMANOVA: *Pseudo* F=2.18; p=0.04). These same differences were identified using the Spearman rank distance (Figure 3b, PERMANOVA: *Pseudo* F=2.28; p=0.02). Diet composition changed between the two periods not only as a function of prey proportions but of the relative order of importance of prey consumed. Significant diet differences were found between sexes based on Bray-Curtis distances (Figure 3a, *Pseudo* F =2.09, p=0.03). Diets were mainly segregated as a function of sex, with male diets and those of small females (CL < 35 mm, all from November) located in the upper part of the MDS plot and diets of large (CL > 35 mm) females in the lower half (Figure 3b). Non-significant differences were found for the factor "sex" using Spearman distances (PERMANOVA: *Pseudo* F=0.70; p=0.69). Among males (and small females), we found the same diet difference between periods of stratification and homogeneity, i.e. diets of January-May and June-November were segregated. Those differences in diet between sexes were only found based on Bray-Curtis distances, so they are mainly attributable to changes in the proportions of the specific prey items. In both males and females, the main prey were *A. foliacea* and the pandalid *Plesionika martia*. Both prey were more important in the diet of females (64% of wet prey weight) than of males (46.5%). The remaining bulk of the female diet consisted mainly of meso-bathypelagic fish (myctophids and *Hymenocephalus italicus*: 20% of diet), accumulating to 84.1% of diet mass. These mobile and relatively large fish contributed less to the diet of males (only 6.1%). In 2-way PERMANOVA models interaction sex-water mass state was not significant (*Pseudo* F=0.62; p=0.80).

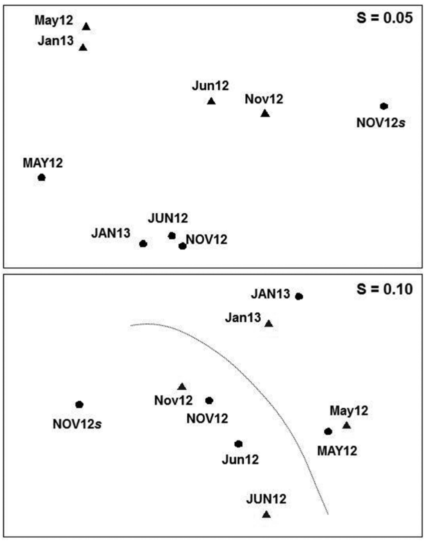

Fig. 3: nMDS analyses based on diets of females and males of *A. foliacea* off Mersin Bay. MDS were performed on shrimp diets based on Bray-Curtis (A, upper plot) and Spearman rank (B, lower plot) distances. (●) females; (▲) males; s label for Nov12 females means "small".

Temporal changes in the diet (weight) consisted in greater consumption of aristeid shrimps, mostly shrimp pieces, in periods of water mass homogeneity (January and May), especially more *Aristeus antennatus* (Table 2). The same tendency was found for cnidarian (siphonophores) and pteropod prey. As regards numbers, more pelagic prey (cnidarians, hyperiidean amphipods and pteropods such as *Creseis* sp., *Atlanta* sp. and *Cavolinia inflexa*, shrimps and small myctophids) were eaten in January and May, before the reproductive period of *A. foliacea* (Table 3). The pelagic shrimp consumed was *Pasiphaea sivado* (in May) and the small myctophids were mainly *Ceratoscopelus maderensis* and *Symbolophorus veranyi*, of TL *ca*. 1.3-4.5 and 2.1 cm respectively (deduced from the size of the otoliths found in stomachs) in January. Moreover, *H. italicus* in *A. foliacea* stomachs in January was small (pre-anal lengths of *ca*. 1.9 cm). In the period of water-mass stratification, especially in June, within the reproductive period of *A. foliacea*, *P. martia* was the main prey. Suprabenthic mysids (mainly *Lophogaster typicus*) also increased in the diet in June-November, while in November, after the *A. foliacea* reproductive period, consumption of benthos increased: polychates, bivalves, benthic gastropods, sponges and benthic foraminifera (Table 3). Myctophids and *H.italicus* were also important

Table 2. SIMPER showing temporal changes in the diet (by weight) of *A. foliacea* off Mersin Bay during in periods of water mass homogeneity (January and May), and water stratification (June-November).

Group HOM
Average similarity: 42,59

Species	Av.Abund	Av.Sim	Contrib%
Aristaeomorpha foliacea	0,08	15,98	37,52
Aristeus antennatus	0,05	9,7	22,78
Plesionika martia	0,02	3,13	7,35
Cnidaria unid.	0,01	2,1	4,93
Macrouridae	0	1,77	4,14
Teleostei	0	1,64	3,86
Ch. appendiculata	0,01	1,36	3,19
Pteropoda	0	1,03	2,43
Hymenocephalus italicus	0,02	1,03	2,43
Myctophidae	0,01	0,52	1,21
Teuthoidea	0	0,5	1,17

Group EST
Average similarity: 43,19

Species	Av.Abund	Av.Sim	Contrib%
Plesionika martia	0,05	16,64	38,53
Aristaeomorpha foliacea	0,07	8,08	18,72
Myctophidae	0,02	5,27	12,19
Hymenocephalus italicus	0,02	2,8	6,47
Lophogaster typicus	0	2	4,62
Teleostei	0,01	1,69	3,92
Cnidaria unid.	0,01	1,38	3,19
Aristeus antennatus	0,01	1,14	2,65

Groups HOM & EST
Average dissimilarity = 62,89

	Group HOM	Group EST		
Species	Av.Abund	Av.Abund	Diss/SD	Contrib%
Aristaeomorpha foliacea	0,08	0,07	1,44	23,33
Aristeus antennatus	0,05	0,01	1,26	14,68
Plesionika martia	0,02	0,05	1,78	12,92
Hymenocephalus italicus	0,02	0,02	1,05	7,98
Other Myctophidae	0,01	0,02	1,39	6,09
Ceratoscopelus maderensis	0,01	0	0,72	2,1
Chaulodius sloani	0	0	0,58	2,09
Lampanyctus crocodilus	0	0	0,74	1,91
Teuthoidea	0	0,01	0,82	1,88
Macrouridae	0	0,01	1,44	1,83
Cnidaria unid.	0,01	0,01	1,19	1,58
Lophogaster typicus	0	0	1,6	1,54
Natantia	0	0	0,58	1,39
Teleostei	0	0,01	1,49	1,38
Ch. appendiculata	0,01	0	1	1,25
Pteropoda	0	0	1,38	1,11
Notolepis rissoi	0	0	0,47	1,09
Myctophum punctatum	0	0	0,84	1,05
Argyropelecus hemigymnus	0	0	0,89	0,99
Pasiphaea sivado	0	0	0,94	0,92
Monodaeus couchi	0	0	0,95	0,87
***Philine* sp.**	0	0	0,55	0,84
Phrosina semilunata	0	0	0,92	0,74
Poriphera	0	0	0,87	0,74

Table 3. Prey identified (by numbers) in the diet of females and males of *A. foliacea* off Mersin Bay and diversity of diets (*S*= no. of prey species; *J*= evenness; *H′*=Shannon diversity).

Aristaeomorpha foliacea	*Levantine Sea*							
	May 2012		**June 2012**		**November 2012**		**January 2013**	
	Females	Males	Females	Males	Females	Males	Females	Males
	n=31	n=32	n=32	n=33	n=27	n=27	n=40	n=21
Size (mm)	35-45	30-35	35-45	30-35	30-45	30-35	35-45	30-35
Cnidaria								
Hydrozoa	0	0	0	0	0	1	1	2
Chelophyes appendiculata	8	11	3	6	12	8	3	9
Other Siphonophora (Diphyidae)	2	3	2	5	0	0	3	0
Cnidaria unid. (nematocysts masses)	12	13	9	8	2	6	4	4
Stephanoscyphus sp.	0	1	0	0	0	0	1	1
Polychaeta								
Glycera sp.	1	0	0	0	0	0	0	2
Harmothoe sp.	0	0	0	0	11	14	0	3
Polychaeta unid.	0	0	0	0	0	0	0	1
Bivalvia								
Taxodonta (*Eunnucula* sp.)	0	0	0	0	0	0	2	0
Abra longicallus	0	1	1	0	1	1	0	0
Bivalvia unid.	0	0	0	0	4	3	0	0
Crustacea								
Ostracoda (Cypridinidae)	0	0	0	1	2	1	0	0
Copepoda Calanoidea	4	7	0	8	1	3	2	9
Amphipoda Gammaridea								
Rhachotropis caeca	0	0	0	0	0	0	1	0
Rhachotropis grimaldii	0	1	0	0	0	0	0	0
Monoculodes packardi	0	0	0	0	1	0	0	0
Gammaridea unid.	0	0	0	0	0	1	0	0
Amphipoda Hyperiidea								
Brachyscelus crusculum	0	0	1	2	0	0	0	0
Anchilomera blossenvillei	2	4	0	1	0	1	0	2
Phronima sedentaria	0	1	1	0	0	0	0	0
Phrosina semilunata	4	8	0	1	1	1	0	0
Isopoda *(Munnopsurus atlanticus)*	0	0	0	1	3	1	1	1
Cumacea								
Diastyloides serrata	0	0	0	1	0	0	0	0
Leucon longirostris	0	0	0	0	1	0	0	0
Procampylaspis bonnieri	0	0	0	0	0	0	0	1
Mysidacea								
Lophogaster typicus	0	0	6	5	10	6	0	1
Boreomysis arctica	0	0	3	2	1	1	2	0
Pseudomma calloplura	0	0	0	1	0	0	0	0
Euphausiacea *(Nyctiphanes couchi)*	0	1	0	0	0	0	0	3
Decapoda								
Aristaeomorpha foliacea	16	11	27	18	8	4	25	9
Aristeus antennatus	11	16	4	5	2	4	1	9
Pasiphaea sivado	11	2	0	1	3	3	1	2
Plesionika gigliolii	0	0	0	0	0	0	1	1
Plesionika edwardsi	0	0	0	0	0	0	1	1
Plesionika martia	2	3	12	13	18	18	11	12
Plesionika sp.	1	0	0	1	0	0	1	0
Processa sp.	0	0	1	1	0	0	0	0
Natantia unid.	2	1	1	0	3	2	0	0
Pagurus alatus	0	0	1	0	1	0	1	0
Ebalia sp.	0	0	0	0	0	0	1	0
Cymonomus granulatus	1	1	0	0	0	0	0	0
Monodaeus couchi	0	1	0	0	0	0	1	5
Munida sp.	0	0	0	0	1	1	0	0
Brachyura unid.	0	0	0	0	1	1	3	4
Crustacea unid.	1	0	0	0	0	0	0	0
Cephalopoda (Teuthoidea)	4	3	1	0	8	8	7	7

(continued)

Table 3 *(continued)*

Aristaeomorpha foliacea	*Levantine Sea*							
	May 2012		**June 2012**		**November 2012**		**January 2013**	
	Females	Males	Females	Males	Females	Males	Females	Males
Gastropoda								
Naticidae	0	8	4	1	0	0	1	0
Rissoidae *(Benthonella* sp.)	0	0	0	0	7	6	1	1
Cymbulia peroni	1	0	0	0	0	0	0	0
Philine sp.	0	0	0	0	4	0	1	0
Clionidae	1	2	1	0	1	1	2	1
Limacina inflata	0	0	1	1	0	2	1	2
Cavolinia inflexa	5	1	0	5	1	2	5	1
Clio pyramidata	0	0	0	0	2	0	1	2
Atlanta sp.	2	6	1	4	0	0	1	8
Cressis sp.	3	26	3	9	2	2	0	2
Pteropod remains	2	3	1	3	0	2	7	4
Echinodermata	0	0	0	0	0	0	1	0
Chaetognatha	6	8	8	22	2	6	0	4
Tunicata *(Pyrosoma atlanticum)*	0	0	0	0	1	0	0	0
Osteychthyes								
Ceratoscopelus maderensis	0	0	0	0	1	0	1	9
Notoscopelus elongatus	0	0	0	0	0	0	1	0
Lampanyctus crocodilus	0	0	0	1	1	1	0	3
Symbolophorus veranyi	0	0	0	0	0	0	1	9
Myctophium punctatum	0	0	1	3	0	0	0	0
Hygophum sp.	0	0	0	0	0	0	3	1
Myctophidae unid.	11	4	12	18	11	12	4	1
Notolepis rissoi	0	0	0	1	0	0	0	0
Chaulodius sloani	1	1	0	0	0	0	0	0
Stomiiformes (*Stomias boa*)	1	2	1	1	0	0	1	1
Argyropelecus hemygymnus	0	0	0	1	0	1	0	1
Cyclothone braueri	2	1	1	0	1	1	0	4
Anguiliformes	0	0	0	0	0	0	2	0
Hymenocephalus italicus	1	1	3	1	12	6	30	10
Macrouridae unid.	10	14	1	4	5	5	1	5
Teleostei remains	9	8	14	6	4	8	2	2
Scales	0	5	0	3	0	1	1	2
Poriphera	0	1	0	0	5	5	0	0
Plant remains	1	0	1	1	1	0	1	1
Organic debris	1	0	1	1	0	1	0	3
Inorganic remains (nylon threats)	2	0	0	1	1	4	1	1
Insecta	0	0	0	0	1	2	0	0
Foraminifera								
Benthic foraminifera								
Uvigerina sp., *Robulus* sp.	1	1	1	0	7	1	2	1
Globigerinidae	0	0	0	2	0	0	0	0
mean nº prey	4,5	5,6	4,0	5,1	5,8	5,6	3,6	7,9
S	34	36	32	40	42	42	46	47
J	0,881	0,8656	0,8175	0,8544	0,8814	0,8915	0,8041	0,9115
H	3,107	3,102	2,833	3,152	3,294	3,332	3,078	3,509

in the period of water-mass stratification, but only fish remains (not entire small fish as in January) were found.

All diversity indexes (S, J, H') showed similar temporal dynamics in both females and males (Table 3), with values being minimal in June (in some cases in May) and increasing (more diverse diets) in November and January. For example, in June, S was 32 and 40 for females and males, respectively, increasing to 42 for both in November and to 46 and 47 in January. Thus, more diverse diets were found in the post-reproductive period.

Trophic position of A. foliacea and the origin of food by stable isotope analyses

Values of δ^{15}N of *A. foliacea* ranged (May-June individuals) between 6.68‰ and 7.96‰ in females, and 7.05‰ and 8.26‰ in males. Females tended to have higher δ^{15}N with increasing size (CL > 44 mm, mean d^{15}N = 7.55±0.16‰; 44 mm < CL > 35 mm, mean d^{15}N = 7.21±0.14‰; *t* test =2.67; *p*=0.01; df=22; Figure 4). Although there was no similarly significant trend, males tended to have an inverse relationship to females regarding size, i.e. larger males had lower δ^{15}N (CL > 34 mm, mean δ^{15}N = 7.38±0.29‰ ; 34 mm < CL > 31 mm, mean d^{15}N = 7.56±0.29‰; *t* test =0.84; *p*=0.41; df= 10; Fig. 4).

Values of δ^{13}C ranged for both females and males within very similar values (-13.91‰ to -15.38‰ in females; -14.15‰ to -15.34‰ in males), which is not a significant difference (Fig. 4). This indicates, basically, the use of the same prey by both sexes, especially in terms of biomass. Among females, both larger (CL > 44 mm) and smaller specimens (44 mm < CL > 35 mm) showed similar mean values (mean δ^{13}C = -14.83±0.61‰ and -14.75±0.27‰, respectively).

Three *A. antennatus* collected in May, sized 33-43 mm CL, showed higher δ^{15}N (8.46‰) than *A. foliacea* (n=18) of comparable size (7.20‰)(*t*=6.4; *p*=10^{-5}).

Environmental changes

Monthly surface T was 21.5 ºC over the fishing grounds of *A. foliacea* in May (Fig. 5) and slightly lower (20.9º C) in the neritic waters of Mersin Bay/Antalya. Temperature increased in June to 25.1-25.2 ºC; it was still high (22.9-23 ºC) in November and then decreased to its lowest values in January (18.5-18.8º C).

Average monthly Chl *a* at the surface peaked inshore in May (0.533 mg/m^3), decreased sharply in June and remained low until September-October 2012 (0.110 – 0.238 mg/m^3), after which it rose again (e.g. in December 2012 it was 0.547 mg/m^3). Offshore, dynamics were similar, with a relatively productive period (0.173-0.251 mg/m^3) in January-May and December-February (Fig. 5), a period of very low surface production in June-September, 0.044 mg/m^3 in August, and then starting to increase, 0.108-0.122 mg/m^3, in October.

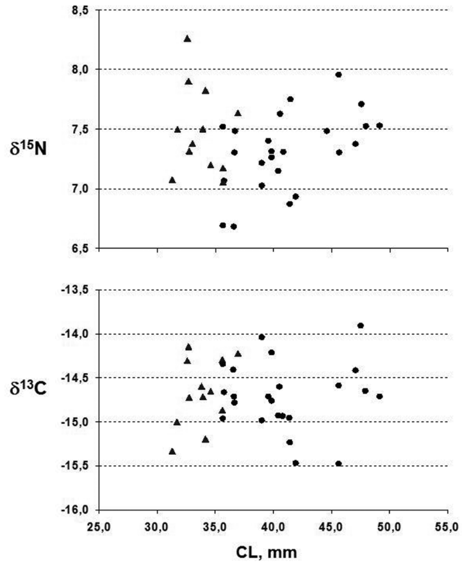

Fig. 4: Isotopic composition (δ^{15}N and δ^{13}C) for *A. foliacea* (May-June individuals) females (●) and males (▲) off Mersin Bay.

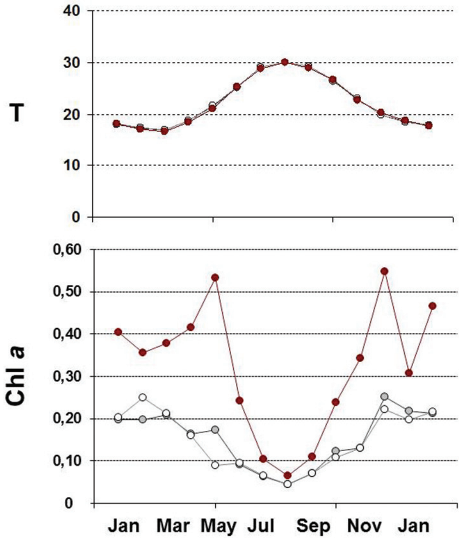

Fig. 5: Monthly surface temperature (T, ºC) and Chl *a* taken off Mersin Bay between January 2012 and February 2013. (●) slope station over 400 m; (○) slope station over 500 m; (▲) shelf station.

Discussion

Spatial heterogeneity in our sampling (between Mersin Bay and Gulf of Antalya) did not seem to have any influence on the intra-annual dynamics of the biological condition and *F* of *A. foliacea*. The two sampled areas off southeast Turkey have similar seasonality, e.g. in the seasons where water masses are homogeneized/stratified (Özsoy *et al*., 1993). Although strong eddies reaching as deep as 500 m can form off the Antalya Gulf in autumn-winter (Özsoy *et al*., 1993), their location is far from the coast, offshore of our sampling area in November, and the expected enrichment of production by eddies moving deep water upward had no positive effect, e.g. on *F* or HSI of *A. foliacea* that reached (both *F* and HSI) their lowest values in autumn-winter. *Aristaeomorpha foliacea* had a biological cycle off southeast Turkey similar to those found in other seasonal or monthly studies on its reproductive biology in the Mediterranean. Belcari *et al.* (2003) found mature females (stage IV) in May in the Tyrrhenian Sea, with mature females (corresponding to high GSI) most prevalent in July. In the Ionian Sea, the reproductive peak was in June-August, with a few mature females in spring (Papaconstantinou & Kapiris, 2003). Off southeast Turkey, gonad maturity seemed to be a little delayed in June compared to other areas (Belcari *et al*., 2003; Papaconstantinou & Kapiris, 2003; Cartes *et al*., 2014b), although the smaller size of females (to 48 mm CL) on 20 May, compared with those of the Tyrrhenian and Ionian Sea (Belcari *et al*., 2003; Papaconstantinou & Kapiris, 2003), could also explain that. Can & Aktas (2005) still found a low proportion (<50%) of mature females (gonad stages S3, S4 and S5) in mid-June close to our study area (Iskenderun Bay). In June, we already found mature females sized 41-42 mm CL off Mersin Bay. Mature females (likely stage IV in Belcari *et al*., 2003; S3 to S5 in Can & Aktas, 2005) had a GSI of 5-12% off Mersin Bay. GSI is a useful measure of shrimp ovary maturity (e.g. Cestari Dumont *et al*., 2007; Farrell *et al*., 2012), allowing interspecific comparisons of potential reproductive capacity of a species. In this sense, GSI_{max} of *A. foliacea* (10-12% in females 42.3-52.3 mm CL) was below the 13-16% GSI of the sympatric species *A. antennatus* (Cartes *et al*., 2008; authors' unpubl. data) in the western Mediterranean. The mean GSI=5.6% in June was less than the GSI=7% of *A. foliacea* in the Ionian Sea (Kapiris & Thessalou-Legaki, 2009). Also, this June GSI was lower than the GSI=7% of *A. antennatus* in the Ionian Sea (Kapiris & Thessalou-Legaki, 2009) and of *P. longirostris* (Bayhan *et al*., 2005) off southeast Turkey. Those two species are on average distributed in shallower (*P. longirostris*) and deeper (*A. antennatus*) waters than *A. foliacea* off Mersin Bay. Although GSI is only a proxy for fecundity, the comparisons suggest relatively low reproductive capability of *A. foliacea* and possibly greater vulnerability to environmental changes, including fishery pressure.

The HSI of *A. foliacea* off southeast Turkey was lower (8.2%) than this ratio in other areas of the Eastern-Central Mediterranean (*ca*. 10-11.5% in the Sicily Channel and the Tyrrhenian Sea), where the species also maintains substantial populations (Cartes *et al*., 2014b). The range of HSI for *A. foliacea* was similar off southeast Turkey to that of *A. antennatus* in the western Mediterranean (in the same period: June-July, Cartes *et al*., 2008; authors' unpubl. data). However, in the Sicily Channel and the Tyrrhenian Sea *A. foliacea* HSI was greater than that of *A. antennatus* (9.5-9.8%). This could be related to higher consumption by *A. foliacea* of pelagic prey (with high energy content: e.g. lipids) than benthos, which is preferentially consumed by *A. antennatus*. This pattern of resource partitioning between *A. foliacea* and *A. antennatus,* i.e. greater consumption of pelagic prey by the former, and of benthic prey by the latter, also seems to be present off southeast Turkey. Examination of four *A. antennatus* guts (females of 33-52 mm CL) in May showed that 39.3% of its diet (by weight) consisted of benthic invertebrates (polychaetes, *Echiurus abyssalis*, sipunculans, bivalves), and only 28.4% was zooplankton (mainly the hyperiid *Phrosina semilunata*).

Aristaeomorpha foliacea had rather low $\delta^{15}N$ (6.68‰ to 8.26‰) in the Levantine Basin, with females tending to have higher $\delta^{15}N$ with increasing size. Considering the $\delta^{15}N$ (2.0–3.1‰) of epipelagic zooplankton found in the Levantine Basin (Koppelmann *et al*., 2003), $\delta^{15}N$ of *A. foliacea* suggests that the species prey there at a moderate level within the trophic web, with estimated TL of 3.53 (Cartes *et al*., 2014b) based on the usually assumed increase of *ca*. 3‰ per trophic step (Minagawa & Wada, 1984; Post 2002). The $\delta^{13}C$ found in the Levantine Sea (-14.85 to -14.68‰) for *A. foliacea* was not especially depleted, so it does not reflect a diet based only on zooplankton. The increase of *A. foliacea* remains in their guts, and of some benthic prey (polychaetes, bivalves, gastropods) after the reproductive period (e.g. in November), would explain this moderate depletion of $\delta^{13}C$. The *A. foliacea* remains in *A. foliacea* guts collected in the Tyrrhenian Sea were from ingestion of specimens as small as CL 19 mm (Cartes *et al*., 2014b). Cannibalism could be greater when *A. foliacea* recruits to the bottom, which happens in March-April off the Tyrrhenian Sea (Belcari *et al*., 2003). Assuming a similar recruitment period in SE Turkey, this would be two months before our $\delta^{13}C$ analyses. However, it is also possible that scavenging due to consumption of fishery discards increases in spring (May-June) off southeast Turkey, a period of more trawling activity off Mersin Bay (Bayhan, unp.). What seems obvious is that consumption of benthic/benthopelagic prey entails parallel $\delta^{13}C$ enrichment. The analyses of 3 *A. antennatus* collected in May, of a size (33-43 mm CL) similar to that of *A. foliacea*, showed higher $\delta^{15}N$ (8.27-8.84 ‰) and slightly more enriched $\delta^{13}C$ (-14.47‰). It is also likely that $\delta^{13}C$ enrichment is due to higher production in inshore-coastal waters, as deduced from satellite imagery data for Chl *a*.

Despite possible consumption of some fishery discards or net feeding (Cartes *et al*., 2014b), the increase of feeding intensity (*F*) in pre-reproductive (May) and reproductive (June) periods seems natural in origin: it was simultaneous to HSI increase, and Kapiris *et al*. (2009) found a similar increase of *F* for *A. foliacea* in spring and a sharp decrease of *F* in autumn after the reproductive period over unexploited depths on the Ionian Sea slope. Also, remains of *A. foliacea*, fish and squid in *A. foliacea* guts were abundant in periods with low or no fishing activity (January and November), with fish consumed in January mainly composed of small myctophids (1.3-4.5 mm TL) and *H. italicus*. Such mobile prey are unlikely a consequence of either scavenging on discards or net feeding, because they are scarcely retained by the 40 mm mesh size used by trawlers. By contrast, remains of fish dominant in by-catch (e.g. *C. agassizi*, *H. mediterraneus*) were not identified in *A. foliacea* guts. Other authors have documented intense predation by *A. foliacea* on swimming prey such as small cephalopods (Bello & Pipitone, 2002). Cephalopods were more important as prey in November off southeast Turkey. Another source of variation in diet results could be related with higher near-bottom zooplankton density in Antalya Gulf (November) due to higher slope steepness. However, any zooplankton prey were more abundant in guts in November than in other seasons sampled off Mersin Bay, e.g. siphonophores were also abundant in May and prey like *P. sivado* and myctophids were more abundant in other seasons than November.

Aristaeomorpha foliacea has been suggested as an indicator species for environmental changes in deep-water ecosystems (Cartes *et al*., 2011b). It seems to have lower reproductive capacity than other deep-water penaeoidean shrimps and a diet more specialized on zooplankton. This last aspect, i.e. capacity to exploit trophic chains directly connected with primary producers, could explain its dominance in oligotrophic areas off Turkey and in the whole Central-Eastern Mediterranean. However, greater dietary specialization and perhaps rather low fecundity would increase species vulnerability to fishery pressure.

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