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 δ15N (6.68‰ to 8.26‰) off southeast Turkey, with females having higher δ15N with increasing size. The δ13C signal (-14.85 to -14.68‰) indicated that diet was mainly though not exclusively based on zooplankton (pelagic shrimps and small nyctophioids 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 δ13C 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 penaeideai living in shallower (*Parapenaeus 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, Udeken 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, Udeken 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, Belcar et al., 2003, Can & Aktas, 2005, Cartes et al., 2011a). *Aristaeomorpha 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, Belcar 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; Belcar 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. *Aristaeomorpha 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 (Skliiris 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 (Gailì & 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 36° 15.38 N - 34° 19.93 E and 36° 42.01 N - 31° 12.21 E) on board commercial trawlers (*Çınar 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
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. foliacea* 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 ($\delta^{15}N$, $\delta^{13}C$) 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 catch deep-sea shrimps (Bayhan, pers. obs).

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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' gut's 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...
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 δ13C and δ15N 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., 2011a), 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 δ15N and δ13C 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., 2011a, b; Fanelli et al., 2013). Experimental precision of estimates was <0.2‰ for δ15N and <0.1‰ for δ13C. Values for δ13C and δ15N were obtained in parts per thousand (‰) relative to Vienna Pee Dee Belemnite (vPDB) and atmospheric N2 standards, respectively, using the following formula: δ13C or δ15N = [(Rsample/Rstandard) – 1] x 10 3, where R = 13C/12C or 15N/14N.

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)

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).

<table>
<thead>
<tr>
<th>Decapod Crustaceans</th>
<th>Number</th>
<th>Weight (WW, Kg)</th>
<th>Size range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aristaeomorpha foliacea</td>
<td>very abundant</td>
<td>20</td>
<td>31-52 mm CL</td>
</tr>
<tr>
<td>Parapeneaus longirostris</td>
<td>very abundant</td>
<td>20</td>
<td>-</td>
</tr>
<tr>
<td>Aristaeus antennatus</td>
<td>abundant</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>Plesionika martia</td>
<td>-</td>
<td>-</td>
<td>distributed deeper</td>
</tr>
<tr>
<td>Fish</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galeus melastomus</td>
<td>7</td>
<td>-</td>
<td>35-50 cm TL</td>
</tr>
<tr>
<td>Sciliorynchus canicula</td>
<td>45</td>
<td>-</td>
<td>20-22 cm TL</td>
</tr>
<tr>
<td>Eumopterus spinax</td>
<td>3</td>
<td>-</td>
<td>20 cm TL</td>
</tr>
<tr>
<td>Raja spp.</td>
<td>12</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Chlaenothalamus agassizi</td>
<td>very abundant</td>
<td>20</td>
<td>10-25 cm TL</td>
</tr>
<tr>
<td>Myctophilae</td>
<td>1</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Conger conger</td>
<td>common</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Hymenoc扯rus italicus</td>
<td>3</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Merluccius merluccius</td>
<td>4</td>
<td>5</td>
<td>-</td>
</tr>
<tr>
<td>Physic blemnides</td>
<td>3</td>
<td>-</td>
<td>20-30 cm TL</td>
</tr>
<tr>
<td>Hoplostethus mediterraneus</td>
<td>very abundant</td>
<td>-</td>
<td>12-15 cm TL</td>
</tr>
<tr>
<td>Trichirius lepturus</td>
<td>12</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Epigonus sp.</td>
<td>1</td>
<td>-</td>
<td>captured on surface</td>
</tr>
<tr>
<td>Helicolenus dactylopterus</td>
<td>abundant</td>
<td>3</td>
<td>17-23 cm TL</td>
</tr>
<tr>
<td>Lepidorhombus bosci</td>
<td>abundant</td>
<td>2</td>
<td>16-20 cm TL</td>
</tr>
<tr>
<td>Lophius piscatorius</td>
<td>common</td>
<td>10</td>
<td>-</td>
</tr>
<tr>
<td>Other invertebrates</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gryphus vitreus</td>
<td>5</td>
<td>-</td>
<td>-</td>
</tr>
</tbody>
</table>

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was inversely proportional to their relative similarity. Females of sizes classes with CL < 35 mm, CL ≥ 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-Wiener 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).

Temporal changes in the diet (weight) consisted in greater consumer of aristeid shrimps, mostly shrimp pieces, in periods of water mass homogeneity (January and May), especially more Aristaeus 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 inflixa, 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: polychaetes, 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

<table>
<thead>
<tr>
<th>Species</th>
<th>Av.Abund</th>
<th>Av.Sim</th>
<th>Contrib%</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Aristaeomorpha foliacea</em></td>
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<td>15.98</td>
<td>37.52</td>
</tr>
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### Group EST
Average similarity: 43.19

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### Groups HOM & EST
Average dissimilarity = 62.89

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<th>Group EST Av.Abund</th>
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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).

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<th>Aristaemorpha foliacea</th>
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<td>Females</td>
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<td>n=32</td>
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<td>3</td>
<td>1</td>
<td>0</td>
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</tr>
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(continued)
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 \(\delta^{15}N\) of \(A. \text{foliacea}\) 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 \(\delta^{15}N\) with increasing size (CL > 44 mm, mean \(\delta^{15}N = 7.55\pm0.16‰\); 44 mm < CL > 35 mm, mean \(\delta^{15}N = 7.21\pm0.14‰; t \text{ 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 $\delta^{15}N$ (CL > 34 mm, mean $\delta^{15}N = 7.38\pm0.29\%o$; 34 mm < CL > 31 mm, mean $\delta^{15}N = 7.56\pm0.29\%o$; t test =0.84; p=0.41; df= 10; Fig. 4).

Values of $\delta^{13}C$ 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 $\delta^{13}C = -14.83\pm0.61\%o$ and -14.75\pm0.27\%o, respectively).

Three *A. antennatus* collected in May, sized 33-43 mm CL, showed higher $\delta^{15}N$ (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 °C over the fishing grounds of *A. foliacea* in May (Fig. 5) and slightly lower (20.9° C) in the neritic waters of Mersin Bay/Antalya. Temperature increased in June to 25.1-25.2 °C; it was still high (22.9-23 °C) in November and then decreased to its lowest values in January (18.5-18.8° 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.

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 homogenized/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. *Aristaedemorpha 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

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

Fig. 5: Monthly surface temperature (T, °C) 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.

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 & Aktaş, 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 higher consumption by $A$. foliacea, preferentially consumed by relatively low reproductive capability of $A$. foliacea and possibly greater vulnerability to environmental changes, including fishery pressure.

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$A$. foliacea had rather low δ¹⁵N (6.68% to 8.26%) in the Levantine Basin, with females tending to have higher δ¹⁵N with increasing size. Considering the δ¹³C (2.0–3.1‰) of epipelagic zooplankton found in the Levantine Basin (Koppelman et al., 2003), δ¹⁵N 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 δ¹³C 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 δ¹³C. 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 δ¹³C 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, unpub.). What seems obvious is that consumption of benthic/benthopelagic prey entails parallel δ¹³C 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 δ¹³N (8.27-8.84 %) and slightly more enriched δ¹³C (-14.47‰). It is also likely that δ¹³C 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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References


