Seasonal changes in the dietary patterns and reproductive aspects of deep-water rose shrimp *Parapenaeus longirostris* in the central Adriatic Sea

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ABSTRACT: The deep-water rose shrimp *Parapenaeus longirostris* is one of the most important commercial species caught by trawl fisheries in the Mediterranean Sea. The species has a warm-water affinity and its landings are increasing in the whole basin. Detailed information on its trophic ecology, niche width and role within demersal food webs is dated or lacking in the Adriatic Sea, the most exploited basin of the Mediterranean. Therefore, to detect seasonal changes in diet and trophic levels, seasonal samplings were conducted in this area from January to December 2021, collecting 400 specimens, and integrating information from both stomach content analysis and stable isotope analyses (SIA). To identify potential links between the biological cycle of the species and fluctuations in energy demand, seasonal changes in fullness, as a proxy of feeding intensity, and gonadosomatic and hepatosomatic indices were assessed. The deep-water rose shrimp is confirmed to be a benthic feeder that predominantly preys on molluscs, crustaceans, fish, echinoderms and polychaetes. According to SIA, *P. longirostris* is defined as a secondary consumer. Observed seasonal dietary changes precede the reproductive periods, likely due to the need for more energetic prey.

KEY WORDS: Stable isotopes analysis · Stomach contents · *Parapenaeus longirostris* · Reproductive patterns · Trophic position · Mediterranean Sea

1. INTRODUCTION

1.1. Geographical and bathymetric distribution

The deep-water rose shrimp *Parapenaeus longirostris* (Lucas, 1846), has a broad geographic range, from the waters off northern Spain to those of southern Angola in the Atlantic, as well as the entire Mediterranean basin and the Sea of Marmara (Holthius 1980, Farfante & Kensley 1997, Sobrino et al. 2005). In the Mediterranean Sea, this species lives on sandy-muddy bottoms at depths between 20 and 840 m (Tom et al. 1988, Politou et al. 2005), although it is mainly distributed between 100 and 400 m (Holthuis 1980, Sobrino

et al. 2005). This species shows a size-related bathymetric distribution, with juveniles (immature individuals smaller than 16 mm carapace length, CL) settling in shallower areas (usually between 100 and 200 m) and larger individuals moving into deeper waters (Mori et al. 2000a, Politou et al. 2008).

1.2. Biology and ecology

The deep-water rose shrimp is an iteroparous species, reproducing several times during the year in different seasons, depending on the region, depth and temperature. In the Atlantic Ocean, reproduction occurs

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mostly in 2 periods (summer and autumn–winter; Sobrino 1998, Sobrino et al. 2005), whereas in the Mediterranean Sea, several periods have been identified throughout the year, with a preference for spring and autumn (Mori et al. 2000b, García-Rodríguez et al. 2009). Both sexes reach sexual maturity during the first year of life across the whole Mediterranean Sea (Sobrino et al. 2005). The smallest females found in the Tyrrhenian and Ionian Seas measured 16 mm CL (Spedicato et al. 1996, De Ranieri et al. 1998, Relini et al. 1999, Mori et al. 2000b). Females are generally more abundant and larger than males (Froglia 1982, Ardizzone et al. 1990). The deep-water rose shrimp shows an affinity for warm water; in the Mediterranean Sea, its trends of abundance and commercial catches are strongly linked to sea temperature fluctuations, which likely affect the survival of larvae during the planktonic phase (Ligas et al. 2011, Colloca et al. 2014).

The deep-water rose shrimp can be considered an active predator of bathypelagic, benthic and endobenthic prey, while also acting as a scavenger (Ribeiro Cascalho & Arrobas 1983, Mori et al. 2000a, Kapiris 2004). It exhibits distinct behaviours during day and night periods. During the daytime, it typically remains close to the seabed, displaying the so-called 'digging phase', predominantly feeding on benthic organisms (Relini et al. 1998). At night, it rises from the seabed to feed on bathypelagic plankton in the water column (Sobrino et al. 2005).

The movement patterns described above are influenced by light; this species is more active during the night, coinciding with reduced activity of predatory species (Hughes 1968). This behavioural trait also significantly impacts its sensitivity to trawling activities, as indicated by Geraci et al. (2021) and Sonderblohm (2011). Furthermore, the deep-water rose shrimp often shares its habitat with the Norway lobster *Nephrops norvegicus* (Linnaeus, 1758) and the sea pen *Funiculina quadrangularis* (Pallas, 1766); the latter acts as a habitat-forming species on muddy bottoms (Bertrand et al. 1997, Nouar & Maurin 2001, Ceriola et al. 2008) and can be affected by bottom trawling activities targeting the 2 decapods (Martinelli et al. 2023). Zacchetti et al. (2022) reported seasonal changes in the diet of *N. norvegicus*; given the coexistence in the same area and possibly similar feeding behaviour, it might be expected that such variations could also be traced in the diet of *P. longirostris*.

1.3. Economic aspects

The Adriatic Sea represents one of the most-exploited fishing grounds for the deep-water rose shrimp fishery within the Mediterranean Sea, with average catches of 11 114 out of 13 900 kt yr^{-1} reported for the entire Mediterranean over the period 2010–2020 (FAO 2021a). Landings of this species have grown consistently during the last years in the Adriatic Sea (Martinelli et al. 2020, Chiarini et al. 2022), likely due to its affinity for warm waters (Colloca et al. 2014).

1.4. Integrated approach to the study of feeding ecology

Given the wide distribution of this species and its significant economic importance in the Mediterranean basin, and especially in the Adriatic Sea, it is essential to highlight seasonal changes in its diet and investigate their potential drivers such as reproductive periods, sex and sizes. This approach is necessary for the optimal management of the species and to anticipate potential impacts on the benthic community and its functioning. This information is essential in view of an ecosystem approach to fisheries (Garcia et al. 2003).

The feeding ecology of a species has mostly been studied through stomach content analysis (SCA) (Hyslop 1980, Welden et al. 2015). However, because of the difficulties in identifying taxa and the amount of unidentified material depending on species' feeding habits and digestion, this approach has several drawbacks (Garrison & Link 2000, Parslow-Williams et al. 2002). SCA only offers a snapshot of the diet at a specific point in time and space, necessitating multiple samples to fully understand the overall feeding ecology of an organism (Fanelli et al. 2010). In the last decades, the use of stable isotope analysis (SIA) has shown to be particularly effective for studies on aquatic food webs, and the most frequently used tracers are stable isotopes of carbon (^{13}C) and nitrogen (^{15}N) (Divine et al. 2017, McCormack et al. 2019). The isotopic composition of a species' carbon provides hints on the origin of the ingested organic matter due to an increase in ^{13}C of approximately 1‰ per trophic level; on the other hand, nitrogen isotope values typically increase by 2.5 to 3.4‰ from prey to consumer and serve as proxies for trophic position of a species (Post 2002, Sweeting et al. 2007, Caut et al. 2009, Layman et al. 2012). If integrated, these methodologies may also be used to assess the trophic status of a species and reduce possible mistakes in diet estimation caused by changes in prey composition, habitat or ontogeny (Genner et al. 1999, Cocheret de la Morinière et al. 2003, Bearhop et al. 2004, Rybczynski et al. 2008). Combining SCA and SIA approaches is strongly advised to properly understand temporal

changes in the feeding ecology of a species (Rybczyn-ski et al. 2008, Fanelli & Cartes 2008, 2010, Fanelli et al. 2022, 2023a, Zacchetti et al. 2022).

2. MATERIALS AND METHODS

2.1. Study area

The Adriatic Sea is a semi-enclosed basin within the Mediterranean, located between the Italian peninsula and the shorelines of Slovenia, Croatia, Montenegro and Albania. Its main axis extends from northwest to southeast, spanning around 800 km in length and 200 km in width. It is classified as an epi-continental basin, and its depth increases from north to south, reaching a maximum depth of 1200 m in the southern part. This depth gradient allows identifying 3 sub-basins (Northern, Central, and Southern Adriatic; Artegiani et al. 1997, Penna et al. 2023). According to the General Fishery Commission for the Mediterranean Sea

(GFCM), the Adriatic is included in 2 geographical sub-areas (GSAs), namely GSA 17 (northern and central sub-basins) and GSA 18 (southern sub-basin; Fig. 1). Specifically, the fishing ground indicated as 'Off Ancona', in the central Adriatic Sea (Fig. 1) is heavily exploited by trawlers (Russo et al. 2018). For a more detailed description of the study area, refer to Zacchetti et al. (2022).

2.2. Field sampling

Sampling of commercial demersal species is regularly carried out in GSA 17 by the National Research Council - Institute for Marine Biological Resources and Biotechnology of Ancona, within the European Data Collection Framework (EU 2008). For this study, we analysed a total of 400 specimens of deep-water rose shrimp, comprising 279 females (F) and 121 males (M), caught in the 'Off Ancona' fishing ground from January to December 2021. Seasonal samplings were
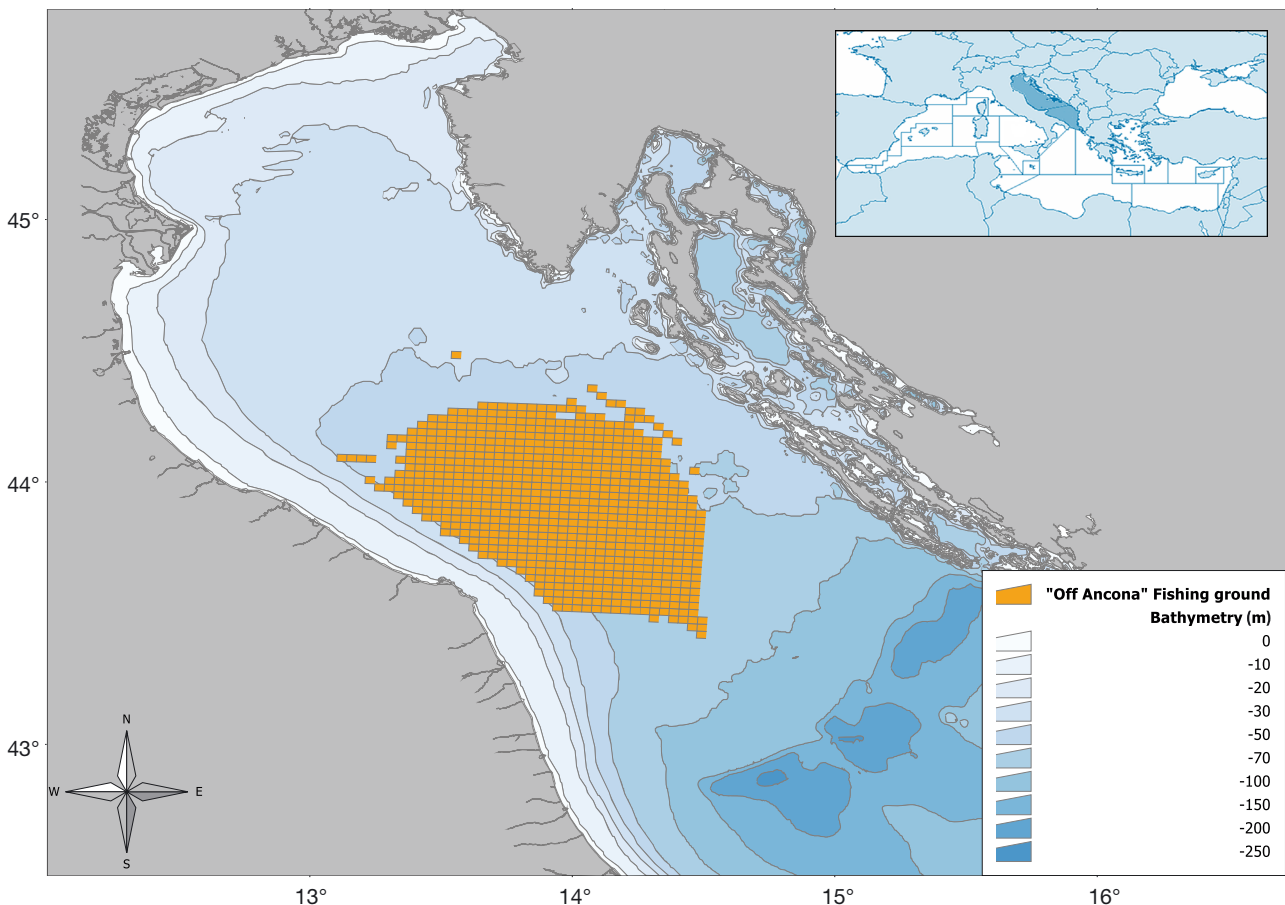

Fig. 1. The Mediterranean Sea and division into General Fishery Commission for the Mediterranean Sea (GFCM) Geographical Sub-Areas (the Adriatic Sea in dark blue; from top to bottom, GSA 17 and 18, respectively) (inset). The 'Off Ancona' fishing ground in the central Adriatic Sea, as defined by Zacchetti et al. (2022) and Angelini et al. (2020), is indicated by orange cells

carried out on board a commercial bottom trawler (overall length: 25 m, tonnage: 98.5 t, engine power: 480 KW) at a depth between 50 and 70 m. According to European and national regulations, the net cod-end had a 50 mm diamond mesh (EU 2006). The analysed samples consisted exclusively of adult individuals and encompassed 100 specimens in winter (February), 81 in spring (early June), 111 in summer (early September) and 108 in autumn (November). All prey considered for SIA were collected in the same fishing ground ('Off Ancona') in 2021.

2.3. Evaluation of ovarian maturity and biometric data

According to ICES guidelines (ICES 2010), sex was determined based on the external morphology of the first pair of pleopods, and macroscopic maturity stages were determined only for females. Furthermore, the gonads of 7 females in winter and 12 females in summer were removed and preserved in Dietrich solution (900 ml distilled water, 450 ml 95% ethanol, 150 ml 40% formaldehyde, 30 ml acetic acid) for histological analysis to validate the sexual development stage at the microscopic level. Gonads were dehydrated, embedded in paraplast, sectioned into 6 μm slices, mounted on slides and stained with Harris haematoxylin and eosin (Pearse 1985). Gonad tissues were observed under a light microscope (Leica DM4000B) at different magnification levels, and the stage of maturity was assigned at a microscopic level according to the ICES scale (ICES 2010). The sex ratio was also estimated as follows: total number of females divided by the sum of the total number of females and males F/(F+M). For each individual, the wet weight (WW, g) was recorded using a precision scale (Radwag WLC 6/F1/K balance, accuracy: 0.1 g) and CL (mm) was measured using a calliper to produce a length–frequency distribution (LFD). Gonads, hepatopancreas and full stomach weights (WW, g) were weighed using a Mettler-Toledo XP204 scale (accuracy: 1 mg) after dissection with laboratory scissors and tweezers to estimate fullness, gonadosomatic (GSI) and hepatosomatic (HSI) indices as follows:

$$\text{Fullness index} = \text{stomach content weight / body weight} \times 100 \tag{1}$$

$$\text{Gonadosomatic index (\%GSI)} = \text{gonad weight / body weight} \times 100 \tag{2}$$

$$\text{Hepatosomatic index (\%HSI)} = \text{hepatopancreas weight / body weight} \times 100 \tag{3}$$

The fullness index is considered a measure of feeding intensity (Fanelli et al. 2009), the GSI is frequently used as a proxy for gonad maturity and to emphasise the various periods of the reproductive cycle, and the HSI is considered a proxy for energy reserves stored in the liver (Jones & Obst 2000). The HSI and GSI were computed for both sexes as well as in relation to season; females spend more energy on reproduction than males, and the liver is crucial for energy storage (Kao et al. 1999, Tsikliras et al. 2010). For each variable, the Games-Howell test was then carried out for non-parametric comparisons of groups (seasons).

2.4. SCA and SIA

All collected specimens were used for SCA. Once the stomach was everted in a Petri dish, each prey item was identified to the lowest taxonomic level possible. The contribution of each prey to the total stomach contents was calculated using the subjective point approach (Swynnerton & Worthington 1940), as many prey items were crushed and heavily digested, making it difficult to weigh them separately. The frequency of prey occurrence (%F = [number of stomachs containing prey / total number of stomachs] × 100), the numerical abundance (%N = [number of prey / total number of prey] × 100) and the prey biomass (%W = [wet weight of prey / total weight of prey] × 100) of prey were then computed. The index of relative importance (IRI) for each prey group, according to Pianka (1973), was then calculated as %IRI = (%N + %W) × 100. This index was expressed as IRI = (IRI*i* / ΣIRI) × 100 (Fanelli et al. 2010). The coefficient of vacuity was calculated according to Hureau (1970) (%V = [number of empty stomachs / total number of stomachs] × 100). Using the Shannon-Wiener index, the trophic diversity was computed per year and per season based on the prey abundance (Shannon & Weaver 1949).

For SIA, a total of 32 individuals (8 per season: 4 females and 4 males) were analysed. A piece of muscle tissue (from the abdomen without exoskeleton) was dissected from the selected specimens and oven-dried at 60°C for 24 h (Fanelli et al. 2010). To obtain $\delta^{13}C$ and $\delta^{15}N$ values, ca. 0.5–1 mg of tissue was placed into tin capsules and introduced in an elemental analyser (Thermo Flash EA 1112), coupled through a continuous-flow to an isotope-ratio mass spectrometer (Thermo Delta Plus XP). $\delta^{13}C$ and $\delta^{15}N$ values were obtained in parts per thousand (‰) relative to Vienna Pee Dee belemnite (VPDB) and atmospheric N_2 standards, respectively, according to the following formula:

$$\delta^{13}\text{C or } \delta^{15}\text{N} = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 10^3 \quad (4)$$

where $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. Based on the standard deviations of internal standards from the International Atomic Energy Agency (IAEA-CH-6, IAEA-NO-3 and IAEA-N-2), the analytical accuracy varied from 0.10 to 0.19‰ for $\delta^{13}\text{C}$, and from 0.02 to 0.08‰ for $\delta^{15}\text{N}$. Additionally, samples of the bivalves *Anadara kagoshimensis* (Tokunaga, 1906) and *Mimachlamys varia* (Linnaeus, 1758), the flatfish *Citharus linguatula* (Linnaeus, 1758) and copepods were prepared for SIA as representative of potential benthic and pelagic prey in order to estimate the trophic position (TP) of *P. longirostris* (see Section 2.6). Additionally, since lipids were not removed from the samples, a correction equation was applied to $\delta^{13}\text{C}$ values for samples with C:N ratios >3, by using the relationship between C:N ratios and the $\delta^{13}\text{C}$ signatures according to Post et al. (2007):

$$\delta^{13}\text{C}_{\text{normalized}} = \delta^{13}\text{C}_{\text{untreated}} - 3.32 + 0.99 \times \text{C:N} \quad (5)$$

where $\delta^{13}\text{C}_{\text{untreated}}$ is the $\delta^{13}\text{C}$ of the bulk (not-defatted) samples.

2.5. Statistical analysis on stomach content data

Univariate analyses were used to test the differences in the sex ratios, %GSI, %HSI and fullness indices by season and sex. First, Levene's test was used to determine if the data complied with the assumption of homoscedasticity. In case of homogeneity, 2-way ANOVAs were performed to test the single effect on each dependent variable and interaction of sex and season (independent variables). If the hypotheses were not satisfied, nonparametric ANOVAs were performed. Welch's *t*-test, which is used to examine the distribution probability of 2 variables, was used to test if there were differences in mean CL between males and females (Underwood 1997). The R packages 'Dplyr', 'ggplot2' and 'car' were used for univariate analyses (Wickham 2016, Fox & Weisberg 2019, R Core Team 2023). Seasonal diet variations were then analysed using multivariate methods following the same 2-way experimental design, described above. First, a non-metric multi-dimensional scaling (nMDS) analysis was carried out on the Bray-Curtis resemblance matrix of fourth-root transformed prey biomass data. Using permutation procedures and a Monte Carlo test to determine p-values, a 2-way permutational multivariate analysis of variance (PERMANOVA, Anderson et al. 2008) was then conducted to examine variations between levels of components (season and sex), with

season (fixed, 4 levels) and sex (fixed, 2 levels) crossed within each other. Permutations of residuals were run under a reduced model, and the significance level was set at $\alpha = 0.05$. Similarity percentage (SIMPER) was used to evaluate the taxa that mostly contributed to the similarity/dissimilarity between and within groups. In order to visualise separation among samples based on hypothesised variables, the factor identified as significant in PERMANOVA (along the 2 axes; Clarke & Gorley 2006) was subjected to canonical analysis of principal coordinates (CAP) (Anderson & Willis 2003). The software PRIMER v6 & PERMANOVA+ was used for all multivariate analyses (Clarke & Gorley 2006, Anderson et al. 2008).

2.6. Statistical analysis on stable isotope data

To assess the isotopic niche width throughout the year, Bayesian statistics, available in the R package 'SIBER', were used to construct standard ellipse areas (SEAs) for the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (Jackson et al. 2011). The posterior distribution of the covariance matrix for each group was then obtained using a Bayesian SEA analysis (Jackson et al. 2011). The SEA corrected for limited sample size (SEAc) was used to estimate the isotopic niches for each species. The R package 'tRophicPosition' was used to calculate the TP (Quezada-Romegialli et al. 2018), including in the analysis the isotopic data of potential prey, sampled in the same study area. Prior to conducting mixing models aimed at identifying the primary dietary contributors for *P. longirostris*, a simulation was performed through the R package 'splancs' (Rowlingson & Diggle 2021). This simulation considered the isotopic signatures of consumers, along with those (plus standard deviations) from potential dietary sources and trophic enrichment factors (Parnell et al. 2013). Furthermore, particulate organic matter (POM) as a potential food source was examined. However, as POM was not collected during this study, POM values from another location within the Adriatic Sea were used (Faganeli et al. 2009), according to other studies carried out in the area (Da Ros et al. 2023, Fanelli et al. 2023b). The mixing polygon was calculated for each iteration of source data, and each point within the polygon played a role in determining whether consumers fell within its boundaries or on its periphery. Iterations continued until the variance of the mixing polygon's area reached a stable point, as per the approach outlined by Smith et al. (2013). This analysis was useful to identify the most suitable food sources for inclusion in the mixing model, which was constructed using the R package 'SIMMR'

(Parnell et al. 2013). The outcomes of this model were then employed to investigate the proportions of different prey items in the diet of *P. longirostris*. This analytical approach effectively discriminates among various food sources by examining the isotope values extracted from the organisms' tissue samples (Parnell et al. 2013). The prey items considered for the mixing models were grouped into 4 categories as follows: (1) copepods, (2) benthic shrimps, including *Solenocera membranacea* (Risso, 1816) and *Processa edulis* (Risso, 1816); (3) benthic fishes, namely *Gaidropsarus biscayensis* (Collett, 1886) and *Callionymus maculatus* Rafinesque, 1810; and (4) bivalves (*M. varia* and *A. kagoschimensis*). All isotope data used in these analyses are provided in Table 1.

underwent shape changes as size increased. EVOs are polyhedral cells with a variable number of highly basophile nucleoli, which migrate towards the border of the cell, while the nucleus remains central; the oocytes show endogenous vitellin platelets in their ooplasma, which becomes more granular (Fig. 3A). As vitellogenesis progresses, the oocytes move toward the periphery of the ovary. The mature stage is characterised by the presence of advanced LVO (ALVO) cells with acidophile lipo-proteic vesicles (yolk globules) of exogenous origin. The nucleus changes its previous spherical aspect, locally undergoes modifications and migrates towards the peripheral area, and then the cortical granules appear (these cells can indicate imminent spawning, Fig. 3B). In the spent stage, the ovary tissue

3. RESULTS

3.1. Allometric and biometric indices

Specimens of *Parapenaeus longirostris* analysed here showed a bimodal LFD, with females larger than males (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m748p099_supp.pdf). Females ranged from 18 to 33 mm CL (mean ± SD: 23.9 ± 3.42 mm), whereas males ranged from 16 to 29 mm CL (20.9 ± 1.98 mm). According to the results of Welch's t-test ($t = 11.164$, df = 366.1, $p < 0.001$), the LFD varied significantly between sexes during the year. The average sex ratio throughout the year was 0.7, with females being prevalent in spring (0.62), summer (0.75) and autumn (0.88), while males and females were equally numerous in winter (0.5).

The highest GSI value for females was recorded in summer (5.86 ± 1.28), while the lowest was recorded in spring (0.59 ± 0.37). The GSI of males was generally lower than that of females, with variations throughout the year ranging from 0.21 to 3.49 (Fig. 2). Females reached 2 GSI maximum peaks in winter and summer; these results were validated by histological analysis, which showed maturing, mature and spent females in these seasons (Fig. 3). The maturing stage was characterised by a quick growth of the oocytes. Early (EVOs) and late vitellogenic oocytes (LVOs)

Table 1. Isotopic values (‰) of all species used for stable isotope analysis

| Species	δ^{15}N		δ^{13}C		Individuals
	Value	SD	Value	SD	
Alloteuthis media	11.9	0.5	−18.5	0.4	1
Anadara kagoshimensis	8.8	0.7	−19.1	0.5	1
Callionymus maculatus	8.4	1	−19.6	0.7	1
Cepola macrophtalma	8.9	0.7	−19.7	0.8	1
Citharus linguatula	10.5	0.6	−17.4	0.4	1
Donax trunculus	4.1	0.7	−19.1	0.6	1
Gaidropsaurus biscayensis	9.1	0.5	−19.6	0.8	1
Mimachlamys varia	8.1	0.3	−19.2	0.2	1
Processa edulis	7.3	0.8	−18.3	1	1
Sepia elegans	7.8	0.6	−18.8	0.5	1
Sepia officinalis	9.9	0.2	−18.9	0.5	1
Solenocera membrancea	8.4	0.1	−18.9	0.1	1
Unidentified large copepods	7.2	0.5	−17.8	0.3	−
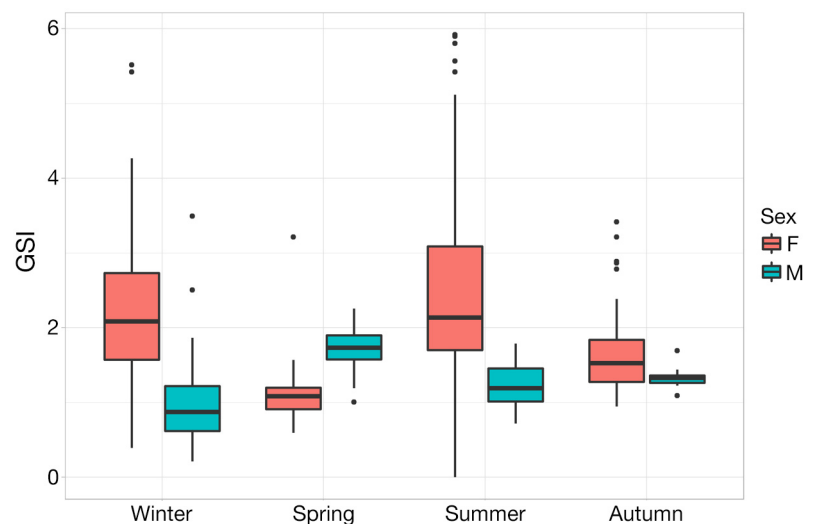
Fig. 2. Seasonal variations in the gonadosomatic index (GSI) of male and female *Parapenaeus longirostris*. Median values are represented by horizontal black lines, values falling outside the interquartile range are marked by vertical black lines, and outliers are indicated by black dots
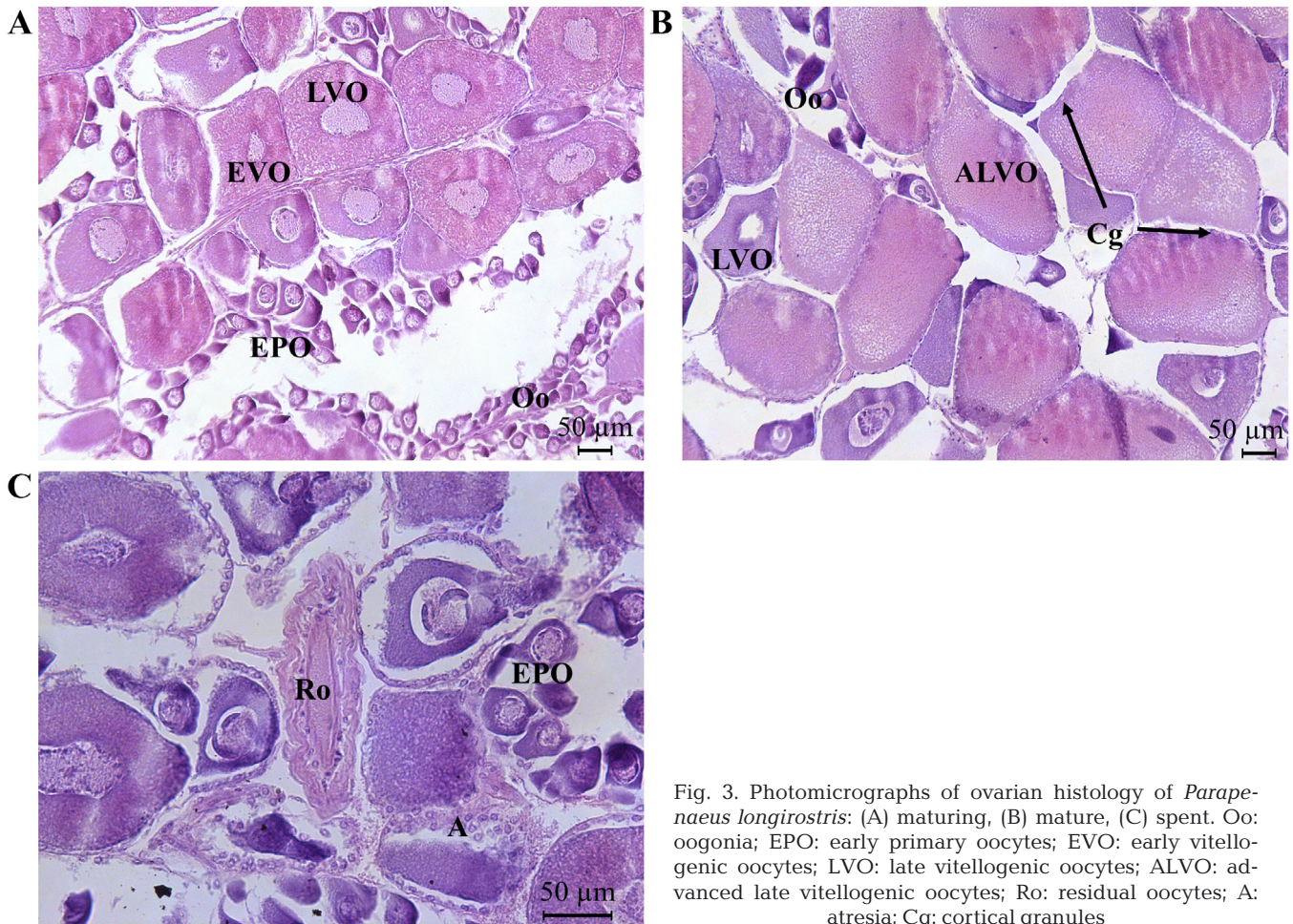
Fig. 3. Photomicrographs of ovarian histology of *Parapenaeus longirostris*: (A) maturing, (B) mature, (C) spent. Oo: oogonia; EPO: early primary oocytes; EVO: early vitellogenic oocytes; LVO: late vitellogenic oocytes; ALVO: advanced late vitellogenic oocytes; Ro: residual oocytes; A: atresia; Cg: cortical granules

appears empty, and residuals of fully mature oocytes can still be seen. Some atretic oocytes were observed at different stages of resorption (Fig. 3C).

The HSI values for females were relatively constant from spring to autumn, while the highest values were detected in winter (Fig. 4). GSI and HSI varied significantly between males and females and among seasons (Table 2a,b). Pairwise comparisons revealed significant variations in the GSI for females across seasons. The index varied significantly between all pairs of seasons in males, except for autumn vs. winter ($p < 0.05$). Pairwise comparisons for females revealed that the HSI varied significantly throughout the seasons (pairwise comparisons: $p < 0.05$).

The fullness index significantly differed among seasons but not between sexes (Table 2c). The lowest values were observed in summer for both sexes

(0.06 ± 0.25 SD for females and 0.07 ± 0.35 for males) and the greatest in autumn for females (2.1 ± 0.42) and in spring for males (2.56 ± 0.52) (Fig. 5).
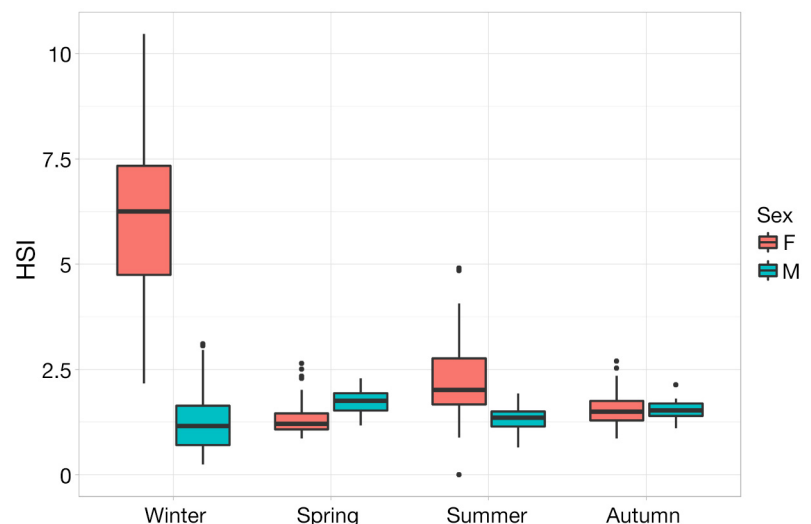

Fig. 4. Seasonal changes in the hepatosomatic index (HSI) of male and female *Parapenaeus longirostris*. Box plot parameters as in Fig. 2

3.2. Diet composition

Out of the 400 analysed stomachs, 284 were full, with the highest vacuity coefficient in summer (55%). In the other seasons, lower numbers of empty stomachs were recorded (26, 32 and 8% in winter, spring and autumn, respectively). In total, 52 taxa were identified in the stomach contents (Box 1). The Shannon-Wiener index showed rather similar values across seasons, with the highest value reached in winter (2.14 ± 0.1 SD) and the lowest in autumn (1.79 ± 0.1). In general, in terms of %W, *P. longirostris* mostly consumed bivalves, caridean shrimps, gastropods and peracarid crustaceans throughout the year. Mollusca and Crustacea were the 2 primary prey groups in every season, with Crustacea being the most represented in spring and Mollusca the most prevalent in winter, summer and autumn (Fig. 6A). Crustacea were mostly represented by Caridea (40.5%), Peracarida (24.2%), Penaeidae (18.3%) and Brachyura (16.9%), while Mollusca mainly comprised Bivalvia (68.7%), Gastropoda (15.8%) and Cephalopoda (15.5%; Fig. 6B,C). The diet composition changed significantly by season and for the interaction term 'Season: Sex' (Table 3a), while it did not vary significantly between males and females. The diet composition in autumn differed significantly from that in other seasons (Table 3b). The CAP analysis revealed a seasonal segregation of samples, with the first axis (CAP1) dividing autumn from the other seasons in the diet of the collected specimens (Fig. S2). The SIMPER test showed that bivalves were the taxon that most contributed to similarity within samples throughout the year, with caridean decapods in second place in winter, spring and summer, substituted by gastropods in autumn (Table S1).

3.3. Stable isotope analyses and Bayesian statistics

Across the sampling period, the sampled specimens selected for SIA had a mean (±SD) CL of 23.75 ± 2.73 mm for females and 20.83 ± 1.22 mm for males.

Table 2. ANOVA carried out for (a) gonadosomatic index (GSI), (b) hepatosomatic index (HSI) and (c) fullness index of *Parapenaeus longirotris* by sex and season. For each variable, the Games-Howell test was then carried out to perform multiple comparisons by season. 'estimate' is the estimate of the average difference between the compared seasons. Conf.low and Conf.high are the lower and upper bounds of the confidence intervals for each comparison. *p < 0.05, **p < 0.01, ***p < 0.001, ****p < 0.00001, ns: not significant

(a) GSI	df	SS	MS	F	p	
Sex	1	37.73	37.73	61.53	4.222×10^{-14}	***
Season	3	42.36	14.12	23.03	9.621×10^{-14}	***
Season:Sex	3	53.41	17.8	29.03	$<2.00 \times 10^{-16}$	***
Residuals	390	239.17	0.61			
group1	group2	estimate	conf.low	conf.high		
Winter	Spring	0.31	0.01	0.63	4.703×10^{-2}	*
Spring	Summer	0.91	0.57	1.25	7.783×10^{-10}	****
Summer	Autumn	0.66	0.32	0.99	7.021×10^{-6}	****
Autumn	Winter	0.06	−0.24	0.36	9.574×10^{-1}	ns
(b) HSI	df	SS	MS	F	p	
Sex	1	98.5	98.53	142.1	$<2 \times 10^{-16}$	***
Season	3	423.1	141.03	203.4	$<2 \times 10^{-16}$	***
Season:Sex	3	355.5	118.5	170.9	$<2 \times 10^{-16}$	***
Residuals	390	270.5	0.69			
group1	group2	estimate	conf.low	conf.high		
Winter	Spring	2.18	1.45	2.91	2.92×10^{-11}	****
Spring	Summer	0.57	0.32	0.82	1.012×10^{-7}	****
Summer	Autumn	0.49	0.26	0.72	1.254×10^{-6}	****
Autumn	Winter	2.1	1.38	2.83	1.013×10^{-10}	****
(c) Fullness	df	SS	MS	F	p	
Sex	1	0.05	0.05	0.31	0.57	
Season	3	15.45	5.15	29.53	$<2.00 \times 10^{-16}$	***
Season:Sex	3	3.36	1.12	6.42	0.001	***
Residuals	390	67.99	0.17			
group1	group2	estimate	conf.low	conf.high		
Winter	Spring	0.07	−0.13	0.26	8.26×10^{-1}	ns
Spring	Summer	−0.32	−0.49	−0.15	1.491×10^{-5}	****
Summer	Autumn	−0.51	−0.63	−0.39	0	****
Autumn	Winter	−0.12	−0.28	0.042	2.233×10^{-1}	ns

$\delta^{13}C$ values ranged from −19.2 to −18.2‰, with highest values in autumn and lowest in spring. $\delta^{15}N$ values fluctuated between 8.2 and 9.6‰, with the highest found in summer and the lowest in autumn (Fig. 7A). Regarding $\delta^{13}C$, significant differences were found among seasons (p < 0.05), but not size and sex. In contrast, $\delta^{15}N$ was significantly higher in males than in females (p < 0.05), but no differences were found among seasons and sizes (Fig. S3). The calculation of SEAc revealed that *P. longirostris* displayed similar trophic niches in all seasons (Fig. 7B), while the analysis of TP indicated that the contribution of the benthic baseline
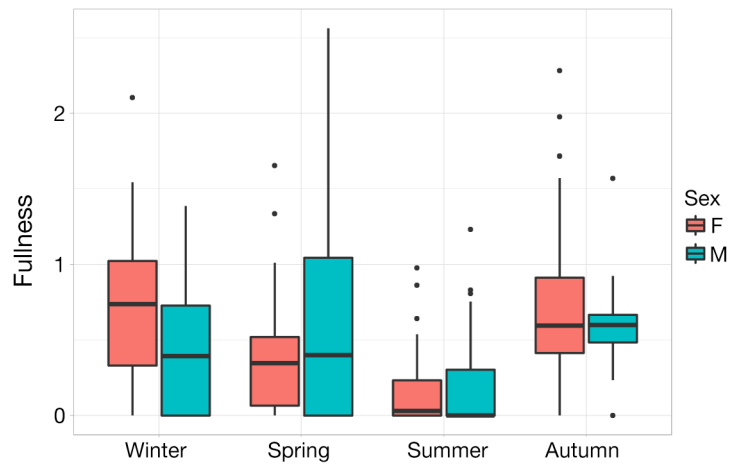
Fig. 5. Seasonal changes in the fullness index of male and female *Parapenaeus longirostris*. Box plot parameters as in Fig. 2

exceeded that of the pelagic baseline (Fig. 8A). According to the 'tRophicPosition' analysis, the deep-water rose shrimp occupied the third trophic level (average TP = 3.35, Fig. 8B), with little variation across seasons (winter TP = 3.33, spring and summer TP = 3.37, autumn TP = 3.34). The mixing polygon simulation indicated that consumer values fell within the 95% mixing region (represented by the outermost contour), enabling us to choose the prey for subsequent mixing models. POM was ultimately removed from the model, since it was determined not to be a probable food source; in fact, its considerable variability made it incompatible within

Box 1. List of prey found in *Parapenaeus longirostris* stomach contents. Asterisks (*) mark unidentified material

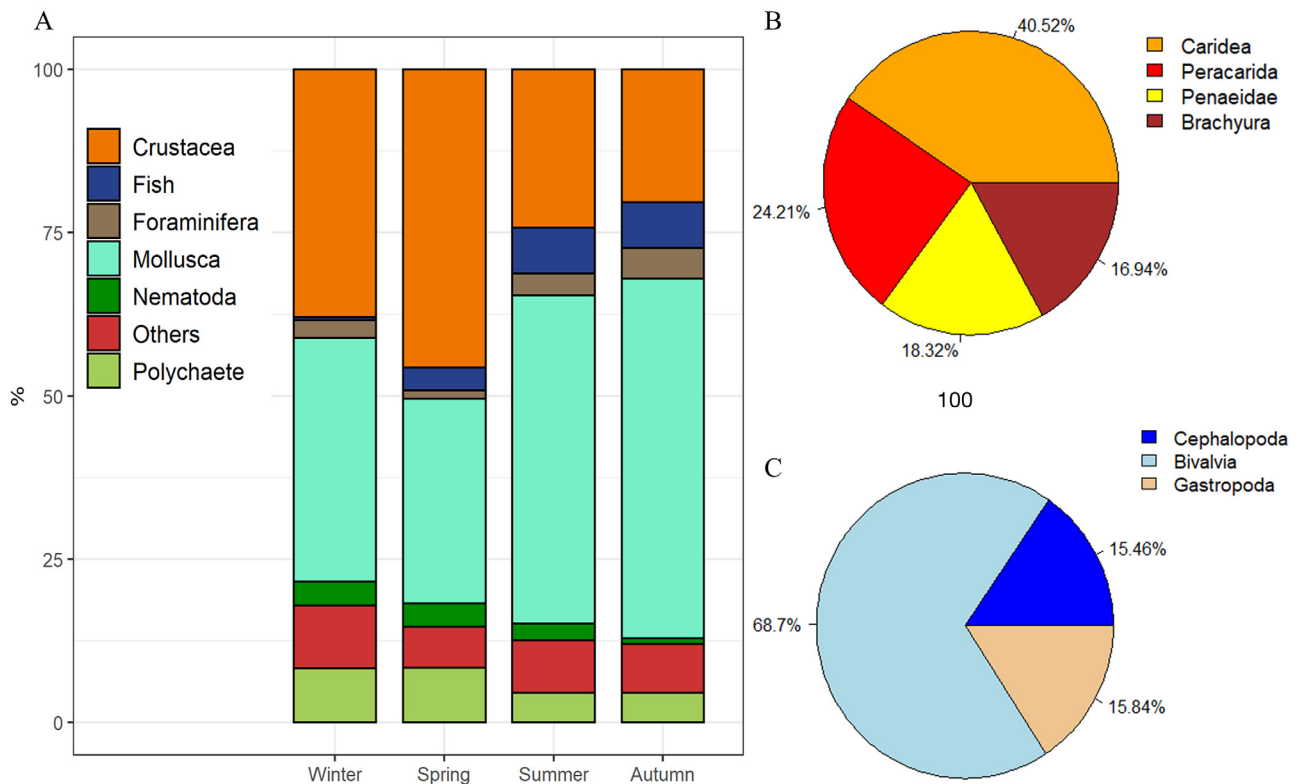|			
FORAMINIFERA		Nereididae	
Foraminifera*		CRUSTACEA	
	Ammonia beccarii	Crustacea*	
	Bolivina sp.	Copepoda	
	Fissurina sp.	Ostracoda	
	Haynesina germanica	Pericarida*	
	Quinqueloculina sp.	Mysida	*Lophogaster typicus*
	Uvigerina sp.	Amphipoda	
BRYOZOA		Cumacea	
Bryozoa*			*Iphinoe* sp.
GASTROPODA		Isopoda	
Gastropoda*		Tanaidacea	
Muricidae		Decapoda*	
	Trophonopsis sp.	Penaeoidea	
Naticidae			*Solenocera membranacea*
Rissoidae		Caridea	
	Alvania sp.	Alpheoidea	
Tricolia			*Alpheus glaber*
	Tricolia pullus	Crangonidae	
BIVALVIA			*Pontophilus* sp.
Bivalvia*		Pandalidae	
Arcidae			*Plesionika heterocarpus*
	Anadara sp.	Processidae	
Cardiidae			*Processa* sp.
	Acanthocardia sp.	Brachyura	
	Laevicardium oblongum		*Goneplax rhomboides*
Veneridae			*Inachus* sp.
	Kelliella miliaris	ECHINODERMATA	
	Timoclea ovata	Echinodermata*	
Pectinidae		Echinoidea	
Scaphopoda		OSTEICHTYES	
CEPHALOPODA		Osteichtyes*	
Chephalopoda*		Carapidae	
Sepiolidae			*Echiodon dentatus*
	Sepiola affinis	Mullidae	
Loliginidae			*Mullus barbatus*
	Alloteuthis media	PLANT DEBRIS	
POLYCHAETAE		Debris of land plant	
Polychaetae*		Algae	
Sternaspidae		PLASTIC REMAINS	
	Sternapsis scutata		

Fig. 6. (A) Dietary composition of *Parapenaeus longirostris* in terms of prey wet weight percentages; taxa are grouped to provide a clearer overview of prey categories. (B) Crustacea encompasses Caridea, Peracarida, Penaeidae and Brachyura; (C) Mollusca is composed of Cephalopoda, Bivalvia and Gastropoda

the polygon. However, this result could have been influenced by the use of values from a different study area. According to the SIMMR output, bivalves contributed most to the diet (Fig. 9A) throughout the year, with some seasonal variations in prey contribution. Benthic shrimps seemed to be preferred in spring, while benthic fishes were preferred in autumn (Fig. 9B).

Table 3. Results of PERMANOVA (a) main test and (b) pairwise comparisons for the diet composition of *Parapenaeus longirostris* by sex and season

(a) Source	df	MS	Pseudo-*F*	p (perm)
Season	3	7602	2.66	0.01
Sex	1	3972.8	1.39	0.23
Season:Sex	3	6485.5	2.27	0.01

(b) Groups	*t*	p (perm)		
Winter, Spring	0.91	0.55		
Spring, Summer	0.75	0.77		
Summer, Autumn	2.5	0.01		
Autumn, Winter	1.84	0.01		

4. DISCUSSION

This study represents the first attempt to combine SCA and SIA to investigate the feeding habits of *Parapenaeus longirostris* at a seasonal scale in the Mediterranean Sea. The obtained results confirm that the deep-water rose shrimp acts as an active predator and scavenger (Mori et al. 2000a, Kapiris 2004). The high variety of prey found in stomach contents revealed a rather generalist diet, with a preference for molluscs, particularly bivalves, gastropods and cephalopods. Although crustaceans, fish and polychaetes also contributed to the diet, they played a secondary role. Entire organisms were occasionally found in the stomachs, particularly small bivalves, and some fish otoliths (identified as *Echiodon dentatus* (Cuvier, 1829) and *Mullus barbatus* (Walbaum, 1792)). This confirms that the species feeds on a large array of organisms, including fish, although benthic and endobenthic prey seem to be preferred. Similar results were reported by Mori et al. (2000a) and Kapiris (2004), although molluscs were less abundant in these studies. This could be linked to the different depth ranges considered in the aforementioned studies (70–600 m) with respect
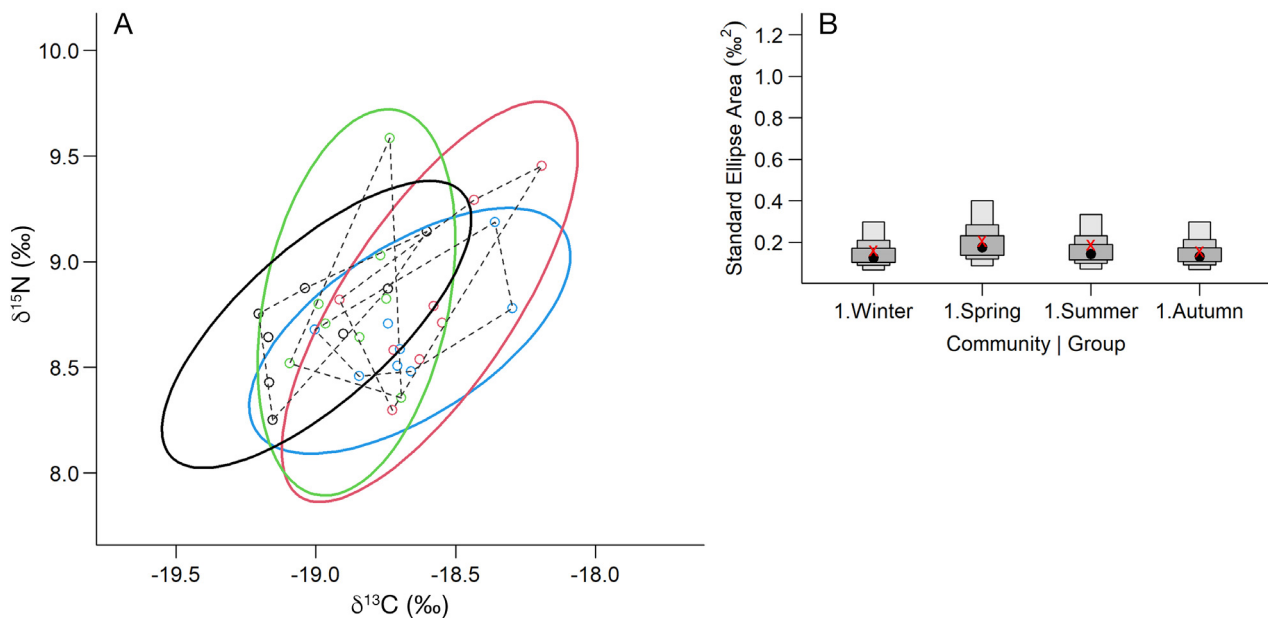
Fig. 7. (A) Standard ellipses depict approximately 95% of the data points independently drawn for each group based on $\delta^{15}N$ and $\delta^{13}C$. Dotted lines encircle the space occupied by each seasonal group (blue: winter; red: spring; green: summer; black: autumn). (B) Standard ellipse area (SEA) serves as a representation of posterior Bayesian SEA estimates for each group. Each box corresponds to the communities, with credible intervals at 25–50 and 75%. The red cross indicates the median, and the black point denotes the mean value, facilitating comparisons among individual groups (seasons)

to our sampling area, leading to the presence of different benthic assemblages.

4.1. Seasonal fluctuations in the physiological state of *P. longirostris*

Historically in this area, deep-water rose shrimp landings showed a fluctuating trend, with increasing values in the last 10 yr (FAO 2021b). In GSA 18, an increase in landings has been recorded since 2002, while in GSA 17, the species has shown an increase since 2011, reaching similar levels to GSA 18 (STEFC 2019). This increasing trend was also observed in the Pomo/Jabuka Pits, where a very high peak was recorded in 2017 (Martinelli et al. 2020). In general, a south–north gradient of expansion is evident in the Adriatic Sea (Martinelli et al. 2020, FAO 2021b, Mannini & Simmonds 2021). The northern sub-basin of the Adriatic Sea is characterised by shallow (average depth of 70 m) and eutrophic waters (Marini & Grilli 2023, Penna et al. 2023). In the study area, the size distribution of *P. longirostris* does not depend on bathymetry (i.e. the so-called bigger–deeper trend observed for other decapod species; Morales-Nin et al. 2003), a pattern already observed in the Tyrrhenian, Ionian and Aegean Seas (Mori et al. 2000a, Politou et al. 2008). The average depth of 70 m may

have significantly influenced the lack of size–depth relationships.

The GSI trend suggested 2 reproductive periods, one in winter and another in summer, similarly to what has been found for the Atlantic Ocean (Sobrino 1998, Sobrino et al. 2005). However, this pattern differs from the reproductive periods reported for the northern Tyrrhenian Sea and the Gulf of Alicante in the Mediterranean Sea (Mori et al. 2000b, García-Rodríguez et al. 2009). Histological analyses conducted on females confirmed these reproductive periods. Advanced stages of sexual maturity were found, characterised by the presence of numerous mature gonads with ALVO cells, indicating reproduction events in these seasons. The HSI values of females were notably higher in winter and summer, corresponding to the known reproductive periods for this species in Portuguese waters (Atlantic Ocean) (Rosa & Nunes 2002). The trend of fullness values followed a pattern consistent with the period of lowest predatory activity identified in this study, namely the summer. During this season, the lowest feeding activity was recorded, with approximately half of the stomachs found empty. This contrasts with the findings of Kapiris (2004) in the Ionian Sea, where summer was identified as the period of peak feeding activity. The decrease in predation activity in summer may be linked to reproduction, as the highest GSI values were found
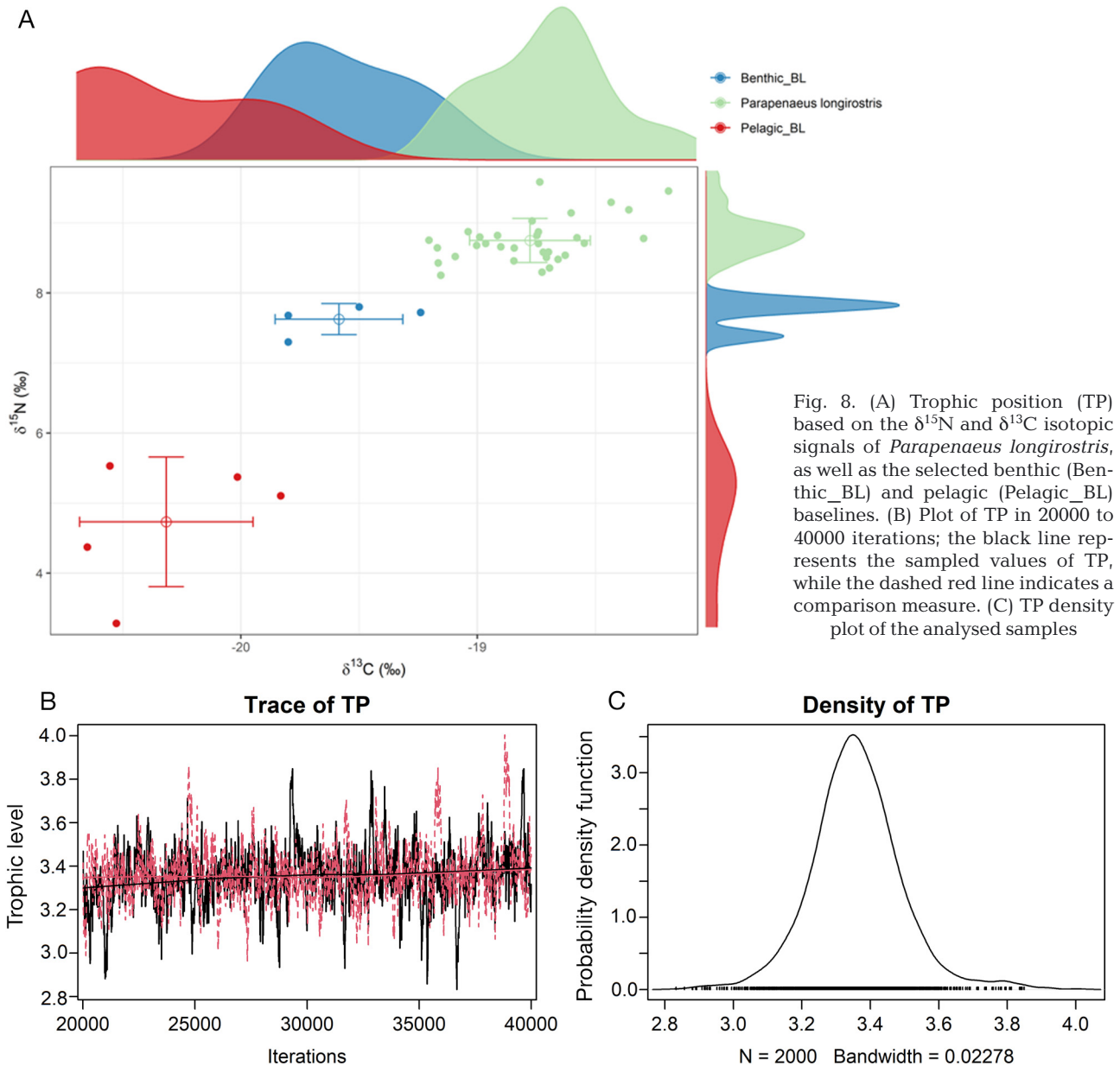
Fig. 8. (A) Trophic position (TP) based on the δ^{15}N and δ^{13}C isotopic signals of *Parapenaeus longirostris*, as well as the selected benthic (Benthic_BL) and pelagic (Pelagic_BL) baselines. (B) Plot of TP in 20000 to 40000 iterations; the black line represents the sampled values of TP, while the dashed red line indicates a comparison measure. (C) TP density plot of the analysed samples

during this season. Gonad growth, especially in females, could cause minimal fullness values due to stomach compression (Kapiris 2004). The metabolic activities of this species, including reproduction, moulting and settling of juveniles, may be connected to the increase in feeding activity observed in other seasons (Dall et al. 1990).

4.2. Seasonal changes in feeding behaviour

With 52 taxa identified (46 when excluding the Foraminifera, which are probably ingested accidentally during the digging phase), the diet of *P. longirostris* displays a moderate diversity, encompassing molluscs, crustaceans, fish, echinoderms and polychaetes. Seasonal variations were only evident in autumn when the highest mollusc intake was recorded, primarily involving small bivalves. Specifically, numerous fragments of bivalves belonging to the genus *Anadara* were found. While some shell fragments may be linked to accidental ingestion during the digging phase, entire juvenile specimens, characterised by their softer texture, are more likely attributed to active predation on these invasive Mediterranean molluscs. These molluscs are highly abundant in the Adriatic Sea, and their bathymetric distribution partially overlaps with that of the deep-water rose shrimp (Strafella et al.
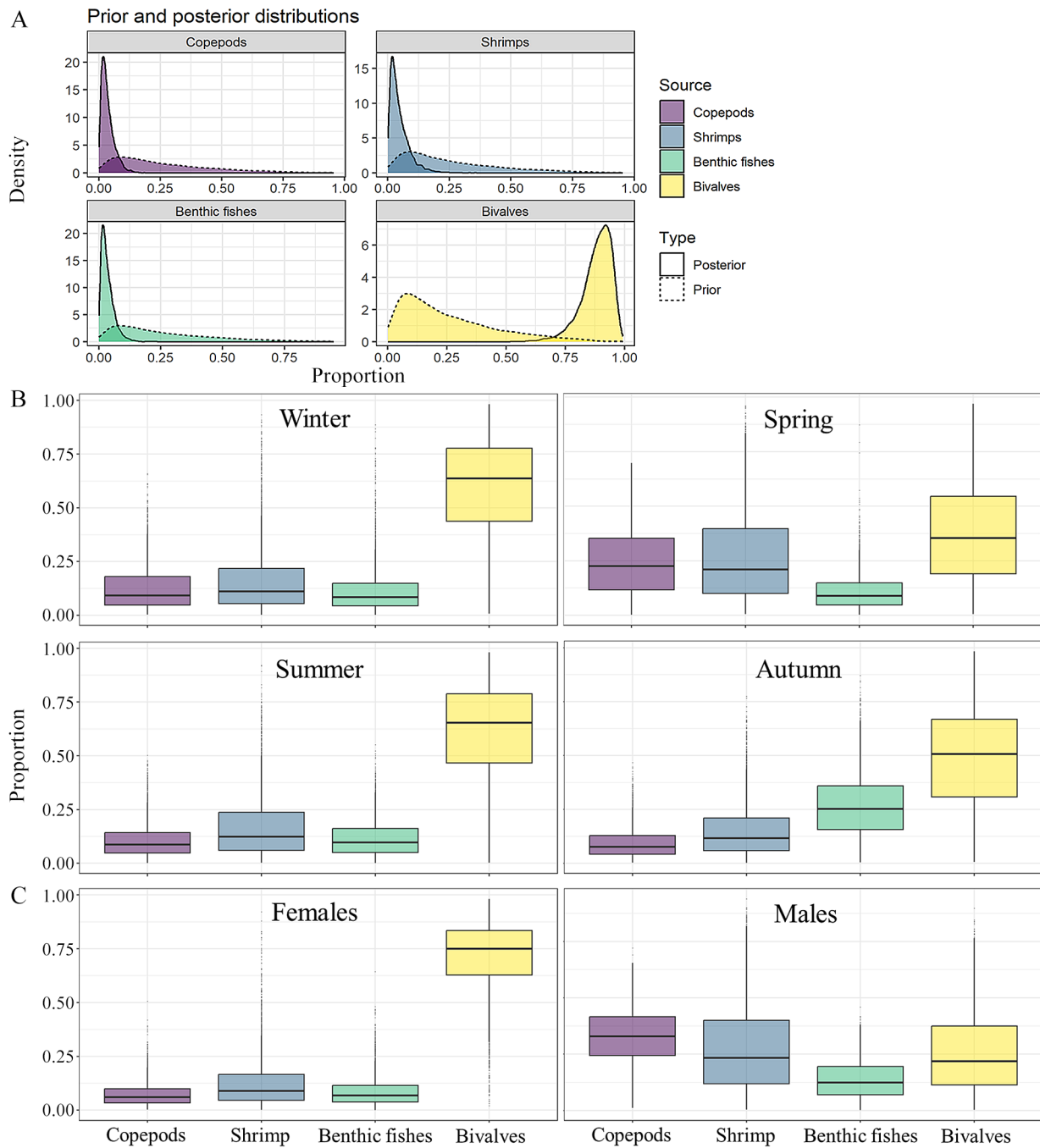
Fig. 9. (A) Prior and posterior distributions of various food sources for *Parapenaeus longirostris* throughout the year. (B) Comparison of the dietary proportions of *P. longirostris* across different sources and seasons, with the colour scheme matching panel (A). (C) Comparison of the dietary proportions of *P. longirostris* between sexes. The box represents the range in which the central half of the data lies. The horizontal line inside the box represents the median (50th percentile). The whiskers extend from the box to minimum and maximum values that fall within 1.5 times the interquartile range of the quartiles. Values outside this range represent outliers

2017). Across seasons, the core components of the diet, Mollusca, remained relatively consistent, with changes occurring in the proportions among the various taxa ingested. A different diet composition was observed in Algerian waters, where a less diversified diet was reported. In this case, the main prey included foraminiferans, polychaetes, radiolarians, algal debris, fish and amphipods, with copepods being particularly

frequent in winter and summer (Nouar et al. 2011). In the Ionian Sea, the diet of the deep-water rose shrimp primarily consisted of polychaetes, decapods, gastropods, amphipods and fish (Kapiris 2004); similar results, but with a greater contribution of bivalves, were observed in the western Mediterranean (Cartes 1995). Many prey items identified in previous studies were also found in our analysed samples. Polychaetes, fish, decapods and copepods made up a substantial portion of the diet, although their abundances varied. The most distinctive component of the shrimp diet were bivalves, which did not represent an important prey item in other studies. These findings indicate that while the deep-water rose shrimp has similar feeding habits across different regions, its diet is strongly influenced by the specific species available in the inhabited area. The generalist predator and scavenger behaviour of this species also provides qualitative information on the biodiversity of the local benthic community; other aquatic organisms with a similar feeding strategy have been used as biodiversity samplers as shown by Siegenthaler et al. (2019) through metabarcoding of DNA extracted from stomach contents. The lack of changes in prey preference according to different sizes suggests that the species exploits the same resources during its entire life cycle. Furthermore, the low bathymetric variability of the area (70 m average depth) may have contributed to this constant prey composition. The differences recorded among seasons can be attributed to intrinsic changes in the benthic community composition throughout the year. SIA results agreed with those derived from SCA. In all seasons, bivalves made the greatest contribution to the diet of deep-water rose shrimp, followed by crustaceans (mostly copepods and small shrimps). Throughout the year, based on Bayesian statistics, benthic fish showed a low contribution, with the exception of autumn, when they became the second most relevant component. Bivalves were isotopically the greatest contributor to the diet in all seasons. Copepods and decapod shrimps showed similar patterns, with a significant increase in contribution in spring. These results suggest that in the seasons preceding the breeding periods, changes in the diet may occur in favour of prey with greater energetic content, as also observed in other decapod crustaceans (Fanelli & Cartes 2008) and fish (Papiol et al. 2014). Furthermore, this seasonal variation in diet is supported by similar changes in $\delta^{13}C$ values among seasons, pointing to different sources for the organic material ingested. Regarding sex, the changes observed were not in the diet itself but in the contribution of various prey to the isotopic

values of the analysed specimens. Specifically, the contribution of the bivalve category decreased in favour of copepods and shrimps in males, explaining the higher $\delta^{15}N$ values. The substantial difference between males and females shown in Fig. 9C may have been obscured in Fig. 9B due to the larger number of female specimens compared to that of males, thus possibly leading to a slight underestimation of the contributions of categories other than bivalves. It can be hypothesised that the slight (not significant) dietary differences between sexes contributed instead significantly to the isotopic signal.

4.3. TP within the benthic food web

The obtained results concerning the trophic level confirmed *P. longirostris* as a secondary consumer. Lower values were recorded in Croatian and Israeli waters (Zorica et al. 2021, Guy-Haim et al. 2022), likely due to different seabed morphology, oceanographic characteristics and different species compositions influencing the feeding strategy. However, the obtained trophic level is consistent with results on the feeding habits of the species, which predominantly feeds on small prey, such as molluscs and crustaceans. The identified fish species ingested by the deep-water rose shrimp indicate that these prey are linked to scavenger activities. The species' capacity to adapt its diet to consume a variety of prey can influence its TP, depending on the specific area and available prey resources. These findings are consistent with those reported by Zacchetti et al. (2022) for the Norway lobster in the same area, where a more diverse diet comprising larger animals at higher trophic levels, such as crabs and fish, corresponded to a higher TP.

5. CONCLUSIONS

This research enhances our knowledge of the trophic ecology of *Parapenaeus longirostris* and offers insights into the primary energy sources supporting its diet in one of the most fished areas of the Mediterranean Sea. According to its dietary preferences, this species is an active predator and a scavenger in the Adriatic Sea. Notably, the daytime digging phase plays a vital role in its foraging behaviour, as it targets various benthic organisms, including molluscs, crustaceans and benthic fishes. The TP calculation determined its role as a secondary consumer within the benthic food web. By assessing key biological indices

and linking the reproductive traits of the species to its seasonal feeding strategy, this study further elucidates the role of *P. longirostris* in the benthic ecosystem of the Adriatic Sea; this information is very important in the context of an ecosystem approach to fisheries. This enhances our understanding of predator—prey interactions within an ecosystem and offers a comprehensive understanding of the ecological dynamics that support the productivity of marine ecosystems.

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