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ORIGINAL ARTICLE

Pelagic forage fish feeding habits in the Adriatic Sea – a stomach content analysis approach

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Abstract: In this study, the feeding habits of seven pelagic forage fish species inhabiting the Adriatic Sea, were evaluated by applying the stomach content analysis. Each month from June 2023 till September 2024 all biological samples were collected along the eastern Adriatic by commercial purse seiner "srdelara". A total of 742 stomach samples were analysed. Small pelagic species such as sardine (*Sardina pilchardus* (Walbaum, 1792)), anchovy (*Engraulis encrasicolus* (Linnaeus, 1758)) and round sardinella (*Sardinella aurita* Valenciennes, 1847) primarily consumed copepods, while medium pelagic species including Atlantic horse mackerel (*Trachurus trachurus* (Linnaeus, 1758)), Mediterranean horse mackerel (*Trachurus mediterraneus* (Steindachner, 1868)), Atlantic chub mackerel (*Scomber colias* Gmelin, 1789), and bogue (*Boops boops* (Linnaeus, 1758)) favoured larger prey such as mysids, euphausids, and decapod larvae. Seasonal variations were observed, with copepods dominating diets during warmer months and larger prey items during the colder part of the year. Lower differences between small and medium species diets occurred in warmer months, linked to increased zooplankton availability in the investigated area. The results obtained in this study indicated potential competition among the observed pelagic species, particularly under resource-limited conditions, highlighting the necessity of adopting an ecosystem-based approach in fisheries management. Such an approach would undoubtedly ensure the sustainable exploitation of these renewable resources in the Adriatic Sea.

Keywords: small pelagic fish; medium pelagic fish; diet; stomach content analysis; eastern Mediterranean Sea

Sažetak: ISHRANA PELAGIČNIH RIBA U JADRANSKOM MORU TEMELJEM ANALIZE ŽELUDACA. Analizom želudaca sedam pelagičnih vrsta koje obitavaju u Jadranskom moru dobiven je uvid u njihovu ishranu. Svi biološki uzorci su prikupljeni mjesečno u razdoblju od lipnja 2023. godine do rujna 2024. godine duž istočne obale Jadranskog mora s komercijalne plivarice "srdelare". Ukupno su analizirana 742 želudca. Sitne pelagične vrste kao što su srdela (*Sardina pilchardus* (Walbaum, 1792)), inćun (*Engraulis encrasicolus* (Linnaeus, 1758)) i srdela golema (*Sardinella aurita* Valenciennes, 1847) su se uglavnom hranile veslonošcima, dok su nešto veće odnosno srednje pelagične vrste kao šnjur (*Trachurus trachurus* (Linnaeus, 1758)), šnjur pučinar (*Trachurus mediterraneus* (Steindachner, 1868)), lokarda (*Scomber colias* Gmelin, 1789) i bukva (*Boops boops* (Linnaeus, 1758)) preferirale krupniji plijen poput rašljonožaca, svjetlara i ličinki desetonožnih rakova. U ishrani navedenih vrsta su uočene sezonske varijacije, pri čemu su veslonošci dominirali ishranom tijekom toplijih mjeseci, dok je krupniji plijen bio zastupljeniji tijekom hladnijeg dijela godine. Manje razlike u ishrani između malih i srednjih pelagičnih vrsta su uočene u toplijim mjesecima, što se povezuje s povećanom dostupnošću zooplanktona na istraživanom području. Rezultati ovog istraživanja ukazuju na potencijalnu kompetenciju među promatranim pelagičnim vrstama osobito u uvjetima ograničenih resursa, zbog čega bi bilo nužno započeti s ekosustavnim pristupom prilikom upravljanja u ribarstvu, čime bi se zacijelo osiguralo održivo iskorištavanje ovih obnovljivih resursa u Jadranskom moru.

Ključne riječi: sitna pelagična riba; srednja pelagična riba; ishrana; analiza sadržaja želudca; istočno Sredozemno more

INTRODUCTION

Small and medium pelagic fish species, often referred to as "forage fish" due to their trophic position in marine ecosystems, play a critical role in transferring energy from primary producers to keystone predators (Alder *et al.,* 2008; Pikitch *et al.,* 2014). Hence, their ecological importance within the ecosystem is immense. Beyond their ecological role, these species are also of great significance due to their substantial contribution to global fish landings (≈30%, FAO, 2011) and their high nutritional value in the human diet (Tacon and Metian, 2013). Pelagic fish are widely distributed across the globe and are often characterised as short-lived, fast-growing species that tend to form large dense schools (Whitehead *et al.,* 1988), which makes them more accessible to fishing (Alder *et al.,* 2008). Furthermore, they seem to be highly sensitive to environmental conditions (Peck *et al.,* 2021; Jurado-Ruzafa *et al.,* 2024). Considering all mentioned, their populations display large boom-and-bust dynamics over the years (FAO, 2011). In the Adriatic Sea, most commercially exploited fish species, including forage fish, are either overfished or overexploited (GFCM, 2024). Over the past two dec-

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ades, numerous studies have focused on understanding the factors driving population fluctuations in these species, which are shaped by a combination of natural and anthropogenic pressures (Engelhard *et al.,* 2014; Grbec *et al.,* 2015). Among the key factors identified there is the availability of planktonic prey, which plays a critical role in shaping fish population dynamics (Toresen and Østvedt, 2000; Chavez *et al.,* 2003).

In this study, we examined the feeding habits of seven forage fish species: sardine (*Sardina pilchardus* (Walbaum, 1792)), anchovy (*Engraulis encrasicolus* (Linnaeus, 1758)), round sardinella (*Sardinella aurita* Valenciennes, 1847), Atlantic horse mackerel (*Trachurus trachurus* (Linnaeus, 1758)), Mediterranean horse mackerel (*Trachurus mediterraneus* (Steindachner, 1868)), Atlantic chub mackerel (*Scomber colias* Gmelin, 1789), and bogue (*Boops boops* (Linnaeus, 1758)).

The biology and ecology of these species, including some aspects of their feeding habits, have been previously studied. Reviewing the literature which refers to their feeding habits it was clear that these fish species, predominantly rely on plankton, ranging from smaller phytoplankton to larger zooplankton species, despite differences in feeding strategies, such as filter feeding and particulate feeding (Šantić *et al.,* 2004; Lomiri *et al.,* 2008; Čikeš Keč *et al.,* 2012; Rumolo *et al.,* 2017; Zorica *et al.,* 2021; Farah and Mavruk, 2024). However, only a limited number of studies, such as those by Stergiou and Karpouzi (2002), Albo-Puigserver *et al.* (2017) and Zorica *et al.* (2024), have addressed the dietary overlap among these species. Most other research has primarily concentrated on two to three forage fish species, typically small pelagic fish. Different authors have employed various methods (e.g., stomach content analysis (Zorica *et al*., 2016.), fatty-acid analysis (Pethybridge *et al*., 2014), stable-isotope analysis (Zorica *et al*., 2024) and DNA-based diet determination techniques (Canals *et al*., 2024)), each with its own advantages and limitations. The application of multiple methodologies offers a more comprehensive and robust understanding of feeding habits. Our recent study (Zorica *et al.,* 2024) revealed the interaction between pelagic species in the central Adriatic applying stable isotope methods. Building on previous research, this study aimed to gain insights into the diverse food sources of the investigated species along the entire eastern Adriatic coast, thereby enhancing our understanding of their feeding ecology. Such an investigation will yield valuable insights into the trophic dynamics and resource competition characterizing the Adriatic Sea ecosystem. The findings may serve as a foundation for future efforts to manage and conserve these essential renewable resources proactively.

MATERIALS AND METHODS

Samples of seven pelagic fish species (small pelagic fish species - sardine, anchovy, round sardinella; medium pelagic fish species - Atlantic horse mackerel, Mediterranean horse mackerel, Atlantic chub mackerel, bogue) were collected onboard of commercial fishing vessel using purse seine net "srdelara". The "srdelara" net is traditionally used to catch sardines and other small pelagic fish species in the eastern Adriatic. Fishing operations occur at night, with fishermen using artificial lights to attract fish schools, which are then surrounded by the net and captured. Biological samples for this study were collected on monthly basis from June 2023 to September 2024, precisely during the cold (November-April) and warm (May-October) season (Table 1). Monthly biological samples for January, February, and May were unavailable due to the enforcement of a fishing ban on "srdelara" purse seines.

Overall, 35 catch operations were obtained from nearly the entire Croatian fishing grounds, including fishing zones A, B, C, E, F, G, and I (Official Gazette of the Republic of Croatia, 2005; Fig. 1). Ten specimens of each fish species (target and by-catch) were randomly selected from the catch, when available. The visceral cavity of each fish was carefully dissected, and specimens of the same species were placed in the same plastic containers and preserved in 10% buffered formalin for subsequent laboratory analysis. In the laboratory, total body length (L, cm) was measured to the nearest ± 0.1 cm, except for the Atlantic chub mackerel, where fork length was recorded. Fish weight (W, g) was measured with a precision of ± 0.1 g. Fish stomachs were carefully excised and weighed (± 0.01 g) before and after removing prey items (total weight of full stomach, Wf, and empty stomach, We). Prey items were identified mostly to the order or class level under a stereomicroscope (Zeiss Discovery V12; magnification 40–80x) using identification keys (Trégouboff and Rose, 1957) and were subsequently counted.

Seven calculated indices described the dietary habits and feeding behaviour of the species under study:

- Fullness index (%Jr) (Hureau, 1970): $(Wp/W) \times 100$, where Wp represents the mass of prey items, calculated as the difference between the mass of the full and empty stomachs (Wf - We), and W is the total body mass of the fish. This index was linearly correlated with fish length to define the eventual ontogenetic shift in diet.
- Vacuity index (%V) (Hureau, 1970): $(E/N) \times 100$, where E is the number of empty stomachs and N is the total number of stomachs analysed.
- Frequency of occurrence (%F) (Hureau, 1970): $(n/N) \times 100$, where n is the number of stomachs containing a particular prey item, and N is the total number of stomachs that contained any prey.
- Numerical abundance (%N) (Berg, 1979): $(np/Np) \times 100$, where np is the number of prey specimens of a specific group, and Np is the total number of all identified prey groups.
- Shannon's diversity index (H') (Ortiz-Burgos, 2016): $H' = -\Sigma(p_i \times \ln(p_i))$, measured the diversity of prey items (i) in each study species based on its pro-

Table 1. Overview of monthly sampling by species and fishing zone from June 2023 to September 2024 with purse seine "srdelara" in the area of Croatian fishing ground.

Month	Fishing zone	1	2	3	4	5	6	7
June 2023	C		■		■			
July 2023	A	■						
	C	■						
	E		■					
	G	■						
August 2023	G		■					
September 2023	A				■		■	
November 2023	A	■				■	■	
December 2023	A					■	■	■
	B	■				■		
	E		■			■		
	G	■				■	■	■
March 2024	B		■		■	■	■	■
	E	■	■					
	F	■	■					
	G	■						
	I	■	■		■		■	
April 2024	B	■	■		■			
	E	■	■					
June 2024	A	■	■	■	■		■	
	B		■		■		■	
	E	■	■					
	F	■	■	■				
	G		■					
July 2024	B			■				
	E	■	■	■				
	F				■			
	G			■				
September 2024	A	■			■		■	
	B	■					■	

1- Sardina pilchardus; 2- *Engraulis encrasicolus*; 3- *Sardinella aurita*; 4- *Trachurus trachurus*; 5- *Trachurus mediterraneus*; 6- *Scomber colias*; 7- *Boops boops.*

portion (p_i) in each species. A higher value of H' indicates greater diversity within the diet composition of investigated species.

- Pielou's Evenness Index (J') (Pielou, 1966): J'=H'/ln(S), where H' refers to Shannon's diversity index, and S is the total number of prey species observed in each analysed species. The index ranges from 0 to 1, where 1 indicates that all prey items are equally abundant and 0 suggests the domination of one prey item completely.
- Levins' normalised index (Bn) was used to define the trophic niche breadth; it was calculated by equation $Bn=1/(R\Sigma p_i^2)$, where R refers to the number of prey species categories and p_i to the relative frequency of each prey type i used by the species (Feinsinger *et al.,* 1981). Bn values range from 0 to 1, where values closer to 1 indicate a more generalised niche and values closer to 0 indicate a more specialised niche.

To investigate the difference in diet between small and medium pelagic fish species, as well as seasonal variations in their diets during the cold and warm periods, stomach content data for the studied species were log-transformed [log(x+1)] and analysed using a Bray–Curtis similarity matrix. This analysis was conducted with the PRIMER 7 *Version 7.0.24* software package (Clarke, 1993; Clarke and Gorley, 2015). The resulting similarity

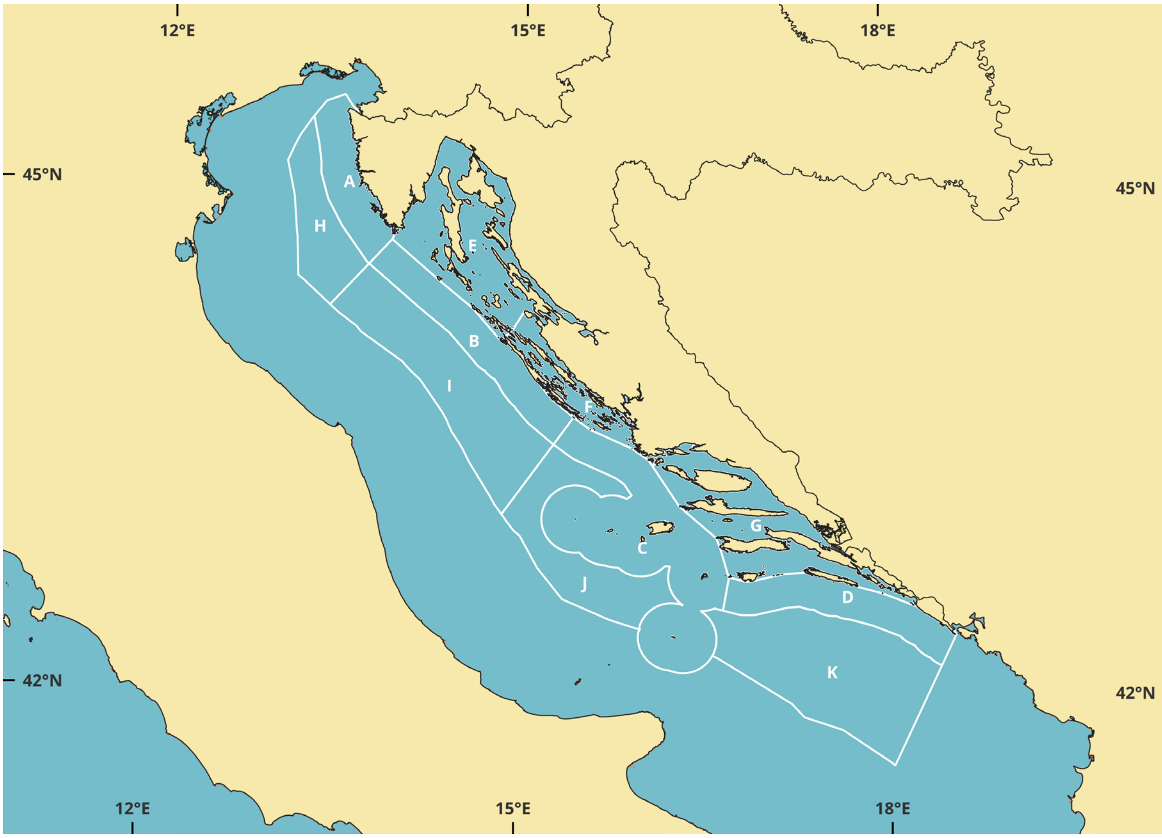

Fig. 1. Overview of the Croatian fishing ground and its fishing zones.

matrix was used to generate a non-metric multidimensional scaling (nMDS) plot to see dietary overlap. To further assess differences in stomach contents, a two-way crossed ANOSIM test was applied, evaluating variations between small and medium-sized pelagic fish and across seasons. Additionally, two-way SIMPER analysis was employed to identify specific prey items contributing to the observed seasonal differences in the diets of small and medium-size fish species.

RESULTS

Stomach content analysis was conducted on 742 specimens of the seven pelagic forage fish species (Table 2). Out of all examined stomachs, 23% (N=171) were empty. The vacuity index was the highest in round sardinella and the lowest in bogue (Table 3). The mean fullness index (%Jr) across all species was relatively low. Furthermore, while %Jr exhibited some correlation with fish body length, the low values of the correlation coefficient ($0.0007<r^2<0.2928$) indicated no clear trend, precisely none of the observed correlations was statistically significant ($0.055<p<0.870$). Based on the relative abundance and frequency of occurrence of prey categories across the investigated fish species (Table 4), the diets of sardine and round sardinella primarily consisted of copepods. Notably, these two species were the only ones that included phytoplankton in their diets, classifying them as omnivores. Copepods were the most frequently occurring prey in anchovy, while mysids constituted the most abundant prey category. The diet of Atlantic horse mackerel was entirely dependent on mysids. Conversely, Mediterranean horse mackerel and bogue predominantly consumed decapod larvae, which were both the most frequent and abundant prey items. Similarly, decapod larvae were the most frequent prey in the diet of Atlantic chub mackerel, but for this species, euphausids emerged as the most abundant prey category (Table 4).

The diversity of prey items varied among the investigated species, but overall it was very low (H'<1.4) and Pielou's evenness index (J') indicated that prey items were unbalanced or dominated by one prey category. Namely, Atlantic horse mackerel and anchovy had the lowest and the highest values of prey diversity, respectively (Table 3). The Pielou's evenness index (J') of those two previously mentioned species also support this as in the diet of Atlantic horse mackerel domination of one prey item was noted, while in anchovy, prey composition was, although unbalanced, still moderately even (Table 3, 4). According to the calculated Levins' normalized index (Bn) values, bogue exhibited the widest dietary niche, with almost well-balanced prey community. In contrast, sardine and Atlantic horse mackerel had the narrowest niche breadth, relying on a more

Table 2. Descriptive overview of seven pelagic forage fish (N – number of individuals, ranges, means and standard deviations (SD) of L – length in cm, W – body weight in g, Wf – weight of full stomach in g, We – weight of empty stomach in g) collected with commercial purse seiners in the eastern Adriatic Sea (Croatian fishing ground) through the whole investigated period (June 2023 – September 2024).

	N	L (cm) Range (Mean ± SD)	W (g) Range (Mean ± SD)	Wf (g) Range (Mean ± SD)	We (g) Range (Mean ± SD)
Sardina pilchardus	216	7.8 – 16.9 (13.69 ± 1.26)	3.90 – 38.30 (20.75 ± 5.96)	0.02 – 1.40 (0.35 ± 0.22)	0.01 – 0.68 (0.21 ± 0.12)
Engraulis encrasicolus	178	9.7 – 16.6 (13.4 ± 1.28)	5.65 – 29.85 (16.37 ± 4.87)	0.03 – 2.23 (0.34 ± 0.34)	0.01 – 0.52 (0.16 ± 0.09)
Sardinella aurita	64	13.8 – 23.0 (17.6 ± 2.25)	22.42 – 96.57 (47.82 ± 19.84)	0.09 – 1.76 (0.67 ± 0.34)	0.08 – 0.93 (0.44 ± 0.20)
Trachurus trachurus	80	8.1 – 23.3 (15.0 ± 3.35)	4.77 – 132.16 (35.51 ± 23.65)	0.06 – 13.14 (1.12 ± 2.01)	0.04 – 2.79 (0.30 ± 0.42)
Trachurus mediterraneus	80	10.4 – 21.3 (15.9 ± 2.40)	9.71 – 78.29 (36.74 ± 14.58)	0.11 – 4.72 (1.14 ± 0.98)	0.01 – 0.90 (0.35 ± 0.21)
*Scomber colias**	89	14.3 – 23.0 (17.9 ± 2.13)	26.23 – 108.85 (57.12 ± 20.08)	0.19 – 10.0 (2.53 ± 2.00)	0.13 – 3.07 (0.74 ± 0.41)
Boops boops	35	11.3 – 20.4 (15.4 ± 1.58)	11.72 – 83.61 (37.83 ± 13.62)	0.22 – 1.67 (0.70 ± 0.33)	0.01 – 0.75 (0.39 ± 0.18)

*fork length

Table 3. Review of the calculated indices (Fullness index (%Jr), Vacuity index (%V), Shannon's diversity index (H'), Pielou's evenness index (J'), Levins' normalised index (Bn)) for the seven investigated pelagic forage fish species caught along the eastern Adriatic Sea with commercial purse seiners, June 2023 - September 2024.

	%Jr	%V	H'	J'	Bn
Sardina pilchardus	0.006	22.69	1.2	0.46	0.1
Engraulis encrasicolus	0.100	21.35	1.4	0.59	0.3
Sardinella aurita	0.005	37.50	0.9	0.42	0.2
Trachurus trachurus	0.015	31.25	0.5	0.20	0.1
Trachurus mediterraneus	0.022	12.50	1.0	0.46	0.2
Scomber colias	0.032	24.72	1.3	0.55	0.2
Boops boops	0.009	8.57	1.3	0.67	0.4

limited range of prey items or even just one (Tables 3, 4).

The analysis highlighted a clear separation between small and medium size species, as well as between seasons (cold and warm). Specifically, the diet of medium pelagic forage fish species varied between seasons, while their diet exhibited greater overlap with that of small pelagic forage species during the warmer season. The obtained results aligned with the results of the two-way crossed ANOSIM test, which demonstrated significant differences in diet composition between small and medium pelagic forage species. The global R-value of 0.385 ($p < 0.001$) indicates moderate but significant differences in prey selection related to small and medium species. Regarding seasonal variation, the ANOSIM test yielded a global R-value of 0.066 ($p < 0.001$), revealing differentiation in diet composition between seasons (Fig. 2).

Small pelagic fish primarily consumed copepods, as shown in Table 4, which contributed 83.12% to the average similarity of their diet. Medium pelagic forage fish had a more diverse diet with decapod larvae (38.84%), mysids (26.92%), and amphipods (14.39%) being the main contributors to their dietary similarity. The two-

Table 4. Frequency of occurrence (%F) and abundance (%N) of prey items found in stomachs of the sardine, anchovy, round sardinella, Atlantic horse mackerel, Mediterranean horse mackerel, Atlantic chub mackerel and bogue collected in the eastern Adriatic Sea (Croatian fishing ground) over the whole investigated period (June 2023 - September 2024).

Species / Prey	*Sardina pilchardus*		*Engraulis encrasicolus*		*Sardinella aurita*		*Trachurus trachurus*		*Trachurus mediterraneus*		*Scomber colias*		*Boops boops*	
	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F	%N
Copepoda	60.42	82.00	53.24	18.42	43.10	71.84	11.67	0.71	10.00	0.68	16.00	7.75	10.00	1.85
Amphipoda	11.11	4.83	18.71	3.43	6.90	2.45	18.33	0.49	60.00	8.47	18.00	3.97	10.00	1.85
Mysida	6.25	1.11	16.55	67.33	1.72	0.41	35.00	96.81	10.00	1.02	20.00	5.10	10.00	1.85
Euphausiacea	-	-	-	-	-	-	1.67	0.03	-	-	18.00	77.57	-	-
Cladocera	11.11	1.76	7.19	0.46	5.17	1.22	-	-	-	-	4.00	0.13	-	-
Cirripedia	0.69	0.07	-	-	-	-	-	-	-	-	-	-	-	-
Decapoda larvae	22.22	4.83	29.50	8.10	5.17	2.45	26.67	1.02	90.00	86.44	24.00	3.53	60.00	85.19
Fish larvae	15.97	4.37	10.79	1.39	32.76	18.78	-	-	-	-	4.00	1.01	10.00	9.26
Pisces larvae	0.69	0.20	-	-	3.45	0.82	8.33	0.95	50.00	3.05	28.09	2.05	-	-
Bivalvia	4.86	0.59	10.07	0.64	5.17	1.63	-	-	-	-	-	-	-	-
Gastropoda	0.69	0.13	1.44	0.21	-	-	-	-	10.00	0.34	2.00	0.13	-	-
Cephalochordata	-	-	-	-	-	-	-	-	-	-	2.00	0.13	-	-
Dinophyceae	1.39	0.13	-	-	1.72	0.41	-	-	-	-	-	-	-	-

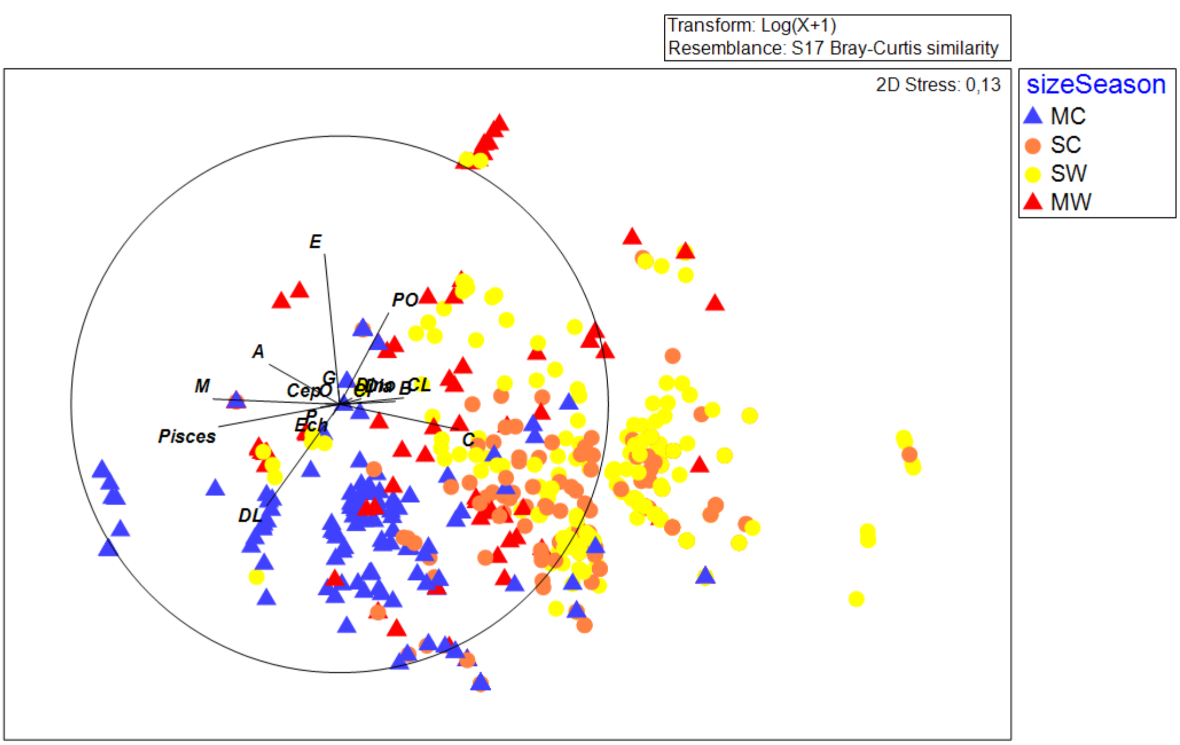

Fig. 2. Non-metric MDS analysis of dietary overlap in small (S) and medium (M) -sized pelagic forage fish across seasons (C-cold; W-warm) in the Adriatic Sea, where the vectors indicate the relative strength and direction of correlations between prey abundance and the nMDS axes. Taxa are identified as: C, Copepoda; A, Amphipoda; M, Mysida; E, Euphausiacea; Cl, Cladocera; Ci, Cirripedia; DL, Decapoda larvae; PO, Pisces ova; B, Bivalvia larvae; G, Gastropoda larvae; Ech, Echinodermata larvae; O, Ostracoda; P, Polychaeta larvae; Cep, Cephalochordata; Dia, Diatomeae; Dino, Dinophyceae; Pisces, Pisces larvae.

way SIMPER analysis further highlighted differences in diet composition between small and medium pelagic forage fish species and across seasons. Namely, copepods were the group that mostly contributed to the observed differences between the diet of small and medium pelagic forage species. Conversely, in medium pelagic fish, mysids and decapod larvae contributed significantly to dietary differences between the groups (Table 5). Within the cold and warm seasons, common prey items-copepods and decapod larvae-were present in the diets of the investigated fish species, but their relative abundance varied between seasons. During the cold season, copepods (44.65%) and decapod larvae (25.61%) contributed most to dietary similarity. In the warm season, copepods became the dominant prey item, accounting for 79.87% of the diet. The dissimilarity in diets between the cold and warm seasons was primarily driven by the higher prevalence of copepods during the warm season (Table 5). Additionally, seasonal differences were influenced by variations in the abundance of decapod larvae and mysids, though to a lesser extent.

DISCUSSION

Species interactions are fundamental to shaping ecosystem dynamics, influencing energy transfer, community structure, and overall ecosystem functioning (Hayden *et al.,* 2019). Understanding the feeding habits of individual species is essential for elucidating their ecological roles and uncovering potential interactions with other species. This study enhances our knowledge by providing detailed insights into the feeding habits of seven pelagic forage fish species and their contributions to trophic dynamics. Considering that this research covers pelagic species, which are known for their fast metabolism due to their lifestyle (Killen *et al.,* 2010), the moderate value of the empty stomach (23%) followed the expected as well as the literature data (Vinson and Angradi, 2011; for pelagic fish species collected during the night the percental range of empty stomach goes from 23% to 33%).

Stomach fullness (%Jr) did not show a significant correlation with total body size, consistent with findings by Zorica *et al.* (2021) for sardines, anchovies, Mediterranean horse mackerel, and Atlantic horse mackerel. However, Vinson and Angradi (2011) noted that larger fish tend to consume larger prey and feed less frequently. This observation aligns with the present study, as the diet of medium-sized pelagic fish species primarily consisted of larger zooplankton such as mysids, euphausids, and decapod larvae. Nonetheless, future research should incorporate a broader range of fish size classes, including juveniles and adults, to provide more comprehensive insights. This particularly refers to all fishes which are not filter feeders and herbivory for which fewer effects of body size were already noted by Sánchez-Hernández and Amundsen (2018).

The stomach content analysis of the investigated species was generally congruent with previous studies done on the same fish species inhabiting the Adriatic Sea (Čikeš Keč *et al.,* 2012; Hure and Mustać, 2020; Zorica *et al.,* 2021; Fanelli *et al.,* 2023; Zorica *et al.,* 2024). Sardine and round sardinella were confirmed as omnivores due to their consumption of both phytoplankton and zooplankton. Their strong preference for copepods suggests that these species function primarily as filter feeders, efficiently exploiting abundant planktonic resources. In contrast, the diet of anchovy exhibited slightly greater variety compared to the other two small pelagic fish. While copepods remained the primary dietary component, the notable abundance of mysids indicated that anchovy employs both particulate and filter feeding strategies, selecting prey based on its availability as previously reported by Bacha and Amara (2009) and Zorica *et al.* (2016). Other investigated species, precisely medium pelagic forage fish, showed reliance on specific prey groups like

Table 5. Results of a two-way SIMPER test on size and seasonal differences in diet of investigated species.

Variable	First group average abundance	Second group average abundance	Average dissimilarity	Standard Deviation	Contribution %	Cumulative %
Medium versus Small size						
Copepoda	0.25	1.51	24.17	1.31	28.45	28.45
Mysida	1.20	0.28	16.04	0.79	18.88	47.33
Decapoda larvae	0.86	0.39	13.47	0.93	15.85	63.18
Amphipoda	0.51	0.30	9.40	0.77	11.06	74.24
Cold versus Warm season						
Copepoda	0.84	1.20	18.54	1.06	26.79	26.79
Decapoda larvae	0.82	0.32	11.57	0.87	16.72	43.51
Mysida	0.67	0.60	10.20	0.56	14.73	58.24
Amphipoda	0.52	0.24	8.10	0.71	11.71	69.95
Euphausiacea	0.01	0.48	6.62	0.39	9.56	79.51

mysids (Atlantic horse mackerel), euphausids (Atlantic chub mackerel) and decapod larvae (Mediterranean horse mackerel and bogue) which indicated that they tend to have specialized feeding strategies as it was following previous studies (Jardas *et al.,* 2004; Šantić *et al.,* 2004; Čikeš Keč *et al.,* 2012; Garrido *et al.,* 2015).

The pelagic forage fish analysed showed low prey diversity (H'), ranging from 0.5 in Atlantic horse mackerel to 1.4 in anchovy. The corresponding Pielou's evenness index indicated that prey items were moderately unevenly represented in the stomachs, with diets often dominated by a single or a few prey categories. The trophic niche breadth of all species was relatively low ($0.1 < Bn < 0.4$), indicating a notable degree of trophic specialization (Petta *et al.,* 2020). Nevertheless, the strict definition of trophic specialists, which describes species that rely predominantly on one or very few prey items (Erlinge, 1986), does not fully apply to the species examined, as they were found to consume up to eleven distinct prey items. Considering the variability in definitions and methodologies for characterizing ecological specialization (Devictor *et al.,* 2010; Kingsbury *et al.,* 2020), analysed species most probably adopt an opportunistic feeding strategy, targeting the most abundant prey items in their ecosystem. Analysis of dietary overlap among the studied species, as assessed through nMDS analysis and ANOSIM and SIMPER, revealed clear differences based on both size category (small *vs*. medium) and sampling season (cold *vs*. warm). Although small pelagic fish diet mostly relied on copepods in both seasons, their higher abundance during the warmer season makes the difference. In the Adriatic Sea, the warm season is characterised by a general increase in average sea water temperatures and higher primary productivity that led to higher abundances of copepods and zooplankton in general (Hure *et al.,* 1980; Bojanić *et al.,* 2005; Vidjak *et al.,* 2012), hence the higher availability of their preferred prey items resulted in their higher intake. Furthermore, the noted increase in zooplankton abundance contributed to higher diet overlap between small and medium pelagic fish within the warm season, although medium fishes showed a preference for larger zooplankton organisms. Conversely, during the colder season difference between the diet of small and medium pelagic forage was more pronounced as the medium size fishes had more decapod larvae and mysids in their stomachs. This pattern is likely attributable to the reduced abundance of zooplankton in the Adriatic Sea during winter (Hure *et al.*, 1980). Under these conditions, medium-sized fish are expected to optimize foraging by selecting prey with higher energetic value, such as decapod larvae, which have their breeding season in the Adriatic during the winter months (Kurian, 1956; Gill, 2003).

CONCLUSION

The results of this study shed light on the trophic interactions and ecological strategies of small and medium pelagic forage fish. The dietary analysis revealed evidence of potential interspecific competition under resource-limited conditions, emphasizing the intricate balance of these species within the ecosystem. This underscores the critical importance of adopting an ecosystem-based approach to fisheries management, particularly in light of the ongoing overexploitation and climate-driven changes that jeopardize the stability of this and other marine food webs.

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