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# Spatiotemporal variability in the feeding habits of anchovy and sardine: a comparison of upwelling and river-runoff driven ecosystems

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European sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) are important components of marine food webs, acting as trophic links between primary consumers and higher trophic levels. However, local factors—such as environmental conditions, human activities, coastal pollution, and more generally, climate change have had a significant impact on their trophic interactions, affecting the energy flow, structure, and function of the marine ecosystems in which they live. Although both species are among the most explored in the Mediterranean Sea, due to their commercial and ecological importance, the spatiotemporal variability in their trophic ecology is still poorly addressed, particularly when combining life stage, sampling year, and geographic location. Here, we propose a spatio-temporal analysis of the trophic variability of juvenile and adult anchovy and sardine in two different areas of the central Mediterranean Sea—the Tyrrhenian Sea (TR) and the Strait of Sicily (SS)—over 4 years (2011, 2014, 2015, and 2017). We used a stable isotope ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) approach to assess variability in feeding behaviour and isotopic niche metrics (niche width and overlap) across space and time. The two study areas are influenced by different water masses with distinct physical and biological properties, leading to local changes in the marine food web and consequently in the feeding behaviour of both fish species at different life stages. In all sampled years, higher  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were found in both anchovy and sardine sampled in the Tyrrhenian Sea (mean values: 8.8‰ and –17.5‰ for anchovy; 9.5‰ and –18.1‰ for sardine) compared with those from the Strait of Sicily (mean values: 6.6‰ and –18.9‰ for anchovy; 6.8‰ and –19.0‰ for sardine). Furthermore, the higher  $\delta^{15}\text{N}$  values observed indicate no significant relationship between isotopic values and organism size. Our results support the hypothesis that the higher isotopic signals observed in both juvenile and adult anchovy and sardine in the Tyrrhenian Sea may be linked to higher trophic-level food sources (e.g., predation on large prey such as krill), potentially associated with persistent local features (e.g., submarine canyons). Moreover, the greater number of cases

showing wider isotopic niches and higher isotopic overlap between species—and between life stages—in the Tyrrhenian Sea than in the Strait of Sicily suggests higher variability in feeding behaviour and access to more diversified food sources. These data contribute to a better understanding of food web dynamics and may be used to improve ecosystem models, which requires an understanding of the ecological processes that control the interaction between species.

#### KEYWORDS

stable isotopes, *Engraulis encrasicolus*, *Sardina pilchardus*, trophic ecology, spatiotemporal variability, feeding habits

## Introduction

Variation in the population dynamics of small pelagic fishes has been widely documented, and progress has been made over the last few decades in understanding the factors driving long-term fluctuations (e.g., Lluich-belda et al., 1992; Chavez et al., 2003; Alheit et al., 2012). However, such changes occur across a variety of scales (e.g., seasonal, inter-annual, decadal), and encompasses fluctuations in both abiotic (temperature, precipitation, light, nutrients) and biotic processes (e.g., migration, growth, reproduction, trophic interactions).

Pelagic food webs can be highly dynamic across space and time, especially at the regional scale and in coastal areas (Hernández-Carrasco et al., 2018), where riverine inputs, upwelling processes, and anthropogenic stressors can deeply modify environmental conditions and the ecological state of the water column (Stenseth et al., 2006; DiBattista et al., 2020). These alterations can have cascading effects on fish populations and pelagic food webs (Cushing, 1995; Russo et al., 2022; Vassallo et al., 2022).

In this context, an important question is whether variability in trophic relationships at the local scale is more strongly linked to spatial or temporal factors in coastal systems. This question has fundamental implications for the ecological study and management of marine ecosystems, including the provision of ecosystem goods and services and the sustainability of economic activities such as fisheries (Lomartire et al., 2021; Nissar et al., 2023).

Small pelagic fish, due to their rapid growth, short life span, and plankton-based diet, are often considered excellent indicators for assessing changes in resource availability associated with rapid, climate-driven environmental shifts in marine systems (e.g., Drinkwater et al., 2010; Peck et al., 2013). In particular, small pelagic fishes such as anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) are key elements both from an economic point of view, representing important species for commercial fishing (FAO, 2022), and for marine ecosystems, linking lower and upper trophic level species (Cury et al., 2000).

Studies on the trophic ecology of these small pelagic fish have largely been conducted based on stomach content analysis (SCA),

which provides insight into the most frequently consumed and abundant prey items (e.g., Borme et al., 2009; Costalago and Palomera, 2014; Costalago et al., 2014). In recent decades, scientists have increasingly used alternative techniques, including stable isotope analysis (SIA), to determine the relative contributions of prey types or trophic positions assimilated over longer periods than those captured by SCA (e.g., Pethybridge et al., 2018). This method provides information about the assimilated prey over a specific time window—ranging from a few days to several months—depending on the tissue type analysed (e.g., liver, white muscle, blood) and its isotopic turnover rate (Hesslein et al., 1993; Bearhop et al., 2004). The ability to isotopically analyse muscle tissue from anchovy and sardine at different life stages offers a time-integrated view of dietary shifts, as this tissue has an isotopic turnover rate ranging from several days to one month (Suzuki et al., 2005; Guelinckx et al., 2007; Buchheister and Latour, 2010). Because stable isotope enrichment occurs along the trophic web, nitrogen stable isotope ( $\delta^{15}\text{N}$ ) have been utilised as an indicator of the trophic position of organisms along the food web, as well as an indicator of the seasonal and spatial variability in trophic habits (Tanaka et al., 2008; Malzahn and Boersma, 2009). Similarly, as different energy sources often have distinct  $\delta^{13}\text{C}$  signatures, carbon stable isotopes can be used to trace the original organic carbon sources at the base of the food web, assess seasonal variation, or detect geographic differences (Vander Zanden and Rasmussen, 1999; 2001; Overman and Parrish, 2001; Castro et al., 2020, and references therein).

In the present study, we compared the isotopic carbon and nitrogen ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) signals in white muscles of juvenile and adult individuals of both sardine and anchovy to investigate the spatiotemporal variability in their feeding behaviour across two Mediterranean areas—the Tyrrhenian Sea and the Strait of Sicily—in the years 2011, 2014, 2015, and 2017. These two areas differ markedly in terms of hydrographic conditions, morpho-bathymetry, and productivity (Bonanno et al., 2016; 2018). The SS area is characterised by highly dynamic circulation, a coastal upwelling system (Bonanno et al., 2014), low coastline complexity, minimal human impact, and limited terrigenous input from river runoff. In contrast, the TR area features a large continental shelf, strong riverine influence from several rivers (e.g., Tiber, Garigliano, Volturno, Sarno, and Sele), and high levels

of urban, agricultural, and industrial activities as well as a high degree of coastline complexity with the presence of Gulfs.

To our knowledge, only a few studies have evaluated the spatiotemporal variability in the feeding habits of these two small pelagic species in the Mediterranean Sea (e.g., [Bachiller et al., 2020](#); [Navarro et al., 2020](#); [Zorica et al., 2021](#); [Fanelli et al., 2023](#)), and these have generally analysed only 1 year of data and/or focused on areas located in close geographic proximity.

Taking all these factors into account, we collected fish samples from both consecutive and non-consecutive years in order to assess the spatiotemporal variability in the feeding habits of anchovy and sardine. We first analysed the inter- and intraspecific differences in the isotopic composition of both species across life stages, areas, and years, focusing on the degree of overlap and the width of the isotopic niches. In a second step, we assessed which factor had the greatest influence on their feeding behaviour (i.e., place or time).

## Materials and methods

### Study area

This study focuses on anchovy and sardine samples collected in the Strait of Sicily (hereafter SS) and the Tyrrhenian Sea (hereafter TR), specifically along the coasts of Campania, Lazio, and Tuscany up to the island of Elba ([Figure 1](#)). The two areas are characterised by differing hydrographic conditions, morpho-bathymetry, and productivity ([Figure 1](#); [Bonanno et al., 2016](#)).

From a morphological perspective, the SS area is characterised by the presence of two broad banks in the westernmost and easternmost sectors of the Adventure Bank and the Maltese Bank, respectively—extending nearly 70 nmi offshore. In contrast, the continental shelf between the two banks is relatively narrow (~8 nmi). This distinct topographic pattern also influences the path of the Atlantic Ionian Stream (AIS; [Robinson et al., 1999](#)), the most important oceanographic feature in the area. The AIS is the primary driver of productivity during the summer season, as it induces a permanent coastal upwelling along the southern coast of Sicily ([Bonanno et al., 2014](#); [Rumolo et al., 2017](#)).

In the SS area, circulation is characterised by a two-layer system flowing in opposite directions: surface Atlantic Water (AW) moves eastward, while Levantine Intermediate Water (LIW) flows westward. The surface flow displays meanders with high spatial and temporal variability ([Manzella et al., 1988](#); [Moretti et al., 1993](#); [Bonanno et al., 2014](#)). Relatively intense local phenomena, including cyclonic and anticyclonic gyres, are frequently observed via satellite imagery ([Champagne-Philippe et al., 1982](#)). In this area, the coastline is also characterised by a low level of morphological complexity and minimal human pressure. Additionally, the input of terrigenous material from river runoff is of minor importance.

The TR area is characterised by a large continental shelf, with surface circulation mainly influenced by the Middle Tyrrhenian Current (MTC), which, upon approaching the coast near Rome, is strongly affected by the Tiber River ([Figure 1](#))—one of the largest rivers flowing into the Tyrrhenian Sea ([Rinaldi et al., 2010](#); [Sammartino et al., 2022](#)).

River discharge serves as a major nutrient source in the TR area, where coastline morphology varies between the northern (i.e., Lazio and Tuscany) and southern (i.e., Campania) sectors.

In the northern TR sector, where coastline complexity is low, the Tiber River outflow is responsible for approximately 20% of the total riverine input into the Tyrrhenian Sea ([Mikhailova et al., 1999](#)). In contrast, the southern sector (i.e. the Campania coast), is characterised by high coastline complexity, due to the presence of three large gulfs: the Gulf of Gaeta, the Gulf of Naples, and the Gulf of Salerno. Several small and medium-sized rivers discharge into these gulfs—including the Garigliano and Volturno rivers (Gulf of Gaeta), the Sarno River (Gulf of Naples), and the Sele River (Gulf of Salerno). These rivers drain catchment areas that are heavily impacted by urban, agricultural, and industrial activities. In this southern Tyrrhenian sector, the combination of low hydrodynamics and enclosed geomorphological features (i.e., gulfs) promotes the retention of nutrients from river discharge on the continental shelf ([Bonanno et al., 2016](#)). The presence of submarine canyons—such as the Cuma Canyon and Dohrn Canyon—also contributes to nutrient retention ([Aiello and Caccavale, 2023](#)).

### Sampling

The Mediterranean International Acoustic Surveys (MEDIAS; [www.medias-project.eu](http://www.medias-project.eu)) programme, established under the EU Fisheries Data Collection Regulation (EC 199/2008), conducts annual acoustic surveys in EU Mediterranean waters to assess the biomass and spatial distribution of anchovy and sardine populations. The biological samples analysed in this study were collected under the MEDIAS umbrella during the “Ancheva” and “Evatir” surveys, which collected acoustic data and biological samples in the Strait of Sicily (including a small portion of the Ionian Sea) and in the Tyrrhenian and Ligurian Seas ([Leonori et al., 2021](#)). Anchovy (hereafter ANE) and sardine (hereafter PIL) samples were collected at specific trawl stations during surveys carried out in 2011, 2014, 2015, and 2017 ([Figure 2](#)).

Specimens of anchovy and sardine were caught using a midwater pelagic trawl net with the following characteristics: 11 m vertical mouth opening, 18 m horizontal opening, and an 8 mm cod end mesh size. During each haul, the net—equipped with an integrated monitoring system (SIMRAD ITI) to control its position in the water column and monitor catch efficiency—was towed at an average speed of 4 knots for 30 minutes. Once the net was retrieved, a subsample of the total catch was selected. For each species, individuals were measured (total length [TL], in cm), assigned to 1 cm length classes, sorted, counted, and weighed (wet weight [WW], in g). Subsamples included 10 individuals per 1 cm length class for each species (sardine and anchovy), when available. All samples were frozen at −20°C for laboratory analysis.

The length thresholds used to classify individuals as juveniles or adults were 11 cm for anchovy and 13 cm for sardine, following [Bachiller et al. \(2020\)](#). In total, 1,337 fish were collected: 173 anchovies and 452 sardines from the SS area, and 406 anchovies and 306 sardines from the TR area (see [Table 1](#) for details).

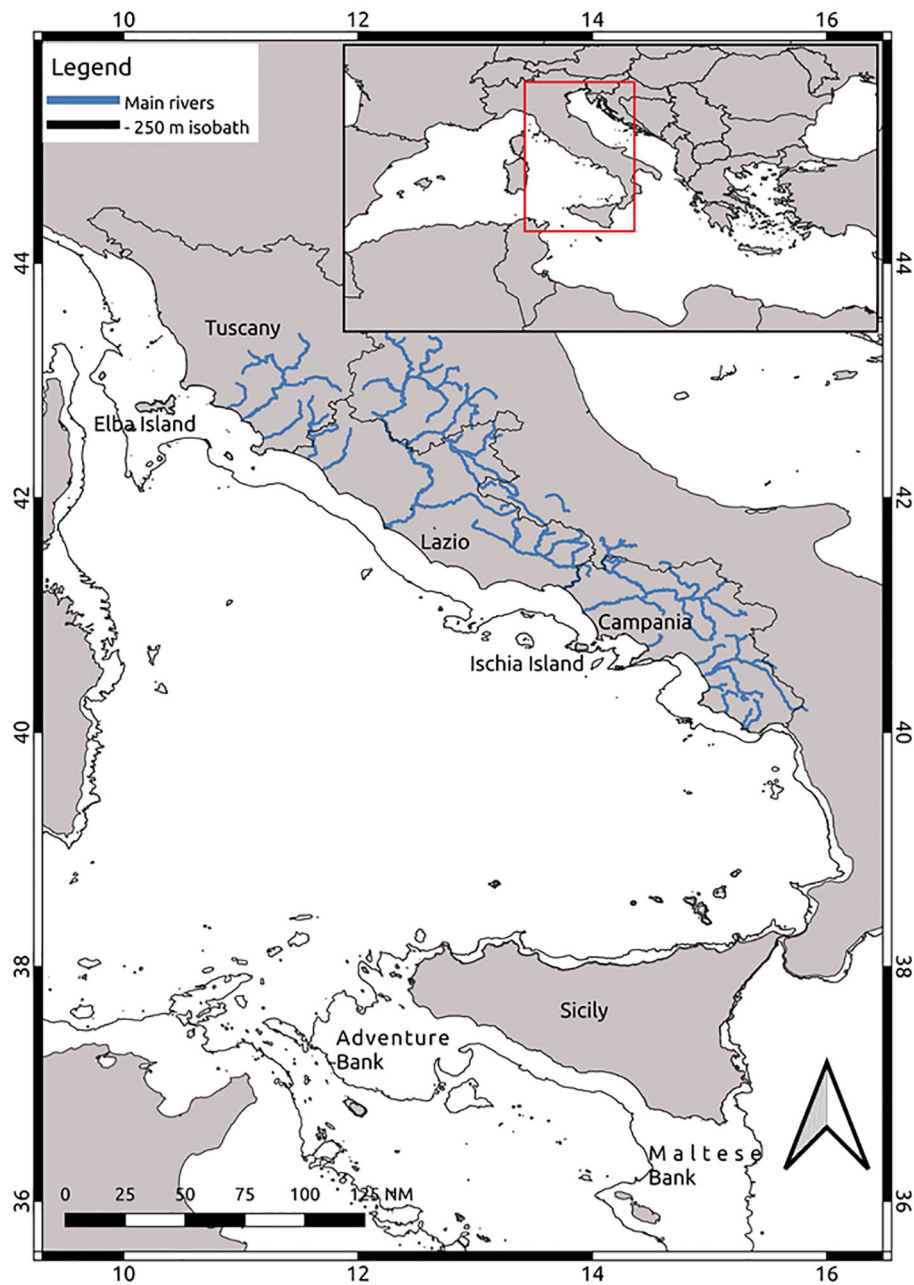


FIGURE 1  
Study area.

## Stable isotope analysis

A portion of white muscle near the dorsal fin was extracted from each individual fish, oven-dried at a constant temperature (60°C for 24 h), powdered, and weighed (0.5 mg) into tin capsules.

Although some authors recommend lipid extraction in fish and zooplankton samples prior to stable isotope analysis (Cardona et al., 2012; Tanaka et al., 2008), we did not apply a defatting procedure, consistent with other studies (Logan et al., 2008; Fanelli et al., 2011; Iitembu et al., 2012; Madigan et al., 2012). Instead, we assessed lipid content using the relationship between C:N ratios and  $\delta^{13}C$

signatures. The method proposed by Logan et al. (2008) to normalise the  $\delta^{13}C$  values from lipid concentration (Rumolo et al., 2016) was used in order to compare the isotopic values of sardine and anchovy collected in similar areas. In particular, Equation (1a) proposed by Logan et al. (2008) was used for white fish muscle with C:N > 3.5.

$$\delta^{13}C' - \delta^{13}C = \frac{a * C:N + b}{C:N + c}$$

where  $\delta^{13}C$  is the isotope value with lipid content,  $\delta^{13}C'$  is the corrected value,  $a = 7.415$ ,  $b = -22.732$  and  $c = 0.746$ .

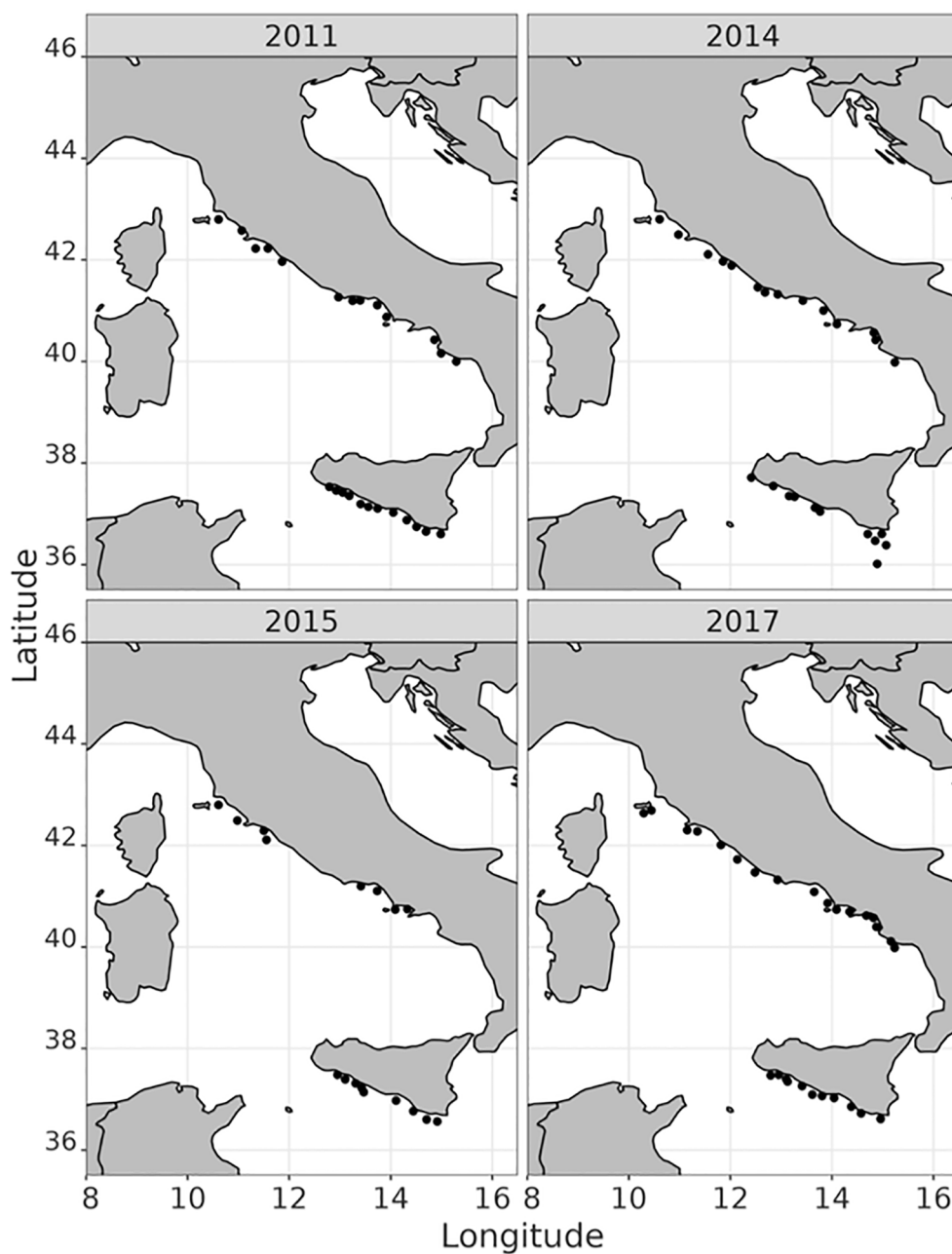


FIGURE 2  
Sampling sites by year.

Stable isotope measurements and C and N concentrations were carried out at the iCONa Laboratory of the University of Campania using a Thermo Fisher Flash EA 1112 elemental analyser coupled to a Thermo Delta V Advantage isotope ratio mass spectrometer (IRMS). Samples were analysed alongside blank tin cups and certified analytical-grade urea of certificated isotopic composition. Three urea capsules were analysed at the beginning of each sequence, and one was analysed every six samples as a quality control measure and to compensate for potential instrument drift. Experimental precision,

based on the standard deviation of replicate internal standards, was  $<0.2\%$  for  $\delta^{15}\text{N}$  and  $<0.1\%$  for  $\delta^{13}\text{C}$ . International IAEA reference standards were used to calibrate sample measurements.

The  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values were obtained in parts per thousand (‰) relative to atmospheric  $\text{N}_2$  and Vienna Pee Dee Belemnite (VPDB), respectively, using the following formula:

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

where  $R = {}^{13}\text{C}/{}^{12}\text{C}$  or  ${}^{15}\text{N}/{}^{14}\text{N}$ .

TABLE 1 Descriptive statistic  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  by area, year, species, and life stage reporting mean, standard deviation (SD), median, inter quartile range (IQR), minimum and maximum values.

Area	Species	Life stage	Year	N	C: N<3.5	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$		
						Mean (sd)	Median (IQR)	Min - Max	Mean (sd)	Median (IQR)	Min - Max
SS	ANE	Adults	2011	36		7.4 (0.4)	7.4 (0.4)	6.6 - 8.3	-18.6 (0.3)	-18.6 (0.6)	-19.0; -18.0
			2014	56		7.2 (0.5)	7.1 (0.6)	6.4 - 9.0	-19.6 (0.6)	-19.7 (0.8)	-20.4; -18.1
			2015	15		7.2 (0.3)	7.3 (0.5)	6.7 - 7.7	-18.0 (0.3)	-18.1 (0.3)	-18.5; -17.2
			2017	5		6.2 (0.2)	6.2 (0.3)	5.9 - 6.4	-19.4 (0.2)	-19.3 (0.3)	-19.7; -19.3
		Juvenile	2011	7		7.3 (0.3)	7.1 (0.4)	7.0 - 7.8	-18.9 (0.3)	-18.9 (0.3)	-19.2; -18.5
			2014	29		5.6 (0.7)	5.9 (0.8)	4.2 - 7	-19.4 (0.4)	-19.3 (0.4)	-20.3; -18.8
			2015	10		6.8 (0.4)	6.9 (0.7)	6.2 - 7.4	-17.9 (0.4)	-18.0 (0.6)	-18.6; -17.1
			2017	15		5.1 (0.5)	4.9 (0.3)	4.6 - 6.2	-19.1 (0.2)	-19.0 (0.3)	-19.5; -18.8
		Adults	All	112	105	7.0 (0.6)	7.2	5.9 - 9.0	-18.9 (0.7)	-19.0	-20.4; -17.2
		Juvenile		61	61	6.2 (1.0)	6.4	4.2 - 7.8	-18.9 (0.6)	-19.0	-20.3; -17.1
		All		173	166	6.6 (0.9)	7.0	4.2 - 9.0	-18.9 (0.6)	-19.0	-20.4; -17.1
		PIL	Adults	2011	50		6.9 (0.3)	6.9 (0.3)	6.3 - 7.4	-18.6 (0.4)	-18.6 (0.5)
	2014			62		6.7 (0.8)	6.8 (1.0)	5.0 - 8.9	-19.3 (0.5)	-19.2 (0.6)	-20.5; -18.1
	2015			25		6.7 (0.3)	6.7 (0.3)	6.0 - 7.5	-19.1 (0.2)	-19.1 (0.3)	-19.6; -18.5
	2017			17		6.7 (0.3)	6.6 (0.3)	6.2 - 7.7	-19.1 (0.2)	-19.2 (0.3)	-19.4; -18.8
	Juvenile		2011	85		6.9 (0.3)	6.9 (0.3)	6.3 - 8.6	-18.7 (0.2)	-18.7 (0.3)	-19.3; -17.9
			2014	146		6.8 (0.5)	6.8 (0.6)	5.1 - 8.6	-19.2 (0.3)	-19.2 (0.4)	-20.2; -18.1
			2015	20		7.1 (0.5)	6.9 (0.5)	6.4 - 8.2	-18.9 (0.3)	-18.8 (0.3)	-19.3; -18.3
2017			47		6.6 (0.5)	6.6 (0.5)	5.8 - 7.6	-19.4 (0.2)	-19.4 (0.2)	-19.7; -18.9	
Adults	All		154	48	6.8 (0.1)	6.8	5.0 - 8.9	-19.0 (0.3)	-19.1	-20.5; -17.7	
Juvenile			298	177	6.9 (0.2)	6.8	5.1 - 8.6	-19.0 (0.3)	-19.0	-20.2; -17.9	
All		452	225	6.8 (0.2)	6.8	5.0 - 8.9	-19.0 (0.3)	-19.1	-20.5; -17.7		
TR	ANE	Adults	2011	87		8.9 (1.1)	8.9 (1.6)	6.0 - 11.1	-17.2 (0.3)	-17.2 (0.5)	-18.1; -16.5
		Adults	2014	62		8.8 (0.8)	8.8 (1.1)	7.0 - 10.5	-18.0 (0.6)	-18.0 (0.7)	-19.1; -16.7
		Adults	2015	31		8.9 (1.0)	8.8 (0.8)	6.0 - 10.7	-17.6 (0.6)	-17.5 (1.1)	-18.7; -16.8
		Adults	2017	44		7.9 (0.9)	7.9 (1.2)	5.9 - 9.6	-17.9 (0.6)	-17.9 (0.8)	-18.9; -16.7
		Juvenile	2011	38		10.1 (1.0)	10.3 (1.4)	7.7 - 11.4	-17.1 (0.3)	-17.1 (0.5)	-17.6; -16.4
		Juvenile	2014	91		9.4 (1.3)	9.5 (1.7)	6.4 - 12.5	-17.7 (0.5)	-17.6 (0.7)	-19; -16.8
		Juvenile	2015	19		9.0 (2.2)	9.0 (3.5)	5.3 - 12.1	-17.3 (0.3)	-17.3 (0.3)	-17.9; -16.6
		Juvenile	2017	34		7.2 (1.8)	6.6 (2.7)	5.0 - 11.3	-17.3 (0.4)	-17.4 (0.5)	-18; -16.3
		Adults	All	224	162	8.6 (0.5)	8.8	5.9 - 11.1	-17.7 (0.3)	-17.7	-19.1; -16.5
		Juvenile		182	108	8.9 (1.3)	9.2	5.0 - 12.5	-17.4 (0.3)	-17.4	-19; -16.3
		All		406	264	8.8 (0.9)	8.9	5.0 - 12.5	-17.5 (0.3)	-17.4	-19.1; -16.3
		PIL	Adults	2011	62		8.8 (1.2)	9.3 (1.5)	6.2 - 10.8	-17.6 (0.3)	-17.5 (0.4)

(Continued)

TABLE 1 Continued

Area	Species	Life stage	Year	N	C: N<3.5	$\delta^{15}\text{N}$			$\delta^{13}\text{C}$		
						Mean (sd)	Median (IQR)	Min - Max	Mean (sd)	Median (IQR)	Min - Max
			2014	28		10.1 (1.4)	10.0 (1.3)	6.7 - 13.5	-17.9 (0.5)	-17.9 (0.7)	-19.3; -17.2
			2015	11		10.0 (0.5)	10.0 (0.9)	9.4 - 10.9	-17.8 (0.3)	-17.9 (0.3)	-18.5; -17.2
			2017	27		8.3 (1.2)	8.4 (2.1)	5.9 - 10.2	-18.6 (0.2)	-18.6 (0.2)	-19.1; -18.1
		Juven ile	2011	51		9.6 (1.4)	9.9 (1.3)	6.1 - 11.0	-17.6 (0.3)	-17.6 (0.4)	-18.2; -17.1
			2014	86		10.4 (1.1)	10.3 (1.6)	7.6 - 13.2	-17.9 (0.5)	-18.0 (0.8)	-18.9; -16.7
			2015	28		10.2 (1.2)	9.8 (2.1)	8.4 - 12.1	-18.3 (0.3)	-18.3 (0.6)	-18.8; -17.8
			2017	13		8.9 (0.8)	9.2 (1.0)	7.5 - 10.1	-18.6 (0.3)	-18.7 (0.4)	-19.0; -18.0
		Adults	All	128	56	9.3 (0.9)	9.6	5.9 - 13.5	-18.0 (0.4)	-17.9	-19.3; -17.1
		Juven ile		178	47	9.8 (0.7)	9.8	6.1 - 13.2	-18.1 (0.4)	-18.1	-19.0; -16.7
		All		306	103	9.5 (0.8)	9.8	5.9 - 13.5	-18.1 (0.4)	-18.0	-19.3; -16.7

SS, Strait of Sicily; TR, Tyrrhenian Sea; ANE, anchovy; and PIL, sardine. All-year statistics by area, species, and life stage, computed from yearly values, are also reported. Number of specimens on which the lipid correction was not applied (C:N<3.5) is also reported.

## Statistical analysis

Exploratory analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values revealed differences in variance between the two areas, as well as significant relationships between isotope values and fish length in specific cases only (Supplementary Figures S1, S2). Consequently, a generalised least squares (GLS)-based ANOVA approach was used to test for differences in  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values across areas, years, life stages, and species, explicitly accounting for (i) possible interactions between factors and length class, and (ii) heteroscedasticity by applying variance weighting according to the Area and Year factors.

For both  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ , GLS-based models were constructed to include all possible interactions among predictors. The best-fitting model was selected based on Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) values. Given the expected significant correlation between length class and isotope values—and the unbalanced nature of the dataset—*post hoc* tests were based on estimated marginal means using the Tukey method.

The standard ellipse area (SEA<sub>b</sub>; Jackson et al., 2011) was calculated to infer isotopic niche width, a proxy for the trophic diversity (or trophic breadth) exploited by the groups considered. Isotopic niche overlap was assessed by calculating the ratio between the area of the geometric intersection of the ellipses and the area of their union. As Bayesian inference techniques provide robust statistical comparisons for datasets with different sample sizes (Navarro et al., 2020), a Bayesian approach was adopted for both niche width and ellipse overlap, allowing formal testing of the significance of observed differences.

All statistical analyses were performed in R (v.4.1; R Core Team, 2023). GLS models were developed using the 'nlme' package (Pinheiro et al., 2023), *post hoc* tests were conducted with the

'emmeans' package (Lenth, 2023), and isotopic niche using the SIBER package (Jackson et al., 2011).

## Results

Summary statistics for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values (mean, standard deviation, median, interquartile range, minimum/maximum values, and number of observations) by area, year, species, and life stage are reported in Table 1. Overall, the differences between the mean and median values of  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  were small (maximum absolute differences were 0.6‰ and 0.2‰, respectively), highlighting the rather symmetric distributions for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values in each group (i.e., area, year, species, and life stage).

Pearson correlation analyses between  $\delta^{15}\text{N}$  (and  $\delta^{13}\text{C}$ ) fish total length (TL) showed both positive and negative correlations for anchovy and sardine across years and areas, when significant ( $p < 0.05$ ) (Supplementary Figure S2). For anchovy in the SS area,  $\delta^{15}\text{N}$  showed a positive correlation in 2014 and 2017, while  $\delta^{13}\text{C}$  showed a negative correlation in 2017 for  $\delta^{13}\text{C}$ ; in TR it was positive in 2017 but negative in 2011 and 2014 in terms of  $\delta^{15}\text{N}$  and always negative in 2014, 2015 and 2017 for  $\delta^{13}\text{C}$ . For sardines, when significant, the correlations were always negative in terms of  $\delta^{15}\text{N}$  in both areas (2015 in SS; 2011 and 2017 in TR). For  $\delta^{13}\text{C}$ , the correlation was negative in 2014 and 2015 and positive in 2017 in SS, and positive only in 2015 in TR.

Preliminary fits of GLS models highlighted the effect of unequal variance and the lack of independence of residuals for both  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ . Consequently, the within-group heteroscedasticity structure was modelled according to area and year factor, while the within-group correlation structure accounted for the autocorrelation at catch operation level. The predictors selected for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  best

models were area and year factors as well as different interactions involving length class and other factors (Table 2).

## $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences between areas considering years, species and life stages

For  $\delta^{15}\text{N}$ , both anchovy and sardine showed lower values in the SS area than in the TR area, with the latter in some cases displaying higher variability (Table 1; Figures 3, 4). In particular,  $\delta^{15}\text{N}$  values for anchovy ranged from 4.2‰ to 9.0‰ in SS and from 5.0‰ to 12.5‰ in TR (mean across all years: 6.6‰ and 8.8‰, respectively). For sardine,  $\delta^{15}\text{N}$  values ranged from 5.0‰ to 8.9‰ in SS and from 5.9‰ to 13.5‰ in TR (mean: 6.8‰ and 9.5‰, respectively).

For  $\delta^{13}\text{C}$ , the SS area generally showed less enriched values than TR, although in 2015 the difference appeared smaller than in other years (Table 1; Figure 5). For anchovy,  $\delta^{13}\text{C}$  values ranged from -20.4‰ to -17.1‰ in SS and from -19.1‰ to -16.3‰ in TR (mean: -18.9‰ and -17.5‰, respectively). For sardine,  $\delta^{13}\text{C}$  values from -20.5‰ to -17.7‰ in SS and from -19.3‰ to -16.7‰ in TR (mean: -19.0‰ and -18.1‰, respectively).

TABLE 2 ANOVA table of the generalized least squares (GLS) models for  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ .

(a)			
	Df	$\chi^2$	Pr ( $>\chi^2$ )
(Intercept)	1	823.1	<0.0001
area	1	41.8	<0.0001
year	3	94.6	<0.0001
area:LC	2	18.9	0.0001
area:year	3	59.5	<0.0001
area:LC:species	2	20.0	<0.0001
area:year:species	6	105.8	<0.0001
area:year:LC:species	12	154.9	<0.0001
(b)			
	Df	$\chi^2$	Pr ( $>\chi^2$ )
(Intercept)	1	1753.5	<0.0001
area	1	19.3	<0.0001
year	3	13.0	0.005
area:species	2	15.8	<0.0001
area:year	3	11.0	0.01
year:species	3	11.6	0.008
area:species:LC	4	13.3	0.01
year:species:LC	6	16.0	0.01
LC:area:year:species	3	35.4	<0.0001

*Post hoc* tests revealed significant differences between the two areas in all comparisons (Supplementary Table S2), except for  $\delta^{15}\text{N}$  in 2014 and  $\delta^{13}\text{C}$  in 2015 in adult anchovies. In all cases where differences were significant, the SS area showed lower average values than TR for both isotopes (Supplementary Table S2). In the case of  $\delta^{15}\text{N}$ , for each species, the difference between juveniles in the two areas was generally higher than the one observed for adults.

## $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences between years considering areas, species, and life stage

Isotopic differences between years were evaluated to highlight the temporal stability of average values at the area, species, and life stage levels (Supplementary Table S3). In the SS area, differences in terms of  $\delta^{15}\text{N}$  values between years were generally not significant for adults of either species. However, significant differences were observed for anchovy juveniles in all pairwise comparisons and for sardine juveniles only in the 2014–2015 comparison. A similar pattern was found in the TR area, though significant differences also emerged for adults of both species.

For  $\delta^{13}\text{C}$  values, significant differences in the SS area were detected for both adults and juveniles of both species. On the contrary, in the TR area, significant differences were less frequent for anchovy (both adults and juveniles) but more consistent for sardine (Supplementary Table S3).

## $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences between life stages (juveniles and adults) of each species considering years and areas

The comparison between adults and juveniles of both species across years and areas (Supplementary Table S4) showed that, in the TR area, differences in  $\delta^{15}\text{N}$  were consistently significant for anchovy in all years but not for sardine. In the SS area, no clear or consistent patterns were observed. For  $\delta^{13}\text{C}$ , differences between life stages were generally not significant for either species in either area.

## $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences between species considering year and area

When comparing  $\delta^{15}\text{N}$  values between species at the same life stage (i.e., adult anchovy vs. adult sardine) within the same area (Supplementary Table S5), significant differences were more frequent in the SS area than in the TR where differences were significant in only one case (year 2014). In terms of  $\delta^{13}\text{C}$ , differences were significant in one case only in both areas (SS: 2015; TR: 2011).

## $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ differences between life stages of the two species considering areas and years

Comparisons between adults and juveniles of the two species at the area and year level (Supplementary Table S6) revealed that, in



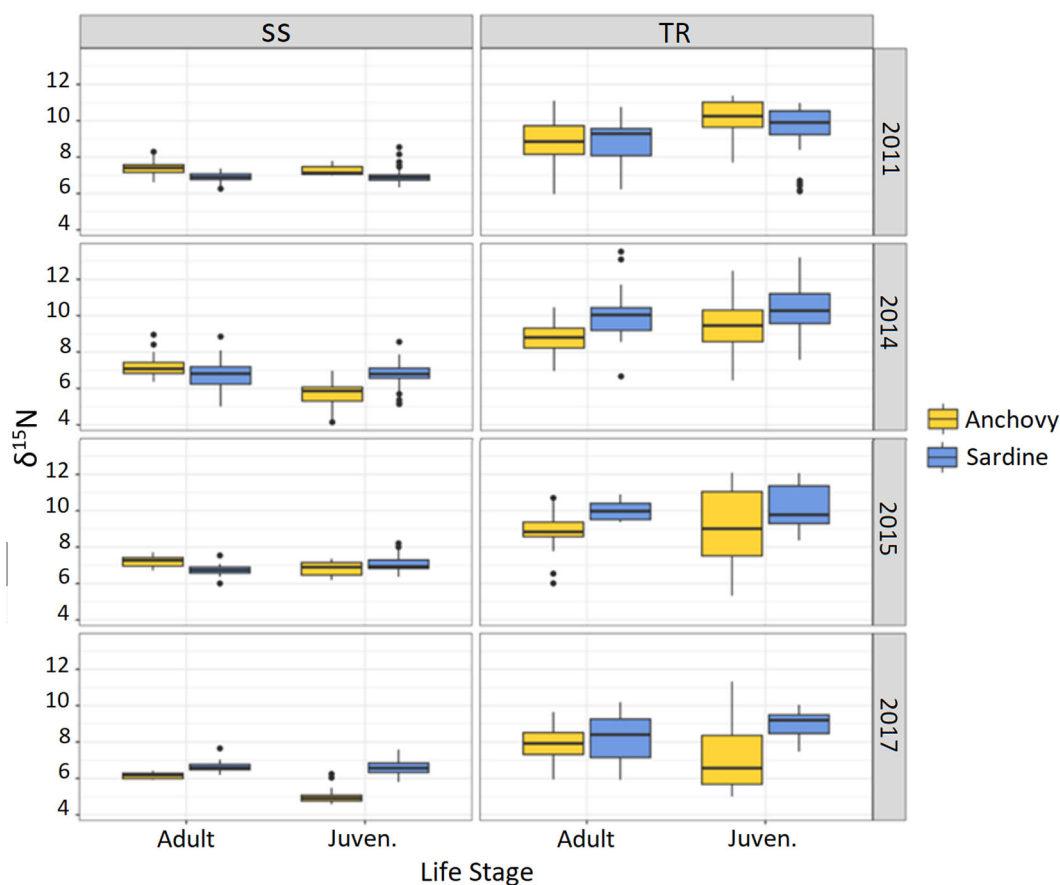


FIGURE 3  
 $\delta^{15}\text{N}$  boxplot by area, year, species, and life stage.

the SS area,  $\delta^{15}\text{N}$  average values were generally comparable between adult anchovies and juvenile sardines, except in one case (2014), where a significant difference was observed. In contrast, significant differences in  $\delta^{15}\text{N}$  were found in three out of 4 years when comparing juvenile anchovies and adult sardines.

In the TR area, the comparison between adult anchovies and juvenile sardines showed significant differences in 2 out of 4 years for both isotopes. Similarly, for  $\delta^{15}\text{N}$ , significant differences were also found in 2 out of 4 years when comparing juvenile anchovies and adult sardines, whereas for  $\delta^{13}\text{C}$ , the difference was significant in only one case.

## Isotopic niche analysis

The width and overlap of isotopic niches were computed by area, year, species, and life stage (Figures 5, 6; Supplementary Table S1). The comparison of isotopic niche width between areas revealed that niche width in TR was and significantly wider than in the SS area (Supplementary Table S2). In contrast, comparison across years showed significant differences in only a few cases, suggesting a certain degree of temporal stability at the area/species/life stage level (Supplementary Table S3).

The comparison of niche width between adults and juveniles of the same species and within the same area (Supplementary Table S4) indicated no significant differences for anchovy in SS, whereas significant differences were observed for sardine in two out of four cases. In the TR area, significant differences in niche width were found for both species. In addition, isotopic niche overlap between adults and juveniles of both species was significant in all cases except one (Supplementary Table S4). On average, in the SS area, sardine showed higher overlap than anchovy (30% and 19%, respectively), while in the TR area, overlap was comparable between species (40% for anchovy and 45% for sardine). For both species, overlap was lower in SS than in TR.

When niche width was compared between adult anchovy and adult sardine, no significant differences were observed in SS, while in TR significant differences were found in three out of four cases (Supplementary Table S5). The comparison of isotopic niche overlap between adults of the two species by area and year, evidenced in the SS area significant overlap in two cases out of four, while in the TR area the overlap was found significant in all cases (Supplementary Table S5).

Finally, when comparing niche width across both life stage and species, significant differences were observed in specific cases only, with no consistent pattern (Supplementary Table S6). In terms of

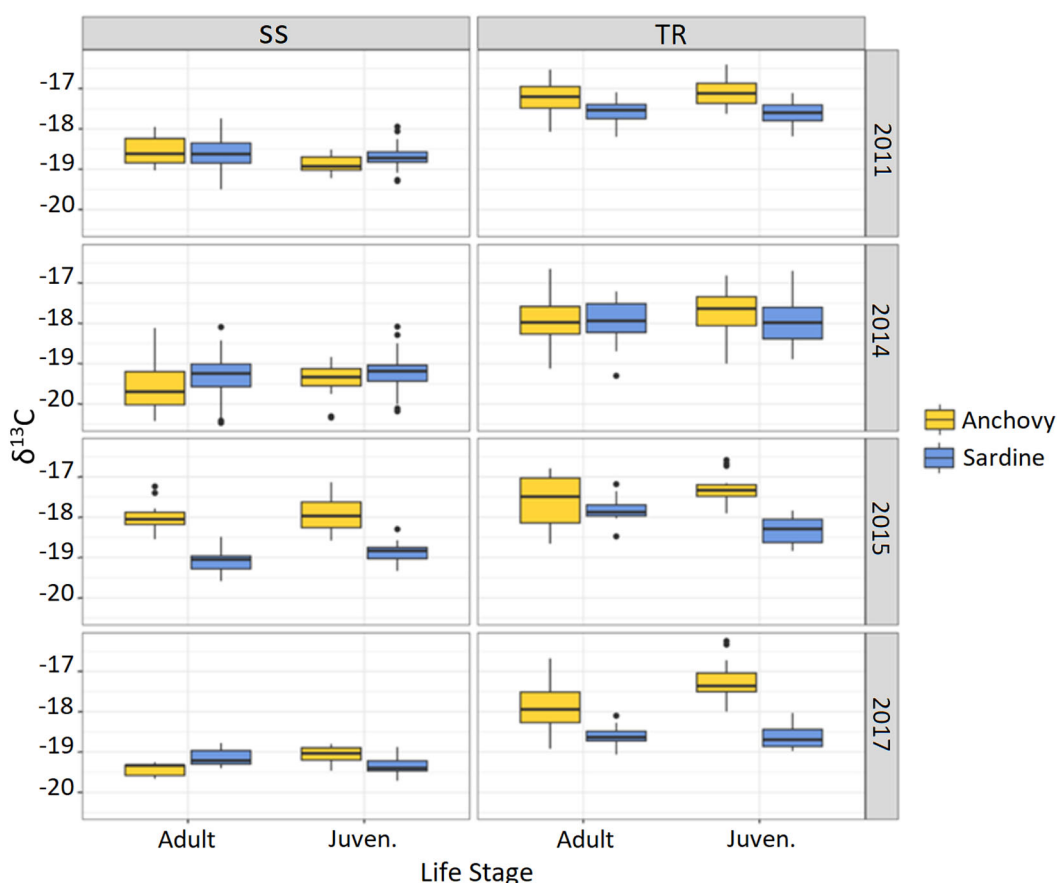


FIGURE 4  
 $\delta^{13}\text{C}$  boxplot by area, year, species, and life stage.

niche overlap, in the TR area significant overlap was found in all cases except one, whereas in the SS area overlap was significant in only half of the comparisons (Supplementary Table S6).

## Discussion

The obtained results showed that differences in isotopic signals between the two species were greater between areas than within areas across all sampled years—except for  $\delta^{13}\text{C}$  in adult anchovy in 2015 (Supplementary Table S2). Specifically, both nitrogen and carbon stable isotopes showed higher values in the Tyrrhenian area (TR) compared with the Strait of Sicily (SS) for both species (Figures 3, 4). It is known that inter-specific variations in the feeding habits of marine fishes are consistent with inter-specific differences associated to local factors that provide variations in the baseline isotopic values in food webs and affect prey presence and abundance (e.g., Costalago and Palomera, 2014; Costalago et al., 2014; Rumolo et al., 2016).

The SS area is less impacted by continental waters, with fewer major cities, effluents, and coastal industries compared to the TR area. Coastal upwelling along the southern coast of Sicily and the presence of offshore banks (Piccioni et al., 1988) generate organic

matter during upwelling events, which—after remineralisation—supports primary production (Alvarez-Salgado et al., 2002; Bode et al., 2004). In sectors as the SS area, phytoplankton generally serves as the main foundation of the food web. Productivity is primarily regulated by oceanographic processes such as upwelling and seasonal changes in stratification and mixing, which fertilise the euphotic zone (Bode et al., 2006).

Although phytoplankton in upwelling regions often becomes enriched in  $^{15}\text{N}$  (Montoya et al., 1990; Goering et al., 1990; Rolff, 2000), resulting in enriched zooplankton, Rumolo et al. (2016) reported low  $\delta^{15}\text{N}$  values in particulate organic matter collected in the SS area. This may be explained by the discontinuous nature of coastal upwelling along the southern coast of Sicily (Piccioni et al., 1988; Bonanno et al., 2014), where summer phytoplankton growth likely relies on regenerated nitrogen—typically depleted in  $^{15}\text{N}$  (Montoya et al., 1990). This mechanism may account for the lower  $\delta^{15}\text{N}$  values found in both anchovy and sardine in the SS area.

In addition, the mean isotopic signals of anchovy and sardine in the SS area were lower than those reported in the literature (Table 3) for other parts of the Mediterranean Sea or similar upwelling-influenced oceanic systems (Bode et al., 2003; Sholto-Douglas et al., 1991; Costalago et al., 2012; Le Bourg et al., 2015; Bachiller et al., 2020, 2021; Lloret-Lloret et al., 2022; Fanelli et al., 2023). In this

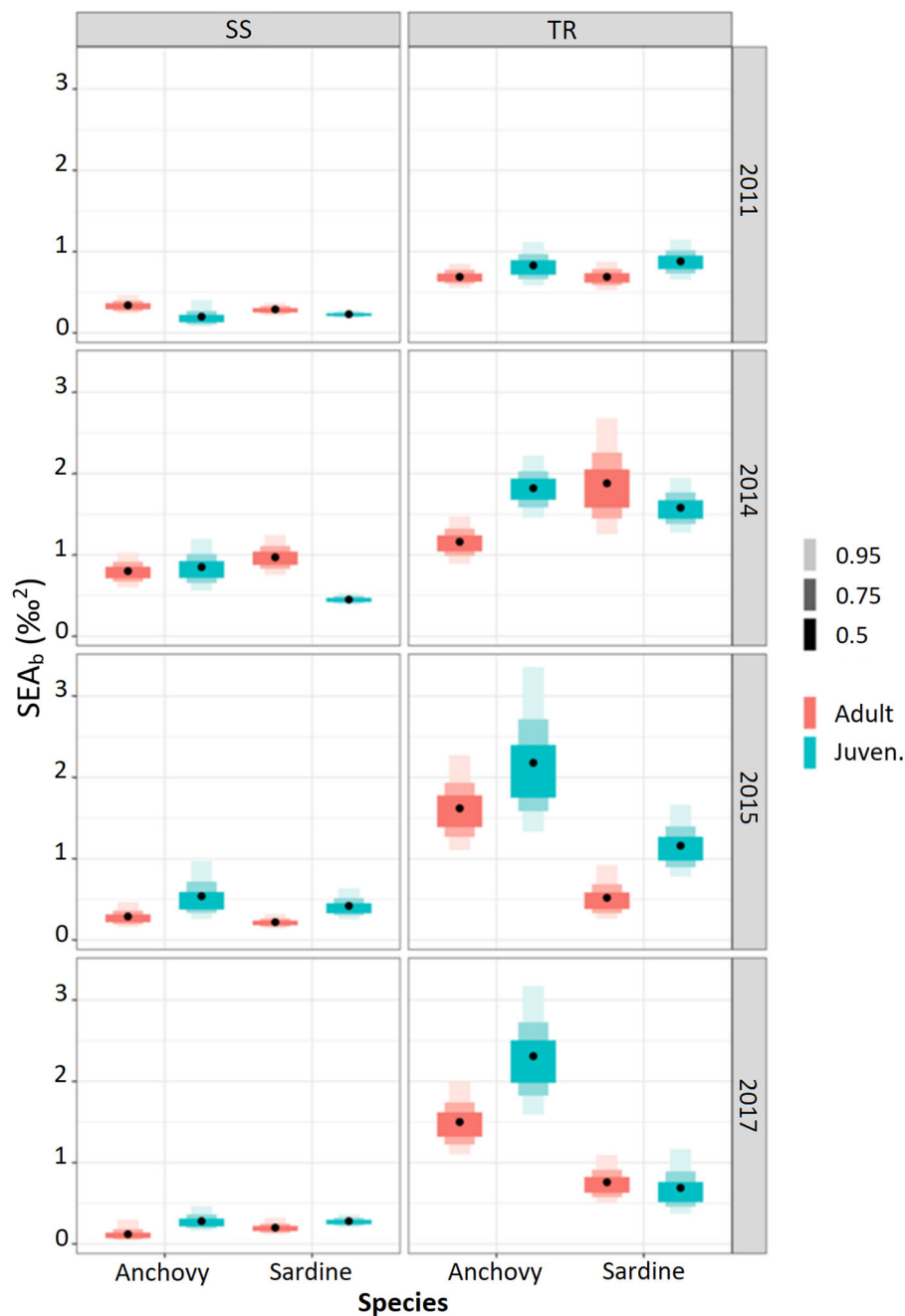


FIGURE 5  
SEA<sub>b</sub> density plot by species area and life stage.

context, the absence of a consistent pattern in the correlation (Supplementary Figures S1, S2) between the  $\delta^{15}\text{N}$  and fish total length (positive, null, or negative across years for both species; Supplementary Figures S1, S2), along with the narrow  $\delta^{15}\text{N}$  range, reinforces the hypothesis that anchovy and sardine in the SS area may exploit similar resources—possibly feeding directly on particulate organic matter with low isotopic signatures and/or on prey occupying lower trophic positions depending on resource availability.

However, while juvenile and adult sardines in the SS area exhibited similar feeding behaviour, as indicated by their isotopic niche overlap, anchovies showed greater feeding variability between life stages, with relatively weak isotopic overlap (never exceeding 30%; Supplementary Table S4). These results align with previous studies (e.g., Tudela and Palomera, 1997; Costalago et al., 2012), which describe juvenile and adult sardines as opportunistic filter-feeders with a more heterogeneous diet than anchovy. For anchovy, several authors have reported high variability in feeding between life

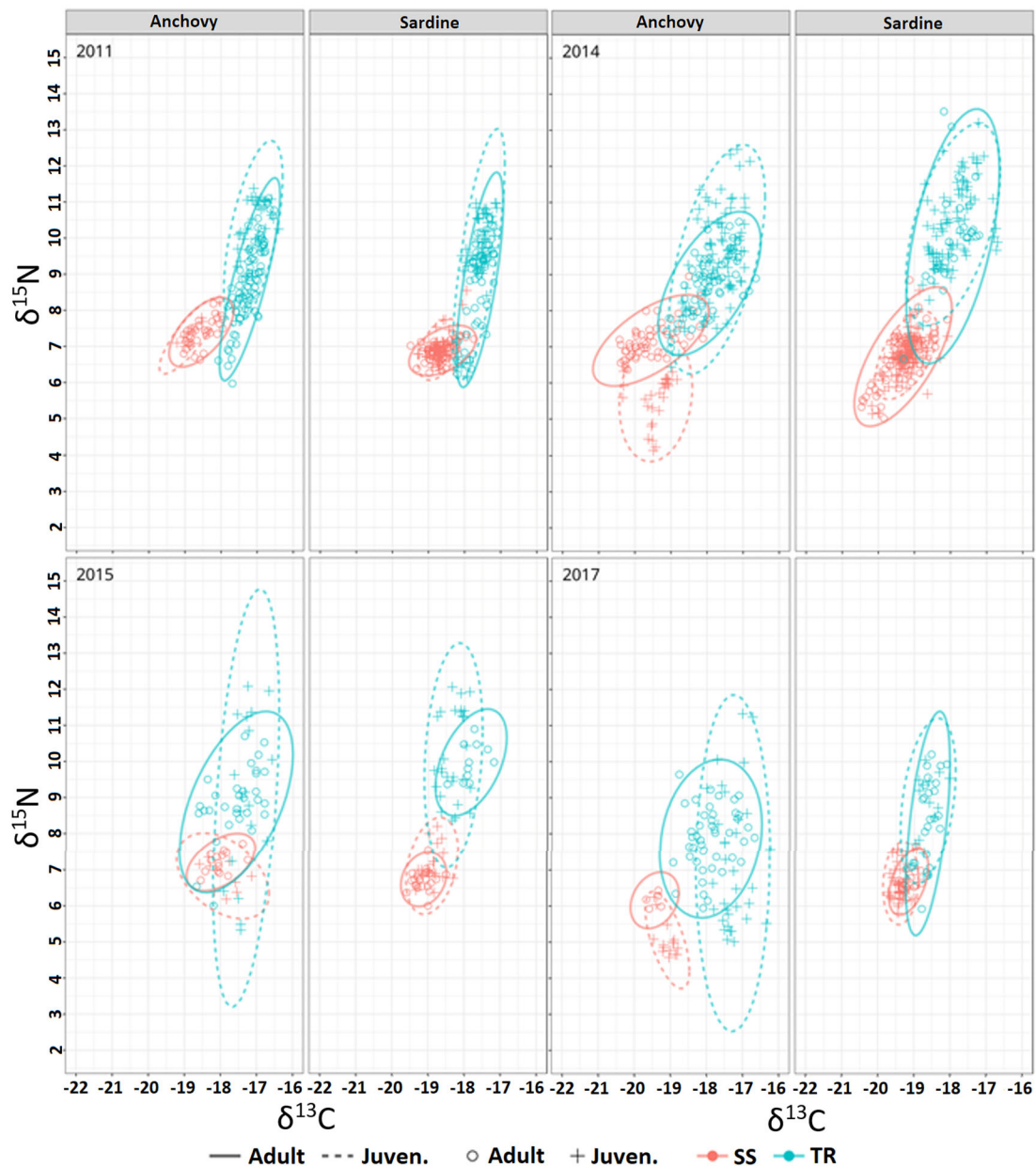


FIGURE 6

Isotopic ellipses (95%) overlap by area (SS: red lines; TR: blue lines), species, life stage (Adults: continuous lines; Juveniles: dotted lines) and year.

stages, sometimes involving ontogenetic shifts (Bacha and Amara, 2009; Pepin and Penney, 1997; Scharf et al., 2000; Bachiller and Irigoien, 2013; Palomera et al., 2007; Plounevez and Champalbert, 1999, 2000), while others reported no ontogenetic shift (Bulgakova, 1993; Tudela and Palomera, 1995, 1997; Plounevez and Champalbert, 1999, 2000; Borme et al., 2009; Van der Lingen et al., 2009; Bacha and Amara, 2009; Catalan et al., 2010).

Regarding  $\delta^{13}\text{C}$ , which is generally considered a conservative tracer of the primary producers at the base of the food web and thus a useful indicator of foraging habitat (France, 1995; Hobson, 1999), the values presented in the SS area for both species were comparable to those reported from other Mediterranean regions (see Table 3).

This suggests that anchovy and sardine in SS likely explored similar habitats and shared food sources.

In contrast to the SS area, the higher  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values observed in anchovy and sardine in the TR area may be attributed either to a strong feeding preference for larger prey items or to feeding within an environment characterised by a more isotopically enriched baseline. Although particulate organic matter (POM) and zooplankton samples were not collected during the 2014, 2015, and 2017 surveys, this study focused on isotopic niche width and overlap in consumers (anchovy and sardine), which revealed greater differences between areas than among years. These area-based differences were also confirmed by Rumolo et al. (2016), who,

TABLE 3  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  values reported in literature from other Mediterranean areas.

Area	Species	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ (‰)	References
Strait of Sicily (SS)	ANE	6,6 ± 0,9 (173)	-18,9 ± 0,6 (173)	This study
	PIL	6,8 ± 0,2 (452)	-19,0 ± 0,3 (452)	
Tyrrhenian Sea (TR)	ANE	8,8 ± 0,9 (406)	-17,5 ± 0,3 (406)	
	PIL	9,5 ± 0,8 (306)	-18,1 ± 0,4 (306)	
NW Mediterranean Sea (Gulf of Lion)	ANE	8,0 ± 0,3 (30)	-18,9 ± 0,9 (30)	Costalago et al., 2012
	PIL	8,2 ± 0,4 (30)	-18,4 ± 1,3 (30)	
Western Mediterranean Sea	ANE	8,1 ± 0,2 (16)	-18,9 ± 0,3 (16)	Bachiller et al., 2021
	PIL	8,5 ± 0,2 (15)	-19,0 ± 0,6 (15)	
Western Mediterranean Sea (Gulf of Lion)	ANE	7,1 ± 0,4 (39)	-19,7 ± 0,4 (39)	Bachiller et al., 2020
	PIL	7,7 ± 0,3 (38)	-19,3 ± 0,7 (38)	
Western Mediterranean Sea (Catalan Sea & Gulf of Valencia)	ANE	8,2 ± 0,5 (24)	-19,3 ± 0,4 (24)	
	PIL	8,8 ± 0,2 (24)	-19,6 ± 0,8 (24)	
Western Mediterranean Sea (Gulf of Alicante)	ANE	8,2 ± 0,3 (22)	-18,9 ± 0,4 (22)	
	PIL	8,2 ± 0,4 (25)	-19,1 ± 0,5 (25)	
Adriatic Sea (North)	ANE	9,8 ± 1,2	-19,1 ± 0,7	Fanelli et al., 2023
	PIL	9,1 ± 0,9	-20,0 ± 0,8	
Adriatic Sea (Central)	ANE	9,0 ± 1,3	-19,0 ± 0,4	
	PIL	8,8 ± 1,0	-19,7 ± 0,7	
Adriatic Sea (South)	ANE	8,2 ± 0,9	-18,9 ± 0,4	
	PIL	8,4 ± 0,8	-19,5 ± 0,8	
Western Mediterranean Sea (Gulf of Lion)	ANE	7,5 ± 0,5	-19,4 ± 0,3	Le Bourg et al., 2015
	PIL	8,1 ± 0,5	-19,8 ± 0,6	
NW Mediterranean Sea (Escala-Catalan Sea)	ANE	7,6 ± 0,4 (10)	-19,3 ± 0,2 (10)	Lloret-Lloret et al., 2022
	PIL	7,9 ± 0,2 (10)	-19,9 ± 0,3 (10)	
NW Mediterranean Sea (Barcelona-Catalan Sea)	ANE	8,0 ± 0,5 (10)	-18,9 ± 0,2 (10)	
	PIL	8,3 ± 0,5 (10)	-19,6 ± 0,6 (10)	
NW Mediterranean Sea (Tarragona-Catalan)	ANE	8,3 ± 0,6 (10)	-19,0 ± 0,2 (10)	
	PIL	8,8 ± 0,3 (10)	-19,6 ± 0,2 (10)	
Eastern Adriatic Sea (Northern area)	ANE	8,1 ± 0,4 (10)	-19,3 ± 0,2 (10)	Zorica et al., 2021
	PIL	8,6 ± 1,0 (8)	-20,1 ± 0,3 (8)	
Eastern Adriatic Sea (Middle area)	ANE	7,8 ± 0,3 (10)	-18,9 ± 0,1 (10)	
	PIL	8,1 ± 0,5 (9)	-20,2 ± 0,5 (9)	
Eastern Adriatic Sea (Southern area)	ANE	7,5 ± 0,6 (10)	-18,9 ± 0,1 (10)	
	PIL	8,2 ± 0,8 (10)	-19,8 ± 0,3 (10)	
West and south coasts of South Africa (upwelling)	ANC	12,9 ± 0,4 (14)	-15,1 ± 0,6 (14)	Sholto-Douglas et al., 1991
Galicia (NW Spain) (upwelling)	PIL	11,3	-	Bode et al., 2003

analysing isotopic data from a single year in the Strait of Sicily and the Tyrrhenian Sea, found higher  $\delta^{15}\text{N}$  values of POM in the Tyrrhenian Sea. This was attributed to riverine input supplying high levels of inorganic nutrients, which can lead to  $^{15}\text{N}$  enrichment in POM (e.g., McClelland et al., 1997), and in turn to enriched  $\delta^{15}\text{N}$  in zooplankton and fish.

Moreover, Rumolo et al. (2016) reported higher isotopic values in adult anchovies and sardines from the Tyrrhenian Sea compared to other Mediterranean regions, linking these values to a higher dietary contribution of mesozooplankton species, particularly chaetognaths and euphausiids. Although the presence of chaetognaths and euphausiids such as *Meganyctiphanes norvegica* in the TR area has not been extensively studied, Wiebe and D'Abramo (1972) found *Euphausia krockhii*, *Nematoscelis megalops*, *Meganyctiphanes norvegica*, and *Stylocheiron abbreviatum* to be abundant in the western Tyrrhenian basin, especially in May and June. Moreover, Mussi et al. (2004) reported the presence of crustacean exoskeletons—belonging to *Meganyctiphanes norvegica*—in fin whale faecal material collected near Ischia Island (Figure 1), close to the Cuma submarine canyon, where marine mammals have been repeatedly observed (Mussi et al., 1999; 2014).

The co-occurrence of large predators and small pelagic fish in the TR area (Leonori et al., 2021) is likely linked to the abundance of large zooplankton species, potentially triggered by the high load of nutrients provided by different mechanisms such as submarine canyon advection and river discharge. Isotopic values of anchovy and sardine in the TR area—particularly  $\delta^{15}\text{N}$ —were consistent with those reported in the northern Adriatic Sea (Table 3), a region with comparable environmental characteristics, including the presence of large rivers and densely populated coastlines (Fanelli et al., 2023; Micheli et al., 2013). In the TR area, anchovy showed no consistent correlation between  $\delta^{15}\text{N}$  and total length (TL); in some cases, higher  $\delta^{15}\text{N}$  values were found in juveniles than in adults (Supplementary Table S4). For sardine, results indicated a negative correlation between  $\delta^{15}\text{N}$  and TL, though not always statistically significant. This trend is difficult to interpret due to the limited availability of isotopic and stomach content data for juvenile small pelagic fish in the Mediterranean (Bachiller et al., 2020). However, some authors (Fanelli et al., 2023; Bode et al., 2003 and references therein) found this negative trend in small pelagic fish interpreting such relationship as the consequence of the increasing consumption of phytoplankton by adults, as most clupeids are known to employ both particle-feeding and filter-feeding (James, 1988).

In the TR area,  $\delta^{13}\text{C}$  values were, on average, more enriched than in other areas of the Mediterranean Sea, suggesting that both species may explore more coastal areas and carbon sources (Table 3). However, our results, which examined dietary variations based on assimilated food (in about one month), did not allow us to estimate individual specialisation linked to habitat use. Such an assessment would require considering the temporal and spatial variability in the  $\delta^{13}\text{C}$  of both prey and consumers.

Taking into account the investigated inter- and intraspecific differences in isotopic composition—by comparing area, life

stage, and year—the patterns of isotopic niche overlap and width for the two species in each area and between areas (Supplementary Tables S2–S6) showed the presence of different feeding systems explored by anchovy and sardine. Although the greater niche overlap observed in TR compared to SS may indicate high interspecific competition, the broader isotopic niche widths indicate dietary plasticity. This plasticity may enable the development of alternative feeding strategies (e.g. division of the niche between juveniles and adults) in response to competition (Andrades et al., 2019; Cathcart et al., 2019).

Moreover, the higher isotopic values and trophic overlap observed in sardine and anchovy in the TR area could also be related to increased consumption of larger prey (e.g., decapods and euphausiids), as previously reported by Rumolo et al. (2016), and/or driven by the presence of other high-trophic-level prey such as siphonophores and jellyfish, as noted by Bachiller et al. (2020) in the western Mediterranean Sea. In contrast, in the SS area, the low isotopic values together with smaller isotopic niche width, suggested the presence of lower trophic levels organisms and less food resources explored by the fish species. Furthermore, the variability observed in isotopic niche overlap may reflect differences in the spatial distribution of the two fish species (Barra et al., 2015).

In addition to the clear difference evidenced between the SS and TR areas, it is important to highlight that observed differences are temporally stable, indicating a certain degree of stability in feeding behaviour. This stability likely reflects underlying ecosystem characteristics rather than interannual variability in environmental conditions. Nonetheless, the high variability observed in the SS area in terms of niche overlap, along with the lower variability in isotopic values compared to TR—suggests that the SS area may be a more sensitive ecosystem, more vulnerable to environmental disturbances, including those induced by climate change.

Given the key role of small pelagic fish in energy transfer along the marine food web, careful management of these resources is should be carefully considered. On the contrary, the TR area could appear to be a more robust ecosystem, capable of handling natural or anthropogenic disturbances. To support this hypothesis, future studies should include isotopic analyses of POM and zooplankton assemblages, using a more targeted sampling design spanning multiple years.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

## Ethics statement

The manuscript presents research on animals that do not require ethical approval for their study.

## Author contributions

PR: Resources, Data curation, Writing – original draft, Visualization, Conceptualization, Writing – review & editing, Investigation, Validation, Methodology, Supervision, Formal analysis. MB: Software, Formal analysis, Writing – review & editing, Conceptualization, Data curation, Writing – original draft, Methodology, Resources, Visualization, Investigation, Validation. AB: Visualization, Data curation, Resources, Writing – original draft, Conceptualization, Investigation, Validation, Writing – review & editing, Methodology, Supervision. SA: Visualization, Data curation, Formal analysis, Methodology, Conceptualization, Writing – review & editing, Investigation, Validation, Supervision. RF: Writing – review & editing, Visualization, Formal analysis, Writing – original draft, Methodology, Supervision, Validation, Data curation, Investigation. AG: Methodology, Data curation, Investigation, Writing – original draft, Formal analysis, Visualization. GB: Writing – original draft, Methodology, Visualization, Data curation, Validation, Investigation, Conceptualization, Writing – review & editing. SGh: Formal analysis, Data curation, Methodology, Writing – original draft, Visualization, Investigation, Supervision. SGe: Formal analysis, Writing – original draft, Methodology, Data curation, Investigation, Supervision. MD: Software, Writing – original draft, Supervision, Writing – review & editing, Investigation, Formal analysis, Conceptualization, Methodology, Validation, Data curation. CL: Writing – original draft, Investigation, Visualization, Formal analysis, Software, Validation, Data curation, Conceptualization, Supervision, Writing – review & editing, Methodology.

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## Supplementary material

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