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Casting light on the European anchovy: from biology to conservation and industry

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This manuscript explores the role of European anchovies (*Engraulis encrasicolus*) in the central Mediterranean Region, shedding light on their ecological significance, conservation challenges, and sustainable utilization. The European anchovy is one of Europe's most important fish resources in the Mediterranean basin, and it is considered a keystone species, playing a pivotal role in both ecological and socio-economic dimensions. However, in recent decades, European anchovy, together with *Sardina pilchardus* (commonly known as European sardine), has suffered a population decline for several reasons. Consequently, it is necessary to improve the management of anchovy fisheries by understanding the reproductive modes and characteristics, the influence of currents on the passive transport of eggs and larvae, the feeding habits, the environmental adaptability (*e.g.*, salinity), and the distribution of ecotypes along the Italian coasts. Such information is fundamental for the management of fisheries, especially artisanal ones, and to control frauds, especially in protected, geographically referred, and traditional high-quality commercial products. Various aspects, ranging from their population dynamics to their industrial processing and the ecological implications of these activities were delved, highlighting the knowledge about anchovy populations and ecotypes and its importance in maintaining ecosystem balance and sustaining human communities. The ecological interaction of anchovies within the food web, as essential data in the conservation actions and management of these resources was emphasized. In addition, the metabolic and stomach contents diversity among anchovy populations and ecotypes was discussed, enhancing our understanding of their adaptability to varying environmental conditions. The manuscript then explores the traditional and industrial processing of anchovies, encompassing aspects ranging from fishing techniques (*i.e.*, methods of capture) to their industrial significance, sustainability concerns, issues of fraud, and the establishment of geographical traceability. Finally, the opportunities for sustainable and biotechnological utilization of anchovy discards were also further explored, demonstrating the potential for waste reduction and resource optimization.

KEYWORDS

Engraulis encrasicolus, ecotypes, Mediterranean, *menaica*, discards, high-value compounds, traceability, trophic ecology

1 Anchovies: ecological significance and challenges in marine ecosystems

Anchovy species are abundant in most of the world's marine ecosystems and are an important food source for other marine organisms (Tudela and Palomera, 1997; Gibson and Atkinson, 2016). Most species are marine, although many tolerate low salinity during one or more stages of their life cycle (Castillo et al., 2019; Liu et al., 2023). In addition, some species are adapted to freshwater environments, as in the case of several American and Asian species (Bloom and Lovejoy, 2017; Cheng et al., 2019). Marine species usually inhabit the continental shelf and adjacent deep-water areas and several of them show a seasonal vertical migration (Giannoulaki et al., 2013). Anchovies have both top-down and bottom-up effects on the ecosystem (Saraux et al., 2019), and mainly feed on zooplankton and, partially, on phytoplankton (Costalago and Palomera, 2014; Awad et al., 2022) although are considered indiscriminate feeders (Koslow, 1981; James, 1987; Borme et al., 2009). Stomach samples from adults show zooplankton, eggs, and small fish as primary prey items, and even some cannibalism activity, whereas larvae primarily consume copepods (James, 1987; Borme et al., 2009; Awad et al., 2022). They contribute to regulate plankton populations, thus influencing the entire trophic pyramid. A clear relationship has been demonstrated among anchovy populations, zooplankton, phytoplankton, and remineralization in the water column (James et al., 1989; Attayde and Hansson, 2001; Oguz et al., 2008; Politikos et al., 2015). Anchovy predation pressure on zooplankton populations helps control their numbers, preventing overgrazing on phytoplankton (Wollrab et al., 2012). Additionally, their role as prey for higher trophic levels, such as seabirds (Velarde et al., 2015), marine mammals (Ouled-Cheikh et al., 2022), and larger fish species (Glaser, 2011; Cardona et al., 2015) contributes to the overall biodiversity and stability of the ecosystem (Lavoué et al., 2022). Anchovies belong to the family of Engraulidae, in the order of Clupeiformes, and are divided into two subfamilies: Coilinae and Engraulinae (Lavoué et al., 2013). The subfamily Coilinae inhabits the Indo-Pacific Ocean, while the family Engraulinae is found in both the Indo-Pacific and Atlantic Oceans (Lavoué et al., 2013).

Into the family Engraulidae, which consists of about 17 genera and 141 species, genus *Engraulis* includes the European anchovy *Engraulis encrasicolus* (Bloom and Lovejoy, 2012). European anchovy is a small pelagic fish that inhabits the Mediterranean and the Black Seas, as well as several African areas (alongside the Moroccan coasts) and the Northeast Atlantic (FAO, 2020). In the Mediterranean Sea, changes in European anchovy' population structure have been registered (Saraux et al., 2019; Fernández-Corredor et al., 2021) coupled with a gradual decline in their populations (Van Beveren et al., 2014). Several hypotheses explaining population decline have been formulated, taking into consideration one or more stressors such as overfishing (Klanjšček and Legović, 2007), habitat degradation (Fujita et al., 2021), food availability (Thoral et al., 2021), alteration in plankton community (Bat et al., 2007), pollution (Savoca et al., 2017; Basilone et al., 2018), microplastics (Collard et al., 2017), and climate-change (Checkley et al., 2017), with consequences on anchovy's abundance and distribution as well as on their behavior, biochemistry, and physiology. Changes in the plankton community affect the diet of this species with consequences on the size of zooplankton species predated (Van Beveren et al., 2014; Queirós et al., 2019; Thoral et al., 2021).

As a case of study, the Black Sea has undergone significant transformations in recent years, leading to notable alterations in both the qualitative and quantitative composition of phytoplankton and zooplankton. These changes have been primarily driven by eutrophication, resulting from an increased influx of nutrients through major rivers over the past few decades (Oguz et al., 2008; Gücü et al., 2017). These changes in the plankton composition are related to interspecific dynamics among pelagic fishes, non-gelatinous and gelatinous plankton (Deibel and Lowen, 2011; Lucas and Dawson, 2013). In fact, in the Black Sea, the presence of non-native species (*e.g.*, the ctenophore *Mnemiopsis leidyi*) has contributed to the decline of anchovy and other pelagic fish populations in the region (Kideys, 1994). The situation has become more intricate with the introduction of other alien species, such as the ctenophore *Beroe ovata* able to feed on *M. leidyi*, creating an ecological feedback system that also impacts other components of the planktonic community (Gücü et al., 2017). In the framework of fisheries management, a multidisciplinary approach is needed for the identification of fish stock units, the presence of subpopulations or sibling species, and the prediction of potential threats (Jemaa et al., 2015; Pita et al., 2016). Such considerations should be integrated from the social and economic point of view, due to the importance of anchovies for regional pelagic fisheries (Ruiz et al., 2017; Falautano et al., 2018; Sartor et al., 2019). In fact, anchovy fishing represents a fundamental resource for many human communities living in coastal areas with economical consequences on industrial and local fisheries in national and international markets. Its nutrient value, and the status of several semi-industrial production as a "protected-food" with characteristics of unicity (FAO, 2018; European Union, 2020) makes its management extremely important in the Mediterranean Basin (Consonni and Cagliani, 2022). This is particularly relevant considering "The Global Deal for Nature" proposal (Dinerstein et al., 2019) that led to the European Union long-term plan (EU's biodiversity strategy for 2030) called "30x30 action", with the aim to protect nature, reverse the degradation of ecosystems, address biodiversity loss and promote sustainable development (Baldock and Charveriat, 2018; Hermoso et al., 2022).

In this review, we focused our attention on European anchovies inhabiting the Mediterranean Sea, highlighting the essential role of anchovies in both ecological and human contexts (Figure 1). This manuscript covers a wide range of topics related to European anchovy including its population dynamics, ecological implications, adaptability to varying environmental conditions, metabolic and trophic diversity. The information presented here are fundamental in the framework of anchovy fishery management, taking into consideration stocks and ecotypes, sustainable and responsible fishing practices, artisanal fisheries, fraud issues, and traditional high-quality commercial productions. Regarding such high-quality productions, this manuscript explores the traditional and industrial processing of anchovies, encompassing aspects such as fishing techniques and their industrial significance. This study also explores the potential of anchovy discards for sustainable and biotechnological utilization, which aligns with the principles of sustainability for green and blue economy, by aiming to reduce waste and optimize the use of resources.

2 Anchovy populations and ecotypes: ecology and research approaches

2.1 The importance of ecotypic diversity in fishery and conservation science

Fishing and connectivity patterns, as well as morphological, behavioral, trophic, and demographic traits of marine species, are commonly used to designate fish stocks (Cadrin, 2020; Huret et al., 2020). The use of population genetic markers is fundamental to improve our understanding of connectivity patterns among marine populations. It could also help to define populations' dynamics across spatial and temporal scales, possibly leading to the identification of ecotypes inside species (Casey et al., 2016; Nordahl et al., 2019).

Although there is widespread acknowledgment about the potential populations' complexity of several marine species, fisheries are frequently managed considering subpopulations into singular management units. The discrepancy between species ecology/genetics and fishing management could result in diminished biodiversity (Benson et al., 2015). When fisheries management fails to account for genetic diversity in natural populations and instead treats them as a single homogeneous unit, it can lead to issues such as overfishing of loss of fixed rare alleles (McKinney et al., 2017), leading to the loss of these unique genetic traits from the overall gene pool (Svedäng et al., 2010). Rare alleles are genetic variants that occur at low frequencies within a population. These alleles may confer specific advantages or adaptations to environmental conditions (Bernatchez, 2016). However, if a

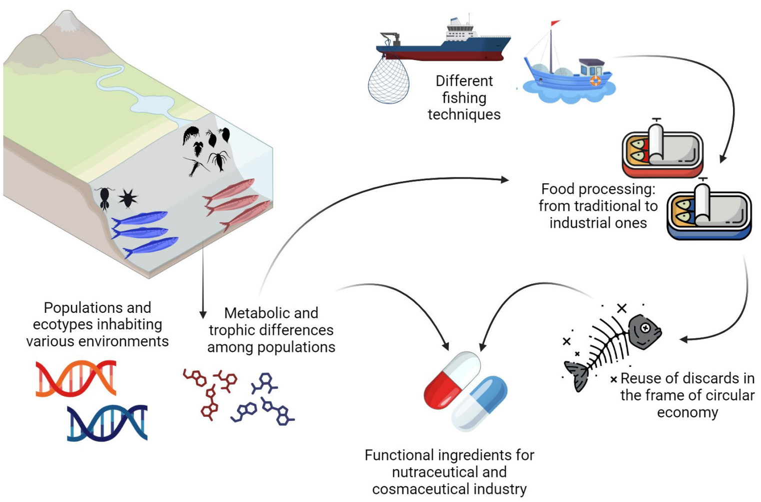

FIGURE 1
The Mediterranean Sea is characterized by different populations of anchovies inhabiting different environments. Through genetic and metabolomic approaches it is possible to identify such different classes of individuals inside the species. At the same time, anchovies are fished using different techniques and, in addition, are processed using industrial and traditional methods. In this review, we propose the reuse of anchovy discards for both nutraceutical and cosmeceutical purposes.

subpopulation with such rare alleles is overfished, it can lead to the loss of these unique genetic traits from the overall gene pool (Svedäng et al., 2010). Indeed, safeguarding genetic resources stands as a pivotal component within conservation endeavors, and neglecting spatial dynamics in fish management could result in unforeseen hazards of overexploitation (Ying et al., 2011). The possibility to consider sub-species level taxonomic units (*e.g.*, ecotypes) for conservation efforts has long been under discussion (Phillimore and Owens, 2006; Burbrink et al., 2022). Ecotypes are defined as populations of the same species that have inherited different traits that are closely associated with environmental parameters, integrating ecological inference with genetic variation (Stronen et al., 2022). Ecotypes correct or refine the delineation of management units and its application to fishery and conservation science, linking together the genetic structure of the population, the trophic preferences, and the behavior, to the exploitation of the fish resource (Stronen et al., 2022). This implies to disentangle predictions on the fate of single populations from that one referred to the species *in toto*, possibly allocating resources to more targeted restoration efforts (Engelhard et al., 2010). Overfishing and habitat degradation can disproportionately affect specific ecotypes, leading to imbalances in the ecosystem (Şahin et al., 2008; Engelhard et al., 2010; Chung et al., 2015).

In the European Union, the exploitation of fish stocks is managed under the Common Fisheries Policy, which ensures that fishing activities are environmentally, economically, and socially sustainable (Casey et al., 2016). European anchovies (*Engraulis encrasicolus*) stand out as an example of a species displaying remarkable ecotypic diversity (Silva et al., 2014; Rumolo et al., 2016; Catanese et al., 2017). Genetic studies of anchovies in the Mediterranean Sea have revealed distinct populations, suggesting limited gene flow between different regions (Magoulas et al., 2006; Huret et al., 2020). This genetic differentiation has led to variations in size, shape, and coloration which likely reflect physiological adaptations to specific environmental conditions, including temperature, salinity, and food availability (Gordina et al., 1997; Tudela, 1999; Turan et al., 2004) with consequences on growth rates, lifespan, and reproductive strategies (Politikos et al., 2015; Raybaud et al., 2017; Bang et al., 2022). The significance of understanding these biological variations, and eventually the existence of ecotypes, is essential for the conservation and management of these key species.

2.2 Populations and ecotypes and putative species

Phylogeographic investigations indicate that marine fish species tend to exhibit less population structuring compared to their freshwater counterparts. However, numerous marine species have revealed an intraspecific diversity among populations, as demonstrated in holothurians (*Holoturia tubulosa*) and clams (*Venus verrucosa*) (Feidantsis et al., 2022) but not in other species, such as European sardine (*Sardina pilchardus*) (Imsiridou et al., 2021) and cuttlefish (*Sepia officinalis*) (Feidantsis et al., 2022). It has been demonstrated that a clear population structuring exists in marine species with limited dispersal capabilities (Doherty et al., 1995; Baus et al., 2005; Cowen and Sponaugle, 2009; Truelove et al., 2017; Gaines and Lafferty, 2020) or living under selective conditions (Zardoya et al., 2004; Bargelloni et al., 2005; Swart et al., 2016; Cheng et al., 2018). This is not always true for species with a strong dispersal potential. The variability in allelic frequencies within natural populations over time and space can be shaped by diverse evolutionary processes, including migration, mutation, selection, and genetic drift (Foll and Gaggiotti, 2006; Jacquard, 2012). Ecological conditions lead to regional scales of local adaptation (Gkafas et al., 2019), giving rise to phylogeographic structures in marine species.

More than two decades ago, mitochondrial clade analysis unveiled a general heterogeneity among European anchovy populations (Magoulas et al., 1996, 2006). Admixture of individuals from different spawning sites (Tudela, 1999), and enhanced population genetic structure has been detected with species-specific polymorphic microsatellite loci (SSRs) (Landi et al., 2005; Zarraonaindia et al., 2009; Turan et al., 2017). Such investigations demonstrated the non-panmictic characteristics of anchovy population in bay of Biscay (Zarraonaindia et al., 2009) but not in the Adriatic sea (Turan et al., 2017), suggesting that European anchovy populations at least in some areas are genetically subdivided. An analysis of allozyme data suggested the presence of two distinct taxonomic entities: a coastal group called by Gulf of Lion' fishermen "white anchovies" and a more pelagic cohort known as "blue anchovy" (Oueslati et al., 2014). Morphological observations also hinted at the existence of a distinct species, identified as *Engraulis rissoi*, inhabiting several lagoons in Sicily Island (Dulzetto, 1947), and Tunisian areas (Quignard et al., 1973; Messaoud et al., 2011). In the Black Sea, researchers identified two distinct geographical "populations" of anchovy (called *Engraulis encrasicolus ponticus* and *Engraulis encrasicolus meaticus*) that have adapted to reproducing in waters with different salinity (Chashchin et al., 2015; Chesalin and Nikolsky, 2023). However, the taxonomic categorization of anchovies living in the Black Sea has been a topic of extended discussion, and the debate continues regarding whether they represent two distinct subspecies, constituting separate stocks, or if they are populations of the same species (Ivanova et al., 2013; Chashchin et al., 2015; Gücü et al., 2017). In the Gulf of Lion, observations raised the potential presence of another species, *Engraulis albidus*, thriving in coastal lagoons (Borsa et al., 2004). In Moroccan coastal sites, researchers described a clear set of morphological and biological traits distinct from the ones of the European anchovy (Kada et al., 2009).

Beyond the potential identification of new anchovy species in the Mediterranean Sea, investigations based on electrophoretic and morphological variances (Bembo et al., 1996a; Borsa, 2002), nuclear ePIC marker CK6-2 (Borsa et al., 2004; Bouchenak-Khelladi et al., 2008) as well as mtDNA (Bembo et al., 1996b), confirmed the presence of distinct anchovy stocks. This idea was supported by other approaches, such as using nuclear and mitochondrial single nucleotide polymorphisms (SNPs), where two distinct groups were identified. The first one was associated with areas of deep-water upwelling on narrow continental shelves, and the second one with wide continental shelves (Zarraonaindia et al., 2012). SNPs markers technique have been utilized to identify population characteristics of adults, juveniles, and larvae of several species and to evaluate the population origin of several species, as in the case of Atlantic cod (*Gadus morhua*) (Jorde et al., 2018) and Atlantic bluefin tuna (*Thunnus thynnus*) (Rodríguez-Ezpeleta et al., 2019). In the frame of the Molecular Ecology Resources Primer Development Consortium, it was developed a SNPs panel composed of 47 nuclear DNA SNPs and 15 mtDNA SNPs of *E. encrasicolus* samples collected in several areas of the species range (Mediterranean, eastern Atlantic, North Sea, and English Channel, Bay of Biscay, Galicia to southern Africa). This tool allowed the researchers to identify two distinct *E. encrasicolus* groups, the first mainly present in the Bay of Biscay, the North Sea, and the English Channel, and the second one present in Mediterranean, with the exception of the Alboran Sea, and the Gulf of Cadiz (Zarraonaindia et al., 2012). Shortly afterward, Montes and colleagues identified in 2013 a much larger number of SNPs (around 19,000) by using a Next Generation Sequencing approach combining transcriptome and genome information of *E. encrasicolus* (Montes et al., 2013). These authors selected a panel of 530 SNPs, which were tested in five populations, four Atlantic and one Mediterranean, using the TaqMan OpenArray technique. This allowed the validation of around 480 markers that could be useful for understanding the genetic structure of the anchovy populations (Montes et al., 2013). Three years later, the same authors proposed the use of a panel of 482 SNPs, 481 from the Montes' previous study and one from the Molecular Ecology Resources Primer Development Consortium (Zarraonaindia et al., 2012), to study both the genetic structure and adaptation of the Bay of Biscay anchovy population (Montes et al., 2016). SNPs panel was also used in the area from the southern Bay of Biscay to the Irish and North Seas across the English Channel (Huret et al., 2020) confirming the results obtained by the previous study (Montes et al., 2016), but with more robust data as the sampling was broader in space and time. Starting from the panel of SNPs used in a previous study (Montes et al., 2013), Catanese and colleagues selected a subset of 96 highly discriminating SNPs that can be used for genetic studies of European anchovy stocks, demonstrating that the SNPs selected based on F_{st} (Bhatia et al., 2013) are efficient in capturing much of the genetic variation identified by a larger SNPs panel (Catanese et al., 2016). Through the SNPs analysis of anchovy populations from the Italian seas (Tyrrhenian, Ionian, and Adriatic Seas), two genetic/ecological ecotypes of *E. encrasicolus* have been identified, namely coastal and offshore (Catanese et al., 2017, 2020). Such ecotypes coexist in several areas occupying partially overlapping niches (Figure 2). Variations in the timing of reproduction and larval growth among distinct ecotypes are notably influenced by environmental factors such as temperature, salinity, and dissolved oxygen (Ruggeri et al., 2016). Transcriptome analysis has further elucidated the presence of adaptive evolutionary mechanisms that drive differential selection between these ecotypes, correlated with fluctuations in salinity, with the coastal ecotype abundant in presence of rivers and higher chlorophyll concentrations (Montes et al., 2016; Catanese et al., 2017). The offshore ecotype, instead, shows enhanced environmental resilience and opportunistic feeding behavior (Catanese et al., 2017). Eleven molecular markers indicated divergent selection between the two ecotypes, with most of these markers being linked to salinity adaptation. Five differently expressed genes were associated with metabolic pathways (*TIMM10*, *eif-2b*, *annexin A4*, *ADH*, and *CHAF1A*) which may be important by enhancing the efficiency of food conversion in low-saline waters (Montes et al., 2013). In addition, two differently expressed genes (*TSSK6* and *basigin*) are involved in a critical stage of fertilization process and could be associated with reproductive isolation of the two ecotypes (Montes et al., 2013).

European anchovy populations exhibit intricate dynamics of egg and larval dispersal, facilitating the transportation and mingling

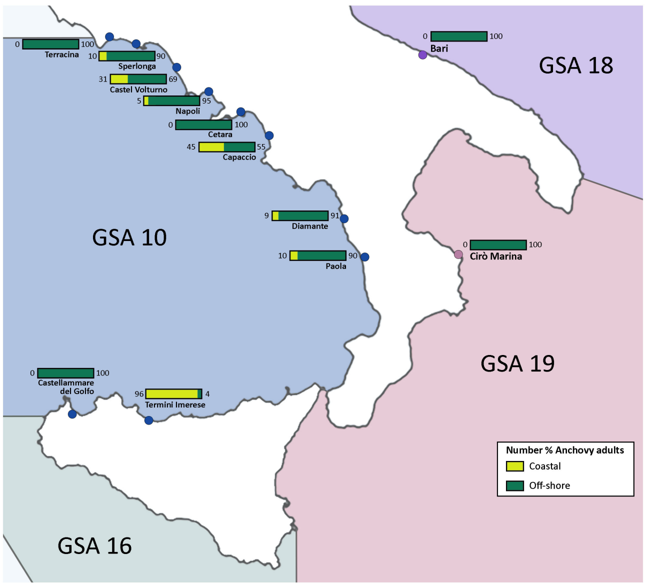

FIGURE 2
Presence in percentage of coastal (in yellow) and offshore (in green) ecotype in various sampling sites in the Central Mediterranean Area (Catanese et al., 2017).

of ecotypes over short and moderate distances (Norcross and Shaw, 1984; Catanese et al., 2020). Such passive transport has consequences on the connectivity of anchovy populations that often consist of individuals from different areas. The presence of individuals belonging to different ecotypes, and presenting distinct ecological attributes and lifestyles poses challenges for effective management actions (Erisman et al., 2017) requiring in several cases a multi-basin integrated approach (Catanese et al., 2020). The differentiated ecotypes, in fact, should be considered as separate fishery stocks, though they coexist within the same population. Phylogenetic studies have concluded that these ecotypes represent a case of partial reproductive isolation, probably due to geographical isolation, which has led to parallel genetic differentiation as effects of quaternary climatic oscillations on evolutionary diversification (Le Moan et al., 2016). Indeed, following the Messinian Salinity Crisis, which devastated the marine fauna of the Mediterranean, the basin was inundated by Atlantic water and biota during the Pliocene around 5.33 million years ago (Roveri et al., 2014; Evangelisti et al., 2017). This fauna underwent significant environmental shifts due to oceanographic and climatic changes associated with the transition from the tropical-subtropical conditions of the Pliocene to the cooler climate of the Pleistocene (Sabelli and Taviani, 2014; Agiadi et al., 2018). The Pleistocene epoch was characterized by numerous glacial-interglacial cycles, leading to substantial alterations in organism distribution (Wilson and Eigenmann Veraguth, 2010), with the Last Glacial Maximum (LGM) occurring approximately between 24 and 16.5 thousand years ago in the Mediterranean Sea (Cacho et al., 2001). The genetic footprint of postglacial recolonization has been identified in numerous marine species with an Atlantic-Mediterranean distribution, such as seabass (Tine et al., 2014) and holothurians (Gkafas et al., 2023). However, the impact of coastal glaciation is not uniform, prompting speculation that species might inherently vary in their capacity to adapt to the environmental shifts linked with glacial cycles (Wilson and Eigenmann Veraguth, 2010). During LGM glacial periods, anchovies found refuge in multiple locations in the eastern Mediterranean seas and, in the Atlantic, in the Gulf of Senegal and Guinea (Le Moan et al., 2016; Evangelisti et al., 2017). In the current interglacial period, an independent secondary contact between anchovy ecotypes in the Atlantic and Mediterranean regions or a post-contact colonization of one or both ecotypes from one region to the other has taken place (Le Moan et al., 2016).

A similar pattern of genetic divergence has been observed in a small intertidal fish, *Coryphoblennius galerita*, that is characterized by the existence of two clades: one in the Mediterranean and another in the eastern Atlantic (Domingues et al., 2007a). Such differences can be explained by the existence of an effective barrier during LGM in Gibraltar Strait or/and the 'Almerian-Oran jet' that prevents gene flow between Mediterranean and Atlantic populations (Duran et al., 2004; Bargelloni et al., 2005; Lemaire et al., 2005). The degree of isolation observed in European anchovy and other marine species cannot be found in other small pelagic fish like European sardine (Imsiridou et al., 2021) and in sparidae such as white seabream (*Diplodus sargus*) (Domingues et al., 2007b). In fact, research has shown that Greek populations of European sardines share haplotypes with those found worldwide, suggesting a single evolutionary unit for this species and no sign of phylogenetic Atlantic-Mediterranean division (Imsiridou et al., 2021). The same situation has been found in white seabream, with Atlantic and Mediterranean populations showing no signs of genetic differentiation (Domingues et al., 2007b).

2.3 Reproduction and passive transport dynamics

Engraulis encrasicolus experiences demographic fluctuations throughout the year (Ma et al., 2019). Interannual variability of the stock biomass in several small pelagic fish species has been related to environmental forcing drivers (Cingolani et al., 1996; Leitão et al., 2014). Such variability is a characteristic of several R-strategist fish species with short life spans, early age at first reproduction, high number of offspring, and low offspring survival rates, which in turn can heavily affect recruitment success and stock biomass levels (Saraux et al., 2019; Patti et al., 2020). These natural fluctuations are of considerable ecological importance, as these fishes make up a significant proportion of the available biomass in the Mediterranean, supporting both fishing activities and the wider ecosystem (Patti et al., 2020). Preserving the reproductive cycle of anchovies and effectively managing it, while addressing potential disturbances, takes on paramount importance to ensure the viability of productive fishing zones. It is the responsibility of governments to manage these disturbances to ensure the survival of these vital species (Ramírez-Valiente et al., 2021). Anchovies are oviparous species with external fertilization and iteroparous strategy, capable of spawning several times within a reproductive season (Regner, 1996). The spawning season for anchovy populations living in the central Mediterranean Sea covers a period from April to October, with spawning peaks during the warmer months (Basilone et al., 2006). The processes of migration from the coast towards deeper waters and the beginning of the reproductive season are temperature-dependent mechanisms (Alheit et al., 2012). During the fertile period, the anchovies expel ellipsoidal-shaped eggs which float between 30 and 100 meters in depth and hatch within 24-36 hours at a temperature of 21°C (Palomera et al., 1988; Dulčić, 1997). Anchovies show a prolonged breeding season that is considered a key adaptation that contributes to its reproductive success. Anchovies necessitate specific spawning habitats characterized by factors called "fundamental triad" such as nutrient enrichment, concentration of larval food distributions, and local retention of eggs and larvae (Bakun, 1997). Consequently, a nexus between environmental conditions and the reproductive process is imperative (Lasker and Zweifel, 1978). In many cases, spawning areas correspond to coastal zones characterized by coastal upwelling events, which are able to enrich the oligotrophic waters (Patti et al., 2010; Torri et al., 2018). A study conducted in the Strait of Sicily, a study examined a 12-year time series spanning from 2005 to 2016, aiming to investigate the relationships between European anchovy density, growth, reproduction, and habitat dynamics within an upwelling system (Basilone et al., 2020). The mechanisms governing anchovy dispersal, encompassing both passive drifting and active swimming, wield substantial influence over their life history, growth, and survival dynamics (Cuttitta et al., 2016).

Evidence suggests a direct correlation between physical phenomena and the abundance of larval populations (Cuttitta et al., 2015). This implies that conducive conditions for the survival of anchovy larvae exist, with implications for adult stocks (Lafuente et al., 2002, 2005; Cuttitta et al., 2015). It can be expected that the early dispersal of the two European anchovy ecotypes is linked to both their physical characteristics and dietary preferences, which play a crucial role in their survival. On one hand, passive dispersal from various spawning grounds and a certain level of active movement capacity influences the spatial distribution of each ecotype. Additionally, their preference for specific prey items, which are influenced by environmental factors, could further influence survival and consequently population structure. Such additional evolutionary force can advantage genetic variants with greater fitness in specific environment maintaining also in early life stages a certain balance among alleles, increasing the level of genetic differentiation between populations (Malavolti, 2017). Nonetheless, fisheries studies focused on analyzing environmentally induced stock fluctuations rely on variables that are comparatively easier to analyze than the other aforementioned driving forces affecting the species' habitat and recruitment variability, which are more challenging to monitor (Lafuente et al., 2002, 2005).

Passive dispersal is a prominent feature of anchovy early life stages. Anchovy eggs and larvae are subject to ocean currents, which can carry them over considerable distances, transporting them from spawning grounds to various nursery areas (Ospina-Alvarez et al., 2012). This passive dispersal can occur on varying spatial scales, depending on the strength and persistence of marine currents, within an estimated distance covered of about regional scales. In any case, these observations underscore the importance of understanding oceanographic processes in predicting anchovy distribution and the central role of ocean circulation in driving recruitment strength and, definitely, resource abundance (Ospina-Álvarez et al., 2013; Ospina-Alvarez et al., 2015). The high rate of egg dispersion caused by marine currents and the different degrees of local retention could explain the genetic heterogeneity observed in the adult populations along the Mediterranean Sea, with different sites harboring coastal ecotype, offshore ecotype, or both of them in different percentage degrees (Catanese et al., 2020). Such clustering could be based on the diet composition of coastal and offshore ecotypes but the presence of different prey in different coastal areas depends on their geomorphology and hydrodynamics, *e.g.*, the presence of rivers (Catanese et al., 2017). The analysis of SNP markers in European anchovy egg samples helped to identify anchovy population parental origins on a small spatial scale (200 km) through the assignment of genotypes to adult anchovy stocks (Catanese et al., 2020). Results underscored the significance of habitat type (offshore versus coastal/estuarine) as a crucial factor in the genetic differentiation among anchovy populations. In the central Tyrrhenian Sea, only two specific locations, called "Capaccio" and "Cetara" by Catanese and colleagues (Figure 2), served as the donor populations for all the sampled adult populations belonging to the offshore ecotype (Catanese et al., 2020). While some degree of mixing among the sampled egg hauls may exist, the assignment of egg groups to adult populations allowed for the differentiation of contributions from distinct ecotypes to new wild generations. The study also described how the high rate of egg dispersion, driven by marine currents, and the varying degrees of local retention could account for the genetic heterogeneity observed within the adult populations, where eggs from neighboring spawning sites tended to intermingle.

As anchovies metamorphose from the larval to juvenile stages, they become more capable of horizontal and vertical active dispersal (Smith et al., 2001) often occurring within specific habitats (Parada et al., 2008). It has been hypothesized that diel vertical migration of both anchovy larvae/juveniles and their prey (copepods) plays an important role in their spatial distribution (Baldó et al., 2006; Ospina-Alvarez et al., 2012; Casaucao et al., 2021). The use of 3D advanced models, that consider vertical daily migrations, biological behavior, egg-buoyancy, and growth, provides a more precise insight into the degree of connectivity between spawning and nursery areas, as well as a better understanding of the species/ecotypes recruitment and management (Ospina-Alvarez et al., 2012; Casaucao et al., 2021). It has been demonstrated that such simulations taking into account juveniles behaviors better describe the formation of schools in anchovy larvae and juveniles, evidencing a transport associated with filaments and meanders depending on the mesoscale oceanographic structures (Ospina-Alvarez et al., 2012). This idea is in agreement with previous researches, who proposed that temperate fish larvae and juveniles, such as anchovies, can detect preferable nursery areas and swim toward them by using a set of sensory cues (infotaxis strategy) (Teodósio et al., 2016).

In the adult stage, anchovies actively move in response to changing environmental conditions, such as temperature and prey availability, influencing their distribution (Guraslan et al., 2017). For all these reasons, success in the reproductive endeavors of pelagic fish, especially those that congregate in sizable schools, hinges upon an intricate interplay of variables. These factors encompass the environment's conditions, the influence of oceanic currents, the salinity of the water, the availability of nourishing sustenance and chlorophyll, etc. The Mediterranean Sea, rife with diverse habitats teeming with anchovies, hosts an assortment of phenotypic and behavioral adaptations among these populations. These distinct groups exploit different ecological niches for the development of their communities (Cardinale et al., 2004; Rumolo et al., 2016; Catanese et al., 2017).

3 Dietary habits and metabolomics

3.1 Trophic ecology and dietary preferences

Engraulis encrasicolus stomach contents offer intriguing insights into their dietary habits and their role within the marine ecosystem thanks to their position as a critical link in the marine food web (Chouvelon et al., 2015; Essington et al., 2015; Awad et al., 2022). Distinct foraging behaviors and dietary preferences are pivotal components of resource partitioning, allowing different species to coexist while reducing competition (Colloca et al., 2010; Liedke et al., 2018; Da Ros et al., 2023). Additionally, different European anchovy prey-preferences impacts the composition of lower trophic levels, influencing the entire food web structure (Colloca et al., 2010; Chouvelon et al., 2015; Rumolo et al., 2016; Awad et al., 2022). Several studies have examined the interactions between various pelagic species, such as *Sardinella aurita*, *Sardina pilchardus*, and *Engraulis encrasicolus*, revealing competition for food resources and overlapping trophic niches among these zooplanktivorous fish species (Bachiller et al., 2020, 2021). While the differences in diet and behavior among sympatric species have been established, it is worth noting that different populations and ecotypes of anchovies may exhibit variations in depth distribution and diet, indicating niche differentiation. This differentiation in resource utilization helps reduce competition, promote species diversity, and enhance ecosystem stability (Awad et al., 2022). Additionally, the presence of distinct ecotypes is influenced by various environmental factors, which in turn shape their physiology, behavior, and interactions with the zooplankton community, thus affecting the trophic web (Catanese et al., 2017). Anchovies exhibit dietary variations in response to environmental food availability revealing a complex mosaic of prey items across various populations (Table 1) (Tudela et al., 2002; Bacha and Amara, 2009; Borme et al., 2009; Raab et al., 2013; Chouvelon et al., 2015; Bachiller et al., 2020, 2021; Basilone et al., 2020; Awad et al., 2022). European anchovy larvae in the north-western Mediterranean primarily feed on copepod eggs, nauplii, and copepodites, with heightened activity during daylight hours. As the larvae grow, their diet broadens to include a variety of prey sizes, particularly an increased consumption of copepodites (Tudela et al., 2002). A study analyzing data from the years 2010-2011 on Northeast Atlantic anchovy's stomach contents, revealed that they exhibited a feeding pattern characterized by copepod-dominated, particularly small and medium-sized organisms. The former study also highlighted trophic segregation as the cause of a negative fluctuation in anchovy abundance during the spring season (Chouvelon et al., 2015).

Raab et al. offered a different viewpoint regarding the European anchovy population in the North Sea. Their study aimed to investigate the influence of temperature, along with food availability, on this particular population (Raab et al., 2013). Through the utilization of spatiotemporal statistical models that correlate anchovy abundance with environmental factors, specifically temperature and food availability, the research revealed that temperature played a more significant role in explaining the distribution and abundance. These findings suggest that, in the case of North Sea anchovies where food resources are not the limiting factor, variations in temperature hold greater significance than alterations in food availability in facilitating the attainment of the necessary size for winter survival (Raab et al., 2013). Two recent studies (Bachiller et al., 2020, 2021) examined the stomach contents of *E. encrasicolus* during the spring of 2018 in the western Mediterranean Sea. The results reveal a significant presence of Calanoidae, order Euphausiacea, and order Decapoda. Diatoms also feature prominently, particularly within the taxonomic families of Chaetocerotaceae, Bacillariaceae, Rhizosoleniaceae, and Thalassiosiraceae (Bachiller et al., 2020, 2021). While the amount of diatoms in anchovy stomach contents is typically limited if compared with *Sarda sarda* (Campo et al., 2006; Fletcher et al., 2013; Albo-Puigserver et al., 2016), it has been demonstrated that these diatoms are abundant in secondary metabolites, which exert diverse effects on the cellular and tissue processes of several species (Mutalipassi et al., 2019; Levy et al., 2021; Bahi et al., 2023). Although the effects of diatoms bioactive compounds on anchovy population have been demonstrated only regarding toxic effects (Scholin et al., 2000; Lefebvre et al., 2001; Fire et al., 2010), it is known that secondary metabolites effects can be elusive to trace and have the potential to alter animal behavior and physiological functions, ultimately influencing population dynamics, as demonstrated in previous studies in other taxa (Gorbi et al., 2014; Lopes et al., 2019; Mutalipassi et al., 2019, 2022; Zupo et al., 2019). Moreover, variations in the frequency of prey ingestion within the same species appear to correspond to a latitudinal signal, suggesting potentially more efficient predation on larger prey like krill. This latitudinal pattern signifies alterations in the trophic ecology of anchovies, aligning with enhanced biological conditions in the southern region of the study area (Bachiller et al., 2020, 2021). An earlier examination of the stomach contents of European anchovies, collected in the Northern Adriatic in October 2002 (Borme et al., 2009), revealed a predominantly zooplanktivorous diet centered around a limited selection of small copepod species (measuring 0.2 to 0.3 or 0.5 to 0.6 mm). Throughout the daylight hours, the copepods *Euterpina acutifrons* and *Oncaea* spp. were the dominant components of the anchovy diet, both in terms of their frequency, abundance, and overall biomass, across all size categories of anchovies. During nighttime hours, bivalve larvae also played a significant role in the anchovy's dietary composition, accounting for more than 69% of the total prey consumed across all anchovy size groups, along with the aforementioned copepods *Oncaea* spp. and *E. acutifrons* (Borme et al., 2009). Bacha and Amara conducted a comprehensive study on European anchovies, examining spatial, temporal, and ontogenetic variations in three regions: Bejaia, Benisaf, and Ghazaouet along the Algerian coast in the southwestern Mediterranean (Bacha and Amara, 2009). Irrespective of factors like season, region, or size, the anchovies' stomach contents were found to consist exclusively of zooplankton, primarily comprising 87% copepods. Nevertheless, the presence and abundance of copepods varied over time. In the first year of life, anchovies consume primarily small to medium-sized copepods. As they matured, these were gradually supplanted by larger decapods and amphipods (*e.g.*, crustaceans). Statistical analyses, including cluster analysis, ANOSIM, and SIMPER, revealed a distinct anchovy diet in Bejaia Bay compared to the other two regions, likely due to differences in hydrological conditions (Bacha and Amara, 2009). Furthermore, differences in diet composition were observed across seasons. Summer and spring exhibited unique prey groups and demonstrated lower dietary similarity compared to the other two seasons. In contrast, winter (with 36 prey species) and autumn (with 30 prey species) featured a more diverse diet. Interestingly no traces of phytoplankton were found in the stomachs of anchovies in this study. The trophic ecology of adult European anchovy in different regions of the central Mediterranean Sea, including the Strait of Sicily and the Tyrrhenian Sea (South Campania, Gulf of Gaeta, South Elba, Strait of Sicily) was examined

TABLE 1 Primary and secondary food source of anchovy living in the Mediterranean and Atlantic Sea.

Area	Location	Anchovy Habitat	Anchovy stage	Primary Food Sources	Secondary Food Sources	Feeding Season	References
North-west Mediterranean	Catalan Sea; Gulf of Lions	Neritic and oceanic domains	larval (Length <4 to 12 mm)	Copepodites, Nauplii; Copepod eggs; Unidentified preys;	Dinoflagellates; Pollen; Tintinids; Cladocerans; Diatoms; Polychaete larvae	Summer (July)	(Tudela et al., 2002)
South-west Mediterranean	Algerian coast	Neritic domain	Adult	Winter: *Oncaea* spp.; *Candacia longimana*; *Corycaeus* sp.; Unidentified copepoda. Spring: *Candacia longimana*; *Oncaea mediterranea*; Unidentified copepoda. Summer: *Candacia longimana*; *Oncaea mediterranea*; *Pleuromamma abdominalis*. Autumn: *Oncaea* spp.	Winter: *Calocalanus* sp.; *Copilia mediterranea*; *Euchirella messinensis*; *Lubbokia aculeata*. Spring: *Arietellus setosus*; *Lubbokia aculeata*; *Phrosina semilunata*; Brachyura (Megalopa). Summer: *Aetideus armatus*. Autumn: *Centropages violaceus*; *Lubbokia aculeata*; *Primno macropa*; *Phrosina semilunata*.	All seasons	(Bacha and Amara, 2009)
Mediterranean	Northern Adriatic Sea (off the River Po delta)	Neritic domain	Adult	Day diet: Copepods (*Euterpina acutifrons*; *Oncaea* spp.). Night, diet: Copepods (*Euterpina acutifrons*; *Oncaea* spp.); bivalve larvae.	Diatoms, dinoflagellates and other microplankton	Autumn (October)	(Borme et al., 2009)
North–east Atlantic	Bay of Biscay	Neritic domain	Adult	Mesozooplanktonic: copepods	Phytoplankton: Dinoflagellates; Diatoms	Spring and autumn	(Chouvelon et al., 2015)
Western Mediterranean	Gulf of Alicante	Neritic domain	Adult	Calanoids; Euphausiacea ord.; Decapoda ord.;	Cyclopoids; Mollusca ph.; Actinopterygii cl.; Diatoms	Spring and summer	(Bachiller et al., 2021)
Atlantic coast	Moroccan coast	Neritic domain	Adult	Copepods; Fish eggs; Crustacean pieces; Mollusks	Dinoflagellates; Diatoms; Ostracods; Annelids	Winter and spring (January and May)	(Awad et al., 2022)

and compared through stable carbon and nitrogen isotope analysis (Rumolo et al., 2016). Results revealed a distinct geographical pattern in anchovy feeding behavior during the summer, characterized by an increasing trend towards the northward where anchovies captured in the northern Tyrrhenian Sea exhibited higher isotope values if compared to individuals sampled in southern region. These elevated carbon and nitrogen values may suggest that anchovies tend to inhabit coastal waters, which contain a greater concentration of ^{13}C derived from benthic primary producers in addition to phytoplankton. The findings of Rumolo and colleagues imply that the feeding behavior of *E. encrasicolus* is influenced, either directly or indirectly, by local factors and resource distribution, in relation to the size of zooplankton.

3.2 Metabolomics for ecotypes identification

The existence of distinct populations was suggested despite the significant considerations given to the interaction between the food web and the distribution of European anchovies, but an exhaustive worldwide assessment is still absent. Nowadays, the distinction between the different ecotypes becomes a categorical imperative, essential to reach a deeper understanding of all economic, ecological, and biological processes related to the presence/absence of one ecotype rather than the other. The development of omics techniques has undoubtedly revolutionized the characterization of the functional responses of biological individuals, populations, or whole communities. Among these techniques, metabolomics represents the endpoint of the omics cascade as well as the level following high throughput and high-resolution analyses of RNA and proteins (transcriptomics and proteomics, respectively) (Macel et al., 2010). As a matter of fact, the set of metabolites synthesized by an organism reflects the surrounding environments representing a helpful tool in studying the mechanisms of interactions between organisms and their environment (Ryan and Robards, 2006; Bundy et al., 2009). Over time, metabolomics has found extensive application in the ecological field, so much that this combination for some authors has given rise to a new discipline, the "ecometabolomic" (Sardans et al., 2021; Uthe et al., 2021). Typically, metabolomics has been applied to explore the effects of pollutants and emerging contaminants and generally to physiological changes (Fasulo et al., 2012; Farré and Jha, 2020; Zhang et al., 2021; Liu et al., 2022), to determine the nutrient profile for aquaculture purposes/effects (Maruhenda Egea et al., 2015), for food security (Yueqi et al., 2023) or to determine habitat qualities (Goode et al., 2020). In addition, metabolomics is supposed to provide reliable information on the geographic origin of the species under examination (Zhao et al., 2020). This methodology has already found widespread application in the field of plant ecology for distinguishing, for example, between ecotypes of *Chenopodium quinoa*, *Ipomoea batatas*, *Arabidopsis thaliana*, and *Cistanche deserticola* (Shekhar et al., 2016; Lalaleo et al., 2020; Sun et al., 2020; Segarra-Medina et al., 2023). However, in the realm of differentiating between ecotypes of marine organisms, its use remains relatively limited. To date, this approach has allowed us to obtain data related to the traceability of geographic origin and detection of species-mislabeling in marine bivalves (Santos et al., 2023) or sponges and deep-sea corals (Vohsen et al., 2019; Bayona et al., 2020; Mohanty et al., 2021). Interestingly, Heal and co-authors demonstrated that in 21 cultured phytoplankton species, the bulk community metabolomes reflect the chemical composition of the phytoplankton community identifying a (chemical) fingerprint of the community across different environmental gradients (Heal et al., 2021). Thus, driven by the close dynamic relationship that exists between the metabolites measured and the physiological status of the whole organism, metabolomic fingerprinting approaches could provide useful information on interspecific relationships (Ivanišević et al., 2011). In this context, the application of fingerprint metabolomics would seem to be a very valid tool for distinguishing and characterizing the offshore and coastal ecotypes of *E. encrasicolus*. Disparities in prey composition closely align with the genetic separation observed between distinct anchovy ecotypes. Offshore ecotype has been demonstrated to predate preferentially larger zooplankton, showing higher environmental tolerance and opportunistic feeding behavior (Catanese et al., 2017). Conversely, their coastal counterparts thrive in the vicinity of river mouths, showcasing a positive correlation with lower salinity and elevated chlorophyll values (Catanese et al., 2017). The dietary preferences of coastal anchovy ecotypes center around smaller prey, including small copepods like *Euterpina*, *Farranula*, *Oithona*, *Acartia*, and various calanoids, along with their nauplii, together with other small-sized prey like bivalve larvae. The diverse prey preferences of anchovy populations have been demonstrated to be not correlated with the difference in prey abundances. These nuanced interactions resonate throughout marine ecosystems, shaping species coexistence, lower trophic levels, and the overall structure and function of marine food webs (Bachiller and Irigoien, 2015; Poiesz et al., 2020). These feeding behavior differences not only have cascade effects along the trophic chain but can confer a different characteristic composition in terms of levels of amino acids, lipids, and other elements such as to allow the possibility of complex biochemical fingerprints for definitively identifying the two different ecotypes. In the context of Protected Designation of Origin (PDO) regulations governing products derived from marine sources, these unique biochemical fingerprints hold immense significance. They emerge as interesting markers that can facilitate the precise classification and authentication of products deriving from specific ecotypes. This intricate differentiation mechanism acts as a safeguard, upholding the authenticity and integrity integral to PDO guidelines. As emphasized by the European Union in 2020, this ensures that consumers consistently receive products that mirror the anticipated characteristics and superior quality associated with their designated origin (European Union, 2020). For example, investigations has demonstrated the prevalence of offshore ecotypes in the vicinity of Cetara juxtaposed with the existence of coastal ecotypes in more distant southern and northern regions (Catanese et al., 2017). This variance underscores the necessity for distinguishing between these populations or ecotypes, a critical aspect in the realm of stock assessment science. Such identification forms a cornerstone in the development of effective fishery management plans, integrating crucial information into the framework of PDO, Protected Geographical Indication (PGI), or Traditional Speciality Guaranteed (TSG) food products (Di Pinto et al., 2019; Minos and Loukovitis, 2019; Girard, 2022). By integrating these findings into regulatory frameworks and management strategies, stakeholders can navigate the nuances of distinct ecotypes, thereby enhancing the precision of product categorization while bolstering sustainable fishing practices. This approach ensures that PDO and related designations uphold their reputation for authenticity, empowering consumers to trust in the specific origin and exceptional quality of the marine-derived products they choose.

In summary, metabolomics is a valuable and evolving approach for distinguishing between two different ecotypes within a species. By revealing the unique metabolic adaptations of these populations, it enhances our understanding of how organisms respond to their environments and provides insights into the ecological and evolutionary processes that shape biodiversity. No less important is the potential support that would arise in distinguishing ecotypes from the perspective of the fraudulent misdescription of seafood, including the mislabeling of raw material, production, and origin. While metabolomics is a promising tool for distinguishing ecotypes coupled also with other molecular techniques, challenges such as sample collection, data analysis, cost-effectiveness, time and standardization must be addressed (Santos et al., 2023). Additionally, to date, the metabolome of anchovies is still poorly explored. Therefore, there is a need to expand the metabolite databases to support a robust comparative analyses also considering the sensitivity of metabolomics to external factors such as age, diet and diurnal and reproductive cycles (Jones et al., 2013).

4 Traditional and industrial processing: from fishing to industries

4.1 Industrial and traditional fishing in the Mediterranean Sea

Engraulis encrasicolus stands as one of the most targeted species of the Mediterranean fishery (FAO, 2022a). This pursuit traditionally employs active techniques such as the *lampara* system, the pelagic trawl (*volante*), or the traditional *menaica* (Cingolani et al., 1996; Tsagarakis et al., 2014; Sartor et al., 2019).

In the *lampara* fishing techniques (Figure 3), anchovies are typically lured by boat equipped with powerful lights, known as *lampara*, and then encircled by a purse seiner (Di Cintio

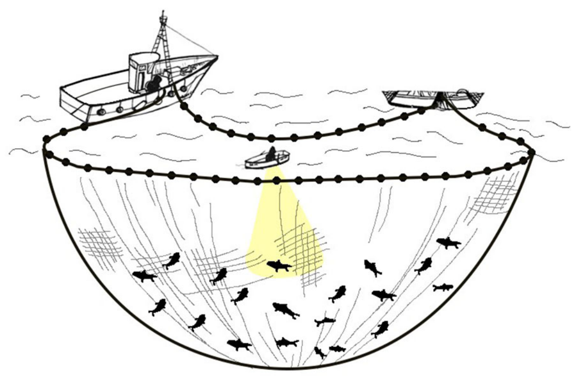

FIGURE 3
Lampara fishing techniques. To catch anchovy using a purse seiner with *lampara*, a large net is deployed around a school of anchovies, encircling them. The central *lampara* light attracts the anchovies towards the net, and then the net bottom is drawn closed to trap the fish, allowing for their easy retrieval.

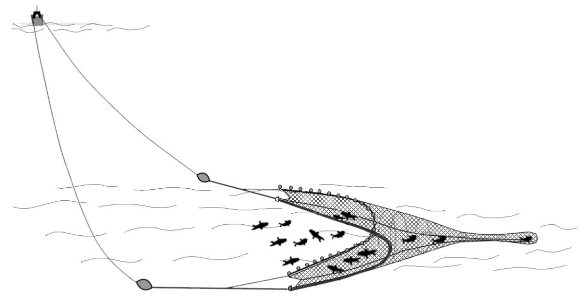

FIGURE 4
Volante fishing technique. To catch anchovy using the mid-water *volante* net technique, a vessel deploys a rectangular net designed to encircle schools of anchovies swimming at mid-depths. The net is suspended horizontally in the water column and equipped with floats and weights to keep it at the desired depth. As the vessel tows the net through the water, the anchovies were caught into the net, and once a sufficient amount is captured, the net is hauled in to harvest the fish, making it an effective method for targeting midwater schools of anchovy.

et al., 2022). In the Tyrrhenian Italian region of Campania, this technique generally is carried out using fishing vessels with a length overall of less than 24 meters (Lucchetti et al., 2017). This technique takes advantage from the attraction to light of several fish species (Fitzpatrick et al., 2013; Nguyen and Winger, 2019) assuming primary roles in triggering a diverse array of stimuli (Marchesan et al., 2005; Liao et al., 2007; Sabbah et al., 2010; Bryhn et al., 2014; Matsui et al., 2016). Light plays a pivotal role in triggering schooling behavior in various fish species, whether as a defense mechanism or a predatory strategy (Pavlov et al., 2000), enabling them to discern prey, seek shelter, and locate conspecifics, standing as a fundamental sensory input vital for their day-to-day survival (Cortesi et al., 2020; Oteiza and Baldwin, 2021). The utilization of light in fishing has emerged as one of the most advanced, efficient, and successful methods for capturing commercially valuable species, as in the case of the *lampara* technique. This fishing activity takes place during the night and fish are attracted to the surface using artificial light. The illumination is created by lamps mounted on auxiliary vessels called *lampara*, which are lowered into the fishing area from the main vessel (Pertierra and Lleonart, 1996; Cingolani and Santojanni, 2003; Edwin, 2019; Giráldez, 2021). In order to maximize fish capture, two auxiliary vessels often can operate both at the same time in a joint fishing operation force for the catch. The illumination system remains activated for a period of approximately 2 hours, during this time anchovies swim relatively close to the surface. When the aggregation is complete, another boat called *stazza* is released at sea from the main vessel quickly as possible moving in a circle to the shoal to close the net by winch. At the end of each fishing operation, fish are hoisted on board with large nets and put into tanks full of water and ice (Cingolani and Santojanni, 2003; Edwin, 2019).

The second method involves towing a net in mid-water without contacting the seabed, called the *volante*, which is used to catch European anchovies and other small pelagic species (Figure 4). At the national scale, this technique represents less than 1% in terms of vessels. This technique is present in the Adriatic Sea fleet, Geographical sub-areas (GSA) 17, which represents the larger *volante* fish fleet in terms of numbers, followed by the Southern and Central Tyrrhenian fleet in the GSA 10 (MIPAAF, 2021). In this case, the fish are captured through the movement of the net towed by the boat. *Volante* vessels fish only in the daytime and land their product every evening. Before beginning this phase, a particular echo sounder installed on board is used to locate and estimate the size of the shoals of anchovies in the water column. The fishing process involves a series of well-coordinated actions that unfold in a particular sequence, each step designed to optimize the capture of anchovies (Pertierra and Lleonart, 1996; Cingolani and Santojanni, 2003; Russo et al., 2015). Firstly, the vessel initiates a deliberate reduction in speed, a crucial maneuver that sets the stage for the subsequent activities. The net is then skillfully deployed at a carefully chosen distance from the seabed. This placement is a strategic decision aimed at increasing the chances of a productive catch. As the trawling operation commences, the vessel's speed is methodically increased. This acceleration is a calculated effort to cover a larger area and ensnare as many anchovies as possible. Once the trawl has been executed, the net is expertly hoisted back onto the vessel. The anchovies, now captured, are gently transferred, as seen for the *lampara* fishing technique, in a container containing water and ice. This careful handling is essential to ensure the anchovies' freshness and preserve their quality until they reach their final destination (Cingolani and Santojanni, 2003; Russo et al., 2015).

However, a third distinct fishing gear, typical of small-scale fisheries with a length overall of less than 12 meters, is notably present along the coasts of southern Italy, particularly in GSA 10 and 19 (Figure 5), and is known as *menaica* or *menaide* (Sartor et al., 2019). The *menaica* method is characterized by scarcely mechanized gear generating an activity strictly correlated with ancient traditions of small fishing fleets (Sartor et al., 2015, 2019). It is performed by a relatively modest *menaica* fleet, which comprises only around 40 boats in Sicily and 19 in Campania (Sartor et al., 2019). In compliance with Italian legislation, which has governed its technical specifications since 2012, *menaica* is a

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passive net categorized as a sub-group of the small-scale driftnet (SSD) passive net subcategory (Lucchetti et al., 2017). As a driftnet, *menaica* was banned in 1998 along with large-scale driftnets targeting swordfish (Ferretti et al., 1995, 2002), the latter producing numerous instances of the unwanted catch of protected, endangered, and threatened species, such as marine mammals and reptiles, generating great environmental concerns (Di Natale, 1995; Di Natale et al., 1995; Tudela, 2004). *Menaica* has been recognized as a highly selective and specialized fishing gear and it has been demonstrated, in fact, that anchovy is the only target species for the fleets of Catania (Sicily) and Cilento (Campania). The European sardine (*S. pilchardus)* is the second target species and it has been reported that it represents the main target species for the *menaica* vessels from Slovenia (Sartor et al., 2019). They have been monitored in certain areas under the context of the European Union Data Collection Regulation (DCR) and subsequent Data Collection Framework (DCF). However, monitoring is limited to specific locations due to the scattered distribution of SSD fisheries and the low level of landings or fishing efforts. For instance, the *menaica* fishery (Figure 6) is monitored primarily in the FAO-GFCM Geographical Sub-Area (GSA) 19 (western Ionian Sea), in GSA 10 (Central-Southern Tyrrhenian Sea) and occasionally in GSA 16 (Central Mediterranean sea, south of Sicily island) (Sartor et al., 2019). The *menaica* method employs a single netting panel made of nylon, deployed no more than three miles from the coast. The net has a maximum length of 500 meters, a height of 10 meters, and a range of mesh size (19 -29 mm) (Sala et al., 2018). Depending on the fishing area and target species, *menaica* operations typically occur from April to September, primarily during the nighttime (Sartor et al., 2019). One of the notable advantages of the *menaica* technique is its inherent selectivity, predominantly capturing adult anchovies while minimizing issues related to by-catch (Sartor et al., 2019). The design of the net prevents larger fish from breaking through it, while allowing smaller ones to pass, contributing to its efficiency in target species retention. Along the South Italian coastline, anchovies caught especially using the *menaica* method are traditionally preserved in wooden barrens in alternating layers separated by sea salt, after being gutted and beheaded by hand (Corona et al., 2022).

4.2 Economic significance and challenges of anchovy fisheries: sustainability, fraud, and geographical traceability

The economic importance of anchovies in the Mediterranean cannot be understated. European anchovies are a vital component of regional fisheries, supporting livelihoods and providing a source of income for coastal communities (FAO, 2018). They are processed into various products, including canned goods, fishmeal, and fish oil, contributing to local and international markets (Dinçer, 2018). The long-term survival of anchovy populations depends on implementing sustainable fisheries management, which includes enforcing catch limits and creating protected zones (Di Franco et al., 2016). Due to its importance in regional pelagic fisheries, this species is highly appreciated in Mediterranean markets. The especially rich nutritional profile contributes to its appeal as a commercial fish species. It is characterized by a high concentration of important polyunsaturated fatty acids (PUFAs), including omega-3 fatty acids like docosahexaenoic acid (DHA) and ecosapentaenoic acid (EPA), as well as omega-6 fatty acids such as arachidonic acid (ARA) (Zlatanos and Laskaridis, 2007). Anchovies, including European ones, are commonly found in the European market as processed food, as in the case of brine-fermented or fileted and canned (preserved in oil) anchovies, in addition to the common use as fresh fish (FAO, 2020). The fisheries industry is vulnerable to dishonest practices, and it is not sufficiently safeguarded. The main factors impeding the fight against fraud include the high level of complexity of the fish supply chain, the large number of parties involved, and the quick perishability of the product. These illegal procedures have adverse economic and sanitary consequences on different levels of the production and supply chain, from producers to transformers and final consumers (FAO, 2018). Consumers' perceptions of fresh or processed fish and seafood items' quality are the result of a variety of objective and subjective elements, and this perception has a direct impact on the product's market and worldwide economic values. The so-called country-of-origin effect, which states that consumers increasingly tend to associate high-quality fish products with specific production areas due to specific sensorial characteristics, and ethical or ecological motivations, is currently encouraging mislabeling or

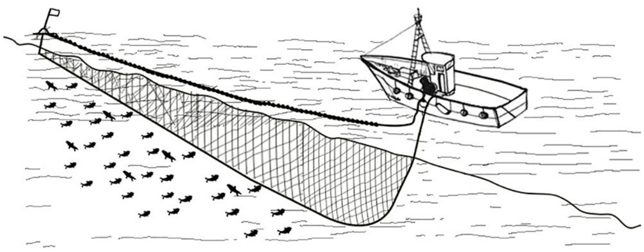

FIGURE 5
Menaica fishing technique. In this fishing technique, a specialized type of drift-net is used to catch anchovies. The *menaica* is deployed vertically in the water, suspended from surface floats and tensioned in the water thanks to the lead-file placed below. Schools of anchovies swim in the net as it drifts, and the mesh size of the gill net is designed to entangle fish with their gills. This fishing gear is highly selective for anchovies and, partially, sardines, and the selectivity is given by the type of mesh used, reducing by-catch to a minimum.

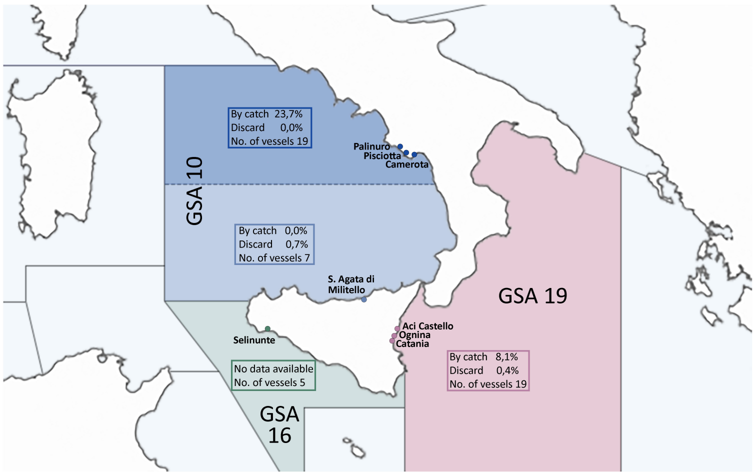

FIGURE 6
Menaica fishing activity in central Mediterranean Sea (South of Italy). The image includes GSA numbers for each specific geographical area, as well as percentage data about bycatch and discards, along with information about the count of vessels engaged in *menaica* fishing in the waters of Italy. Notably, the image also brings attention to the ports where *menaica* vessels have been recorded (Sartor et al., 2015, 2019).

misrepresenting the origin of fish products (Varrà et al., 2021b). According to several authors, fraud is a common occurrence concerning processed fish products made from the industrial transformation of the extremely valuable European anchovy (Velasco et al., 2016). Using misleading labels or other dishonest marketing techniques in the seafood supply chain about the quality, origin, quantity, or species it is a widespread problem in European and American fisheries (Petrossian and Pezzella, 2018). Up to one-third of all seafood consumed in the United States has been misidentified and sold as something different from what these customers thought they were buying, according to recent estimates of species substitution (Silva et al., 2021). Additionally, substitute rates for seafood vary by species, with some substitutions being as high as 70%. Anywhere in the seafood supply chain can experience seafood fraud (Silva et al., 2021; Lawrence et al., 2022). European legislation (General Food Law, regulation (EC) No 178/2002) mandates the identification of species through distinct commercial names solely in fresh and prepared fishery products. However, in processed products, generic designations can be used instead of specific species names leading to misleading information given to consumers and several techniques has been develop to identify species in processed products (Muñoz-Colmenero et al., 2016; Cutarelli et al., 2018). This pertains to European anchovy paste, where the PCR-RFLP technique has revealed the presence in different percentage of undisclosed species, spanning from *Sardinella aurita* to *Sprattus sprattus*, and *S. pilchardus* (Rea et al., 2009). In other investigations, COI-DNA barcoding was used in combination with PCR-RFLP method to investigate labeling species accuracy in different processed food (*i.e.*, anchovy fillets in vegetal oil, canned anchovies, and anchovy paste) demonstrating that up to the 14% of samples contains unlabeled species, *e.g.*, *Engraulis japonicus*, *S. aurita* and *S. pilchardus* (Pappalardo and Ferrito, 2015). Similar results has been achieved using BLAST techniques where other species belonging to *Engraulis* genus has been found in mislabeled anchovy products, such as anchoveta (*E. ringens*), Argentine anchovy (*E. anchoita*) and Japanese anchovy (*E. japonicus*) (Giusti et al., 2019).

Despite the successful application of various techniques for fish species identification (Black et al., 2017), detecting fraud associated with fishing areas remains challenging for the majority of commercial species found in the fish market. Scientific research dealing with the identification of fish and seafood origin used several different approaches. Among these approaches, methods involving inorganic components like stable isotopes (Carrera and Gallardo, 2017), trace elements (Smith and Watts, 2009), a combination of the two previous techniques (Li et al., 2019; Varrà et al., 2021b), or the use of multi-elemental analysis (Rodushkin et al., 2007) have proven successful in several cases. In particular, the multiple identification of elements using techniques such as inductively coupled plasma-optical emission spectroscopy (ICP-OES) and inductively coupled plasma-mass spectrometry (ICP-MS) was used successfully to track back to the origin of processed or highly processed products (Varrà et al., 2021b). Furthermore, near-infrared (NIR) spectroscopy has been employed to evaluate the geographical traceability of salted ripened anchovies originating from diverse Mediterranean regions. Disparities in protein, peptide, amino acid, and proteolytic compound signatures, and particularly in fatty acid profiles, signify distinctive features of aquatic environments, influencing the overall chemical composition of the final product (Varrà et al., 2021a).

Another different approach is linked to the possibility of imposing the use of monitoring software for fishermen to track their fishing activity. These reports are expected to encourage fishing vessel owners to practice self-control and accountability and to increase their perception of being caught and sanctioned if they contravene the law (Petrossian and Pezzella, 2018). In addition, it should be important to check licenses, gear, fish caught, and catch registered through the support of local port authorities to ensure that the fishers take the necessary steps and follow the regulations more carefully, as this will "alert conscience" about possible penalties if they fail to do so (Petrossian and Pezzella, 2018). Several food items have been objects of interest for the European Union, which decided to protect foods with characteristics of unicity. For this reason, PDO, PGI, and TSG labels have been adopted to avoid fraudulent practices (Consonni and Cagliani, 2022). European anchovies are not immune to this activity, especially considering that such high-quality commercial products require a clear statement of Geographical traceability and consequently of the fishing areas, as in the case of traditional Italian anchovy sauce with PDO called "colatura di alici di Cetara". On the Amalfi Coast (Italy), since 1807, anchovies caught are gutted, beheaded by hand, and placed in wooden vats in alternating layers separated by sea salt. Once the layers are ready, a wooden disk with weights is placed on top of the vats, and the aging process starts. A clear liquid called "colatura", obtained from pressed anchovies matured in wooden vats under salt for at least 9 months, is finally collected (Corona et al., 2022). During the maturation process, lipolytic and proteolytic activities exert a significant influence on the commercial attributes of the product, leading to the formation of distinctive volatile compounds and the production of biogenic amines, such as histamine. This phenomenon represents one of the foremost hygienic and health concerns in fish products belonging to the Engraulidae family and their enzymatic maturation-derived products. Preliminary investigations suggest that elevated histamine levels, surpassing safe level thresholds, have exclusively present in processed anchovies that have not undergone evisceration (D'Anza et al., 2023). These findings pinpoint a specific condition associated with histamine accumulation, highlighting the significance of the processing method in mitigating histamine content.

4.3 Valorization of anchovy discards in a circular economy: challenges and opportunities for sustainable and biotechnological utilization

Recently, the Food and Agriculture Organization estimated that, in 2020, fisheries and aquaculture production reached 214 million tones and it is forecasted to grow for another 14% by 2030. Asian countries are at the top of the world ranking with 75% of production in 2020, followed by countries in the Americas (10%), Europe (8%), Africa (6%) and Oceania (1%) (FAO, 2022b). Such increasing global fishery production has resulted in several consequences related to the massive production of waste deriving from industrial processing and by-catch of inedible species. Discards may represent up to 70% of processed fish, depending on the size, species, and type of processing, including heads (9–12% of total fish weight), viscera (12–18%), skin (1–3%), bones (9–15%) and scales (5%) (FAO, 2022b). Due to the increasing attention towards such concerning issues, many EU policies and strategies, in terms of fishing management, have been addressed to a strong reduction of waste and re-utilization of them for industrial and biotechnological purposes (Damalas, 2015; Soto-Oñate and Lemos-Nobre, 2021). Within this context, a circular bio-economy approach has been introduced to promote the production of high-value-added compounds from renewable biological resources (Cooney et al., 2023). Several parts of fish and seafood are generally discarded although they store a lot of important compounds including proteins and peptides, enzymes, oils, and biopolymers of biotechnological interest, *e.g.*, collagen, chitin, chitosan (Coppola et al., 2021; Racioppo et al., 2021; Nag et al., 2022; Lal et al., 2023). At present, a concrete alternative to incineration is the re-use of fish wastes as fishmeal for aquaculture purposes and as a fertilizing agent since the rich content in oils, minerals, and essential amino acids reported good results in gonad/tissue fattening and plant growth (Beheshti Foroutani et al., 2018; Ashraf et al., 2020; Ciriminna et al., 2021).

Chemical methods are conventional approaches that have been used for the isolation of high-value compounds from fish discards, although a high quantity of solvents is needed (Ideia et al., 2020). For this reason, green and more sustainable approaches are starting to be applied such as supercritical carbon dioxide (SC–CO_2) extraction, microwave-assisted extraction (MAE), and enzymatic hydrolysis (Bruno et al., 2019; Ozogul et al., 2021; Thirukumaran et al., 2022). So far, fish protein hydrolysates have been widely obtained through the addition of endogenous or commercial enzymes that cleave the aminoacidic bonds with highly selective reactions (Ozogul et al., 2021). Interestingly, to reinforce the circular economy approach such enzymes have also been extracted from fish viscera and other parts to obtain protein hydrolysates with antioxidant properties (Khiari, 2022; Borges et al., 2023). Recent findings also allowed the development of novel eco-friendly bioconversion processes taking advantage of microbial fermentation or algal metabolism to recover valuable ingredients and produce biofuels from seafood discards (Marti-Quijal et al., 2020; Vázquez et al., 2020; Venugopal, 2021).

So far, several seafood by-products have reported valuable biological activities and potential applications in marine biotechnology by offering new solutions to improve human health and well-being (Atef and Mahdi Ojagh, 2017; Ashraf et al., 2020; Mutalipassi et al., 2021; Cardeira et al., 2022; Siahaan et al., 2022). For instance, depending on fish species, hydrolysis condition, isolation, and so on, protein hydrolysates rich in amino acids, proteins, peptides, and antioxidants, have shown great potential in aquaculture since a significant improvement of growth, immune function, and disease resistance was observed (Siddik et al., 2021; Moya Moreira et al., 2023). Protein hydrolysates, from sources that are normally discarded during industrial processing such as shrimp shells, reported antioxidant properties and potential applications in nutraceutical and cosmeceutical fields (Henriques et al., 2021; Messina et al., 2021).

Concerning anchovies, high-value compounds have been isolated from discards with different applications in biotechnological fields (Table 2). Chemical approaches have led to the isolation of bioactive compounds from wastes of Cantabrian individuals. In particular, hexane, aqueous, butanol, and ethyl-acetate fractions, from the methanol extract of gut and head, showed anti-mutagenic, antifungal, anti-bacterial, and antioxidant activities (Burgos-Hernández et al., 2016). Extensive chemical analyses from head, frame, and viscera of the European anchovy from the Black Sea also reported good potential in the fabrication of protein powder and hydrolysates, fish oils, and mineral supplements (Gencbay and

TABLE 2 Valorization and potential use of anchovy discards: different geographical areas, different species materials, bioactivity and field of application.

Geographical localization	Species	Source	Compounds	Isolation method	Bioactivity	Application	Reference
Cantabria, Spain	*E. encrasicolus*	Gut, head	Not determined	Methanol extraction combined to fractionation with hexane, ethyl acetate, and butanol	Antimutagenic, antifungal, antioxidant, antibacterial	Pharmaceutical and food	(Burgos-Hernández et al., 2016)
Black Sea	*E. encrasicolus*	Head, frame, viscera	Amino acids, fatty acids, minerals	HCl hydrolysis for amino acids and minerals; Separation by mixture of chloroform and methanol for fatty acids	Not determined	Nutraceutical	(Gencbay and Turhan, 2016)
Sicily, Italy	*E. encrasicolus*	Viscera	Protein hydrolysates	Hydrolysis with commercial proteases	Not determined	Nutraceutical	(Mangano et al., 2021)
Sicily, Italy	*E. encrasicolus*	Viscera	Protein hydrolysates	Hydrolysis with commercial proteases	Antiobesity, antiatherogenic	Nutraceutical	(Abbate et al., 2020, 2021)
Sicily, Italy	*E. encrasicolus*	Viscera	Protein hydrolysates	Hydrolysis with commercial proteases	Anti-inflammatory	Nutraceutical	(Giannetto et al., 2020)
China	*E. japonicus*	Whole body	Protein hydrolysates	Hydrolysis with commercial and endogenous enzymes	Antioxidant	Nutraceutical	(He et al., 2014)
China	*E. japonicus*	Cooking wastewater	Protein hydrolysates	Hydrolysis with commercial protease	Antimicrobial	Pharmaceutical, nutraceutical	(Tang et al., 2015)
Argentina	*E. anchoita*	Head, frame, viscera	Proteins	Water extraction, alkaline solubilization, isoelectric precipitation	Antimicrobial	Food packaging	(Rocha et al., 2013, 2014, 2018)
Turkey	*E. encrasicolus*	Head, frame, viscera	Proteins	Water extraction, NaOH solubilization, HCl precipitation	Antioxidant	Food packaging	(Tural and Turhan, 2017b, a; Tural et al., 2020; Yilmaz et al., 2020)
Sicily, Italy	*E. encrasicolus*	Mixed discards	Oils	Mechanical homogenization followed by d-limonene extraction	Not determined	Biofuel, fertilizers	(Ciriminna et al., 2019; Paone et al., 2021; Muscolo et al., 2022)
Argentina	*E. anchoita*	Salting-ripening residues	Oils	NaCl treatment followed by desalting process	Not determined	Biofuel	(Marchetti et al., 2021)
Malaysia	Mix of species: *Encrasicholina heteroloba*, *Encrasicholina punctifer*, *Stolephorus commersonii*, *Stolephorus andhraensis*	Mixed discards	Proteins	Drying process	Improvement of body indices	Feed	(Ahmad et al., 2018, 2023)
Cetara, Italy	*E. encrasicolus*	Salting-ripening residues calle "Colatura di alici"	Amino acids, histamine, volatile compounds	NaCl treatment for 12, 24 and 48 months	Not determined	Nutraceutical	(Corona et al., 2022)

Turhan, 2016). The majority of products isolated from anchovy wastes are protein hydrolysates with interesting bioactivities that make them suitable functional ingredients for biotechnological purposes (He et al., 2014; Rodrigues Freitas et al., 2016; Mangano et al., 2021).

In the European anchovies, several studies have been already done on protein hydrolysates characterization and bioactivity screening in both *in vitro* and *in vivo* models. High-performance liquid chromatography with diode array detection (HPLC-DAD), nuclear magnetic resonance (NMR), and inductively coupled plasma mass spectrometry (ICP-MS), led to the characterization of protein hydrolysates with high nutritional value obtained through enzymatic digestion of viscera (Mangano et al., 2021). Such protein hydrolysates showed anti-obesity properties and a significant reduction of atherosclerotic plaques in dysfunction-associated fatty liver disease (MAFLD) $ApoE^{-/-}$ mice models with a considerable enhancement of lipid metabolism after 12 weeks of administration (Abbate et al., 2020, 2021). In addition, a clear reduction of protein levels and gene expression of pro-inflammatory mediators such as COX-2 and cytokines *TNF-α*, *IL-1 α*, *IL-1 β*, *IL-6*, in LPS-induced RAW264.7 treated cells and ApoE knockout administered mice, was also observed (Giannetto et al., 2020). The aminoacidic composition and antioxidant capacity were also evaluated in protein hydrolysates obtained from the Chinese anchovy *E. japonicus*. DPPH assay revealed a radical scavenging activity with higher efficiency in hydrolysates obtained with commercial enzymes in comparison to endogenous ones (He et al., 2014) and, interestingly, similar results have been reported from the anchovy sprat *Clupeonella engrauliformis* (Ovissipour et al., 2013). Antimicrobial peptides were instead identified in the hydrolysates obtained from the cooking wastewater of *E. japonicus* (Tang et al., 2015) and tissues of the half-fin *Setipinna taty* (Song et al., 2019).

Discarded parts of European and Argentine anchovies were used for the extraction of proteins and the development of edible films to be used in food packaging (Rocha et al., 2013; Tural and Turhan, 2017b). To improve the physiochemical, mechanical, thermal, antioxidant, and antimicrobial properties, some modifications have been applied such as the addition of cross-linking agents (Yilmaz et al., 2020), essential oils (Tural and Turhan, 2017a; Tural et al., 2020), and organic acids (Rocha et al., 2014, 2018).

Fish oils also represent an important source of functional ingredients due to the high content in omega-3 polyunsaturated fatty acids which exert several benefits for humans (Pike and Jackson, 2010). The accomplishment of green extractions through renewable solvents, plus the re-use of both fish oils and solid biomass, allows the highest standards of a circular economy approach. High-quality oils have been successfully extracted from anchovy discards in the fileting process by using limonene obtained from orange peel (Ciriminna et al., 2019). The remaining solid waste was employed for biogas production through microbial anaerobic digestion (Paone et al., 2021), and for the manufacturing of nutrients-rich fertilizers promoting the growth of Tropea's red onion with higher efficiency in comparison to common organic and chemical products (Muscolo et al., 2022). Oils from anchovy discarded tissues have been also used for biodiesel production with good combustion properties and reduced pollutant emission (Behçet, 2011). As already mentioned, industrial processing produces plenty of residues that are commonly wasted although such material could represent a resource of compounds for animal feed or nutraceuticals. For instance, by-products generated by salting-ripening procedures of fresh anchovies (*E. anchoita*) harvested from the Southwestern Atlantic Ocean were found rich in proteins, EPA, and DHA that can be recovered through desalting processes (Marchetti et al., 2021). Recently, feeding experiments on the Red-Hybrid Tilapia (*Oreochromis* spp.) with dried materials obtained from Malaysian anchovies were found to give a significant protein supply and growth performance improvement (Ahmad et al., 2018, 2023). In the Gulf of Salerno, Cetara anchovies have been highly consumed food since 1800 due to their undeniable taste. The salt ripening process that takes, at least, 9 months, allows the production of the so-called "colatura di alici", a savory liquid that received the status of PDO by the European Union in 2020 and is currently used as dressing sauce for several dishes. A very recent study analyzed the chemical content of Cetara anchovies' sauce to investigate its nutritional value and safety. Interestingly, when the ripening process was applied for up to 48 months, the "colatura di alici" was found richer in essential amino acids and volatile organic compounds, enhancing nutritional properties and flavor, while histamine significantly reduced by improving sauce safety (Corona et al., 2022). Since the Cetara anchovy is highly appreciated and widely consumed food by both locals and foreigners, every year a lot of discarded material is produced. However, there are no studies on the possible re-use of such discards for biotechnological applications, although recent chemical analyses have suggested a good nutritional value of its salt-ripening sauce (Corona et al., 2022). Furthermore, it is important to note the absence of available data pertaining to variations in metabolite compositions among distinct populations and ecotypes situated along the expanse of the Mediterranean Sea. Therefore, there exists a compelling imperative for future investigations aimed at comprehending any disparities, should they exist, in the potential utility of anchovy catches in diverse geographical regions.

5 Conclusions

In conclusion, this comprehensive review provides valuable insights into the biology of the European anchovies (*Engraulis encrasicolus*), and the essential role they play in the central Mediterranean Region. The research sheds light on the ecological significance, conservation challenges, and sustainable utilization of *Engraulis encrasicolus*, highlighting its status as a keystone species critical for both ecological and socio-economic dimensions in the Mediterranean basin. The declining numbers of European anchovy, along with *Sardina pilchardus*, have raised concerns, emphasizing the urgent need for improved management of anchovy fisheries. This improvement calls for a deep understanding of their reproductive modes, passive transport dynamics influenced by ocean currents, feeding habits, adaptability to environmental conditions, and the distribution of ecotypes along the Italian coasts. Anchovies are pivotal for maintaining ecosystem balance and supporting human communities reliant on marine resources. Information reported in this review serves as a basis for improving effective fisheries management, based as first on the correct identification of management units, *i.e.* populations and ecotypes.

Management also involves the identification and valorization of artisanal practices, and the prevention of fraud, particularly in the context of protected, geographically specific, and traditional high-quality commercial productions. Reported information about anchovy population dynamics, their industrial processing, and the ecological implications of these activities, ultimately contributing to our knowledge of anchovy populations and ecotypes. It is imperative to proceed with research to develop a more straightforward way to identify anchovy ecotypes. This would greatly enhance our ability to understand and manage these distinct populations and ecotypes, helping in the identification of fishery frauds, for example through the development of ready-to-use population/ecotype identification kits. Special attention should be given to their ecological interactions within the food web, with a focus on metabolic and stomach contents diversity among anchovy populations and ecotypes, thus enhancing our understanding of their adaptability to varying environmental conditions. It's essential to pay attention to potential metabolic differences among populations and ecotypes. This could open doors to the production of nutraceutical and cosmeceutical products, further enhancing the value and sustainability of anchovy resources. Furthermore, there is a clearly reported importance for traditional and industrial processing of anchovies, spanning from fishing techniques to the economic significance and sustainability challenges of anchovy fisheries. It also addresses issues of fraud and the establishment of geographical traceability. It is important to work toward creating a circular economy around anchovy discards, forging agreements with food processing industries. This would not only reduce waste but also contribute to sustainable resource utilization, creating opportunities for the sustainable and biotechnological utilization of anchovy discards, highlighting the potential for waste reduction and resource optimization.

Author contributions

MM: Conceptualization, Data curation, Supervision, Writing – original draft, Writing – review & editing. ED: Conceptualization, Data curation, Supervision, Writing – original draft, Writing – review & editing. MP: Writing – original draft, Writing – review & editing. RF: Data curation, Writing – original draft, Writing – review & editing. CM: Data curation, Writing – original draft, Writing – review & editing. NR: Data curation, Writing – original draft, Writing – review & editing. CP: Data curation, Writing – original draft, Writing – review & editing. GP: Investigation, Supervision, Writing – review & editing. TR: Investigation, Supervision, Writing – review & editing. AT: Funding acquisition, Project administration, Writing – review & editing. VP: Conceptualization, Investigation, Project administration, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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