Food Control 184 (2026) 112028

Contents lists available at ScienceDirect

Food Control

journal homepage: www.elsevier.com/locate/foodcont

Are squid rings made from squids? Amplicon-sequencing HTPS method to identify cephalopod species in processed squid products

Carmen G. Sotelo *, Ana Sanchez, Begoña Correa, Marta Perez Testa, Ricardo I. Perez-Martín

Instituto de Investigaciones Marinas (CSIC), Eduardo Cabello 6, 36208, Vigo, Spain

A B S T R A C T

Cephalopods are widely consumed marine species, yet their fisheries remain poorly regulated, and species-specific catch data are often unavailable. Although a variety of processed squid products are available on the market, frozen squid rings and pieces are among the most popular in the EU and other countries worldwide. This study aimed to assess the diversity of cephalopod species in these processed squid products sold in the Spanish market and to evaluate their compliance with EU labelling regulations. We analysed the labelling and species composition of 63 commercial products by examining their adherence to EU labelling requirements and identifying the cephalopod species present in them by using a metabarcoding approach based on High Throughput Sequencing (HTS). While mislabelling rates were relatively low (11.1%), we observed a high diversity of commercial names that could mislead consumers. Products labelled simply as "squid" included species from both the Loliginidae and Ommastrephidae families, with 50% containing Jumbo flying squid (*Dosidicus gigas*). These findings underscore the need for clearer labelling to ensure transparency and promote sustainable seafood consumption.

1. Introduction

Cephalopods, a significant group of marine invertebrates within the phylum Mollusca, are highly important in marine ecosystems, with relevant global fisheries due to their popularity as seafood in some cultures (Barrett et al., 2022; De la Chesnais et al., 2019; Hunsicker et al., 2010). Cephalopod global capture in 2022 was about 2.76 million tons (FAO, 2024), the highest volumes (1.08 million tons) were of the Jumbo flying squid (*Dosidicus gigas* A. d'Orbigny, 1835), and the Argentinian squid (*Illex argentinus*, Z.J.A. Castellanos, 1960) (334 thousand tons), both belonging to the family Ommastrephidae (FAO, 2024).

In Mediterranean regions, squids are a common sight in fish markets and are consumed after a variety of preparations (Paiva et al., 2024). In fact, recent market reports indicated that squid represents the 59% of the cephalopods consumed in coastal and urban areas of the world and there is a growing trend for the market of processed squid (https://www.businessresearchinsights.com/market-reports/fresh-squid-market-115746). Processed squids have become widely distributed globally seafood products worldwide. The most representative of all of them could probably be squid rings. This is one of the most popular dishes in Mediterranean countries (Pérez-Lloréns et al., 2021). The European squid (*Loligo vulgaris*, J.B. Lamarck, 1800) is renowned for its delicate and tender meat. This makes Loligo species more appreciated and demanded by consumers in Europe and, therefore, also more expensive. Because of that, *Loligo vulgaris* is often substituted in processed products with cheaper species from the family Ommastrephidae, making it difficult to visually detect such change. Within the Ommastrephidae family, there are numerous species of varying quality and price that could be used to produce "squid" rings (Sales et al., 2011).

Like other seafood products, the cephalopod supply chain relies on fisheries operating across diverse regions worldwide. This global sourcing drives substantial imports of squid to processing facilities, which are primarily concentrated in China and other Asian countries. In Europe, Spain is a major player, hosting processing plants and engaging in significant trade, importing approximately 850 thousand tons and exporting 526 thousand tons of squid products in 2022 (EUMOFA, 2025). Over the past decade, imports have risen notably in markets such as the USA, Japan, and Spain. However, the origin of these imports differs: while the USA and Japan predominantly source cephalopods from China, Spain's main suppliers in 2022 include the Falkland Islands, India, Morocco, China, and Argentina (EUMOFA, 2025). Growing demand, coupled with occasional supply constraints, has led to sharp increases in squid prices in recent years (FAO GLOBEFISH Highlights, 2023, pp. 2–2023). This dynamic often encourages the indiscriminate use of umbrella terms like "squid" to market products that may encompass multiple species, each with distinct biological and ecological traits.

* Corresponding author.
E-mail addresses: carmen@iim.csic.es (C.G. Sotelo), asanchez@iim.csci.es (A. Sanchez), begonacorrea@iim.csic.es (B. Correa), mtesta@iim.csic.es (M. Perez Testa), ricardo@iim.csic.es (R.I. Perez-Martín).

https://doi.org/10.1016/j.foodcont.2026.112028
Received 9 October 2025; Received in revised form 22 December 2025; Accepted 31 January 2026
Available online 11 February 2026

However, fisheries of these species are not well studied or managed, and there is controversy regarding the uncontrolled capture of cephalopods in international waters or areas close to Exclusive Economic Zones (EEZ) by some countries (Lishchenko et al., 2021). Additionally, Illegal, Unreported, and Unregulated (IUU) fishing exacerbates issues related to seafood mislabelling and fraud (Helyar et al., 2014; Kroetz et al., 2020). Furthermore, IUU fishing negatively impacts the sustainability of marine stocks, including cephalopods, and the whole marine ecosystems. The situation for cephalopods is particularly dramatic, as there are no comprehensive assessments of their stocks, and even data about all species are not segregated in FAO reports (FAO, 2024). Consequently, the status of some cephalopod species remains unknown.

Seafood traceability and labelling regulations are essential not only for the protection of marine resources (Gleadall et al., 2024), but also for the accurate identification of species and their origin. These tools enable consumers to make informed purchasing decisions and allow authorities to enforce fisheries management policies effectively (Borit & Olsen, 2020). Regulations such as EC 1169/2011 (European Union, 2011) and EC 1379/2013 (European Union, 2013) establish that both commercial and scientific names of species must be included on the packaging, depending on the type of product. However, compliance levels may vary depending on retailers, product categories, and even across EU member states (Paolacci et al., 2021). A major inconsistency in this regulation is that only less processed products, such as frozen squid, require both commercial and scientific names, as well as geographic origin. In contrast, processed products are only required to display the commercial name (EC 1379/2013; D'Amico et al., 2016).

Processed squid products may contain a single species or a mixture of pieces from different species in the same package. Highly processed products may involve blending multiple specimens and species into a paste that can be extruded into various forms.

DNA barcoding has increasingly been used as a tool to control traceability information and prevent seafood fraud (Filonzi et al., 2023). Sanger DNA sequencing is the gold standard for species authentication (Fernandes et al., 2020). However, this technique is typically suitable only for identifying products containing a single species. Processed products often involve multiple ingredients (species), making it challenging to use Sanger DNA sequencing for identifying of each ingredient (Klapper et al., 2023). To address this issue, several researchers have proposed using amplicon sequencing using High Throughput Parallel Sequencing (HTPS) instead of Sanger sequencing (Giusti, Armani, & Sotelo, 2017; Toxqui-Rodríguez, Naya-Català, Sitjà-Bobadilla, Piazzon, & Pérez-Sánchez, 2023).

The objective of this work was to determine the diversity of cephalopod species present in cephalopod seafood products, while noting that the methodology employed may also reveal the presence of other Metazoa. For that, we analysed the market in Vigo, one the most important cities of Galicia (Northwest of Spain), with one of the most important fishery port and fish market, not only in Spain but in the EU. Vigo has a population of about 300,000 (National Statistics Institute, 2023) and area of 11,000 ha.

The aim was to determine the presence of unexpected or undeclared cephalopod species in commercial products, in light of concerns about uncontrolled and unregulated cephalopod fisheries worldwide. We have also investigated the level of species mislabelling and evaluated the diversity of species in these squid products marketed in Spain, which have not been previously investigated. To achieve these goals, we applied DNA metabarcoding using previously validated DNA markers (Chapela et al., 2002) and high-throughput sequencing (Illumina MiSeq platform), which enables the detection of multiple species in mixed or highly processed samples.

2. Material and methods

2.1. Samples

Different types of cephalopod-based products were evaluated and analysed (Fig. 1), including:

a) squid rings both battered and non-battered),
b) cephalopod pieces (finger-shaped and cube-shaped), with or without batter,
c) formed products that simulate squid rings

Fig. 2 provides a graphical overview of the experimental workflow, encompassing market evaluation, sample preparation, DNA sequencing, and bioinformatic analysis.

A total of 13 supermarkets in Vigo (Spain) were visited to assess the variety of cephalopod products available. This market survey identified 86 products, primarily refrigerated and frozen items made from squid, with a smaller representation of cuttlefish. Canned products were excluded from the study. For each product, the following information was recorded: product name, type, category according to EC Regulation N° 1379/2013, declared ingredients, brand, and supermarket code (see Table S1). The visited supermarkets represented well the market of seafood products in Spain, with the 90% of the supermarkets operating at national level (Spain), and the 75% at regional level (Galicia). Additionally, in this work we sampled the 50% of the total retailers in Vigo.

Based on this initial market assessment, representative product types and brands were selected to reflect the diversity of processed squid products available in Spain. One common product type is the "ring," obtained by transversally slicing the squid mantle. These rings are marketed either as non-battered or as battered and pre-fried. Cephalopod pieces may also be battered or non-battered and shaped as fingers ("rabas"), cubes, or irregular forms. Additionally, we identified products shaped like squid rings and fingers but manufactured from a mixture of cephalopod mantle pieces combined with technological adjuvants and moulded into ring shapes and pieces with the shape of finger. These are referred to as "formed" products in this study.

Following product selection, samples were purchased from major supermarkets in Vigo. A total of 63 samples representing different brands and commercial denominations were collected for further analysis (Table S2). For each sample, comprehensive label information was recorded, including geographic origin of capture, fishing gear used, allergen declarations, and photographic documentation.

The analysed samples correspond to categories "c" and "i" of Annex I of EC Regulation N° 1379/2013 (EU, 2013), which defines the fishery products covered by the Common Market Organization. Category "c" (CN 0307) includes molluscs, whether shelled or not, live, fresh, chilled, frozen, dried, salted, or in brine. Category "i" (CN 1605) includes crustaceans, molluscs, and other aquatic invertebrates, prepared or preserved. Of the 63 samples, 21 (33%) belonged to category "c" and 42 (67%) to category "i".

All battered and formed products observed in the market were included in the analysis. For products with visible muscle structure, only a representative subset was analysed. The selected samples included products explicitly labelled as containing squid or those with commercial names commonly associated with cephalopods (e.g., "Aros a la romana").

Positive controls to validate species identification via amplicon sequencing and to minimize the risk of false positives were sourced from the IIM-CSIC mollusc tissue collection, developed over years of sampling cephalopod species (Table S3). Following Klapper et al. (2023), species representing less than 5% of the total assigned reads in a sample were considered non-significant, potentially resulting from cross-contamination during processing or analytical artefacts.

Fig. 1. Some types of samples analysed. A: non-battered squid rings, B: battered squid rings, C: formed squid rings, D: battered squid pieces (fingers) and E: non-battered squid pieces (cubes).

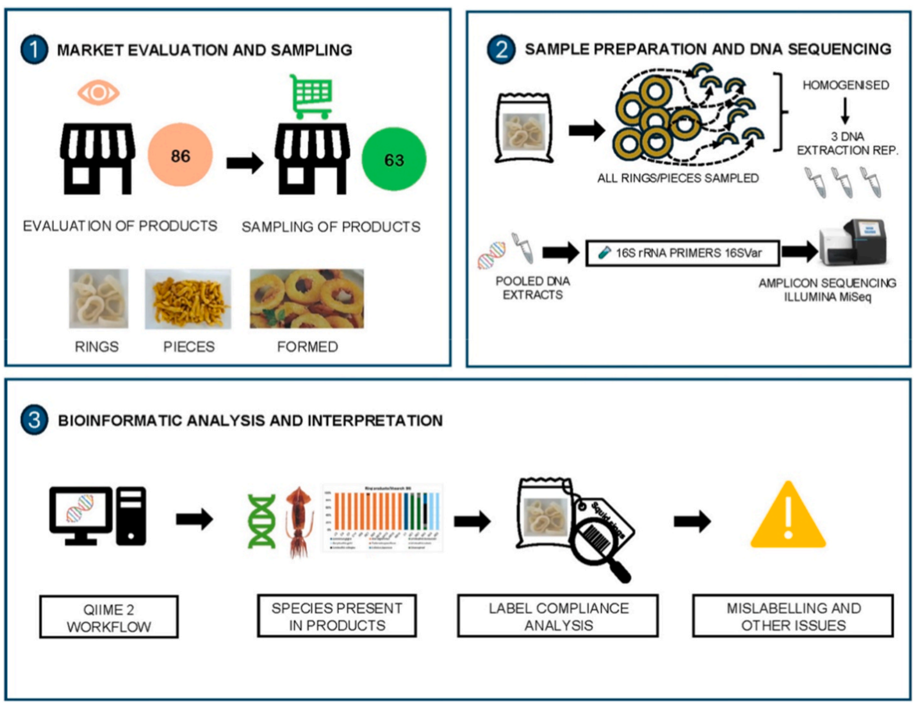


Fig. 2. Graphical representation of the experimental workflow applied in the cephalopod study. The workflow is divided into three main stages: (1) *Market evaluation and sampling*; (2) *Sample preparation and DNA sequencing*; and (3) *Bioinformatic analysis and interpretation*.

2.2. Sample preparation and DNA extraction

For the DNA analysis of squid products, a prior homogenization step was performed to capture all possible biological variability within each sample. To obtain a representative subsample from each product, one piece from each ring or portion present in the commercial package was taken. These pieces were homogenized using a domestic grinder (AD560120, Moulinex) until a uniform paste was obtained for each sample. Different species might be present within the same package, either as separate pieces of squid mantle, as in the case of ring or pieces products, or as a mixture of minced meat, as in the case of formed rings. In the case of battered products, the batter layer was removed before homogenizing the muscle tissue.

DNA was extracted from each homogenized product sample by triplicate, following the MPure system tissue DNA extraction kit protocol (MP Biomedicals, LLC) with some modifications. The method includes the following steps: digestion of 200 to 400 mg with 860 μL of a lysis buffer (1% SDS, 150 mM NaCl, 2 mM EDTA, 10 mM Tris-HCl pH 8), 100 μL of guanidium thiocyanate and 40 μL of proteinase K (20 mg/mL) at 56 °C. Extra proteinase K was added to each sample after 3-4 h and left overnight. Finally, samples were centrifuged, the supernatant transferred to the sample tubes included in the MPure kit and loaded with the reagents in the MPure-12 automated nucleic acid purification system (MP Biomedicals, LLC). The same procedure was followed for a control blank sample without tissue. The quality of the eluted DNA was analysed by UV-spectrometry using a Nanodrop spectrophotometer (ThermoFisher Scientific). DNA was quantified by fluorometry using a Qubit v3.0 fluorimeter and a Qubit dsDNA HS/BR assay kit (Thermo-Fisher Scientific). DNA concentration was normalized to 12.5 ng/μL.

2.3. Library preparation and amplicon sequencing using HTPS

For taxonomic assignment short fragment (164–228 bp) of the mitochondrial 16S rRNA gene was amplified using the following 16S rRNA primers 16SVar (Chapela et al., 2002). This region was selected because it provides sufficient interspecific variability for reliable species-level identification while producing short amplicons suitable for degraded DNA typical of processed seafood products.

Amplicon library preparation and sequencing were carried out at the Sequencing and Genotyping Unit of the Genomic Facility, University of the Basque Country (EHU). Libraries targeting the 16SVar marker were generated using primers 16SVar-F (GACGAGAAGACCCTAATGAGCTTT) and 16SVar-R (CAAATTACGCTGTTATCCCTATGG) (Chapela et al., 2002). Each primer included locus-specific sequences and Illumina overhang adapters for subsequent indexing: Forward overhang: 5′ TCGTCGGCAGCGTCAGATGTGTATAAGAGACAG-(locus-specific sequence); Reverse overhang: 5′ GTCTCGTGGGCTCGGAGATGTGTATAAGAGACAG-(locus-specific sequence). PCR amplification was performed using KAPA HiFi HotStart ReadyMix (Roche Kapa Biosystems) under the following conditions: initial denaturation at 95 °C for 3 min; 35 cycles of 95 °C for 40 s, 60 °C for 40 s, and 72 °C for 40 s; and a final extension at 72 °C for 7 min. Each 25 μl reaction contained 1.5 μl of each primer (10 μM). PCR products were assessed by electrophoresis and purified using magnetic beads (CleaNNA NGS kit). Indexing was performed with Illumina® DNA/RNA UD Indexes following the manufacturer's protocol. Indexed libraries were checked by electrophoresis (LabChip GX Touch HT, Revvity), purified, pooled, and quantified using Qubit. Sequencing was conducted on an Illumina MiSeq platform with a 150 bp paired-end protocol (MiSeq v2 chemistry). Libraries were loaded at 4 pM, and 15% PhiX was added to increase sequence diversity and improve run performance.

2.4. Bioinformatic analysis

Forward (F) and reverse (R) strand FASTAq files for each sample were provided by the HTPS sequencing service. Sequence quality was assessed using FASTQC (Andrews, 2010), and all sequences passed the Q20 quality threshold. The sequences were then imported into QIIME2 (Bolyen et al., 2019) in “Casava 1.8 demultiplexed paired-end” format using the plugin tools import. Sequences were subsequently denoised, dereplicated, and chimeras removed using the DADA2 plugin with the denoise-paired method (Callahan et al., 2016). After these initial steps, 88% of the sequences were recovered, with an average of 137,157 ± 42, 648 reads per sample.

Taxonomic assignment was performed using the *feature-classifier classify-consensus-vsearch* plugin in QIIME2, applying default parameters except for a minimum coverage threshold of 50% and identity thresholds of 97% and 99%. The query sequences were compared against a custom reference database that included 16S rRNA sequences from cephalopod species in our internal sequence bank, as well as 16S rRNA sequences downloaded from GenBank (July 2021) for the Metazoa taxonomic group (NCBI Taxonomy ID: 33208; 319,798 sequences). The database was curated using the RESCRIPt plugin (Robeson et al., 2021).

The VSearch classifier was selected over BLAST + after testing, due to its superior performance in handling insertions and deletions (indels), as it performs global alignments using the full length of the query sequence against the reference database for taxonomic assignment (QIIME2 documentation). Default parameters were used for the classifier, except for the minimum coverage threshold, which was set to 50%, and the identity thresholds, which were set to 97% and 99%.

Taxonomic composition was visualized using interactive bar plots generated via the QIIME2View interface. Relative abundance was calculated as the proportion of reads assigned to each taxon relative to the total number of reads per sample, including both assigned and unassigned reads. This approach provides a semi-quantitative estimate of the contribution of each species to the overall DNA content of the product and was used to infer the composition of ingredients. The methodology follows the approach described by Lorusso et al. (2024), which considers that the read count distribution reflects the relative representation of species in the sample, although it may be influenced by factors such as DNA extraction efficiency, primer bias, and amplification dynamics. Species percentages were calculated using Microsoft Excel.

Labelling was considered accurate when the declared species matched the dominant species identified by DNA sequencing, accounting for more than 95% of the reads. Conversely, mislabelling was defined as either the absence of the declared species among the dominant sequences (i.e., less than 95% of the reads), or the presence of undeclared mixtures of species.

3. Results

3.1. Characterisation of cephalopod products in Spanish market

The first step in our study was to gather information about different cephalopod products available in the markets, excluding canned products. A total of 86 items were recorded, encompassing various presentations: raw and battered rings (n = 25, 29.1%), finger-(n = 13, 15.1%) and cube-shaped (n = 28, 32.6%) pieces, and formed products (n = 20, 23.3%), those resembling squid rings but made from minced cephalopod or a mixture of cephalopod and fish.

The most frequently indicated species on product labels was the jumbo flying squid (*Dosidicus gigas*), appearing in over 50% of the items surveyed. The second most declared species was the Argentine shortfin squid (*Illex argentinus*), present in 17% of the samples (Fig. 3).

3.2. Squid samples analysed

The second step involved selecting samples for analysis from the list of observed samples. The 63 samples selected included all types of products observed in the market (Table S2).

In the Spanish market, various products declare squid as an ingredient, as this group of species is very popular in the Spanish gastronomy. Probably the most popular dishes consist in pieces of squids (rings or pieces) that are battered (with flour or a mixture of flour and egg) and fried in oil (Fig. 1).

The percentages of the analysed samples (Table 1) generally resembled the percentages observed in the visual analysis of the market, except for the formed samples, which were intensively sampled to detect undeclared mixtures of species. In this case, the formed samples represented 31.7% of the analysed samples. Of the analysed samples, 65% were battered, while 35% were non-battered. Some samples (5 out of 63) contained different species, such as products for preparing “paella” or “fish soup.”

The labels indicated that *Dosidicus gigas* was present in 50% of the analysed products, while *Loligo* genus was present in the labels of 19% of the samples (see Table S2).

3.3. Compliance of samples with labelling legislation

As mentioned earlier, 33% of the samples analysed belonged to the “c” category, which must comply with both EC 1379/2013 and EC1169/2011 (Table 2). In contrast, for “i” category products (67% of the samples analysed), the mandatory information only refers to compliance with EC1169/2011.

We analysed whether both types of products included the information required on labels according to Regulations EC1379/2013 and EC1169/2011, particularly the items listed in Table 2. For products in category “c) CN307”, most mandatory information was present in 100% of the samples. The commercial designation and scientific name of the species should be indicated according to the Spanish official commercial names list (Spanish Ministry of Agriculture, Fishing, and Food, 2023). However, some scientific names were used incorrectly; for example, *Loligo patagonicus* or *Doryteuthis patagonica* appeared instead of the approved name *Doryteuthis gahi* (A. d’Orbigny, 1835), which is the approved name. Furthermore, important consumer information, such as the origin, was present in only 38% of these products (2 products declared China, 3 India, 1 Morocco, 1 Argentina and 1 Spain). Additionally, the declaration of the allergen type, specifically the word “mollusc” in bold, was present in just 55% of these samples.

Regarding category “i) CN1605” (prepared products), the commercial designation of the species and its scientific name are not required; only the name of the food is mandatory. In this case, we observed a high variety of commercial names referring to essentially the same product. For instance, in the case of battered squid rings, names such as “chipiron,” “chipirones,” and “anillas a la romana” were found. The

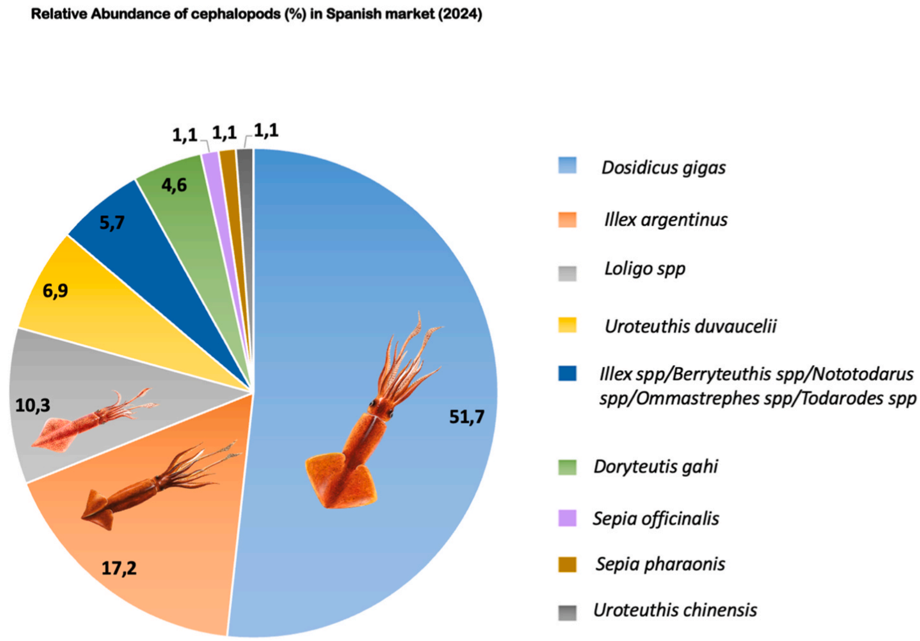


Fig. 3. Relative abundance (%) of species declared on the labels of the products observed in the visited markets.

Table 1
Total number of squid samples analysed for this work with the specification of the type of product (shape).

TYPE OF PRODUCT	NUMBER	%
RINGS (raw and battered)	17	27.0
PIECES (finger, raw and battered)	11	17.5
PIECES (cube, raw)	15	23.8
FORMED	20	31.7
TOTAL	**63**	

Table 2
Some of the Required label information for squid products according to EC 1379/2013 and EC1169/2011 (mandatory ✓, non-mandatory ☒, ✓*catch area is voluntary in i) CN 1605, ✓** is voluntary in both c) CN 307 and i) CN 1605).

Information category	c) CN 307	% Comp.	i) CN 1605	% Comp.
Name of the food (EC1169/2011)	☒	100	✓	100
Commercial designation of the species and its scientific name (EC 1379/2013)	✓	100	☒	NA
Category of fishing gear used in capture of fisheries (EC 1379/2013)	✓	100	☒	NA
Catch area/country and body of water (EC 1379/2013)	✓	100	✓*	5
Country of production (EC 1379/2013) Voluntary	✓**	38	✓**	0
Allergen declaration (EC1169/2011): indication of mollusc in bold	✓	55	✓	60

packaging photographs are essentially the same for these different names; however, the species can vary significantly (Fig. 1S).

The name, "chipiron," according to the approved commercial names in Spain (Spanish Ministry of Agriculture, Fishing, and Food, 2023), refers to any species of the genus *Loligo*, including *Loligo vulgaris*, which also has two other admitted commercial names in the Spanish list: "Calamar" (squid) or "Calamar Europeo" (European squid). In some regions of Spain, "chipiron" is also the accepted name for *Loligo vulgaris*. Therefore, the use of the same denomination for both the genus and a particular species could lead to consumer confusion, as they might expect *Loligo vulgaris* if the label states "chipiron." However, this does not correspond with the actual content of most products as determined by genetic identification.

The term "anillas" is always associated with battered squid rings in Spanish processed products, reminding consumers of the traditional batter mix of flour and egg prepared with *Loligo* spp. However, species from the Ommastrephidae family are often found in the ingredient list.

Another issue in that 40% of "i) CN1605" products do not include the word "mollusc" in the ingredient list; usually, only the species name is underlined or shown in bold. Some consumers may not recognize an unfamiliar species name as a mollusc, potentially failing to identify the product as allergenic.

3.4. *Species identification results*

16S rDNA variable region was selected because it provides sufficient interspecific variability for reliable species-level identification while producing short amplicons suitable for degraded DNA typical of processed seafood products. Previous studies have demonstrated the effectiveness of these primers for cephalopod identification using both Sanger sequencing (Chapela et al., 2002) and metabarcoding approaches (Giusti et al., 2017a, 2017b).

The sequencing results were adequate, with an average number of reads per sample of 155,351 and a coefficient of variation (CV) of 30%. After quality filter, denoising and chimaera removal, 88% of the sequences were available for further bioinformatic analysis. In all the cases, the sequence number per sample was sufficient for obtaining reliable identification results (Klapper et al., 2023). Amplicon length ranged between 164 and 228 bp (average 179 bp), which was expected since the selected DNA marker, 16S rDNA, exhibits length variation depending on the species (Chapela et al., 2002).

3.5. *Positive control species analysis*

DNA from IIM cephalopod tissue collection was used to evaluate the performance of the sequencing approach and bioinformatic analysis. Results showed that VSearch, using 99% level, was able to identify all positive control samples, except for *Illex illecebrosus* (A. Leseur, 1821) that is classified as *Illex argentinus,* and *Illex coindetii* (J.B. Verany, 1839) that is classified as *Illex* spp. (taxonomic level genus) (Table 3). There

Table 3
Identification of positive control samples using the taxonomy classifier VSearch with two identity thresholds: 97% and 99%. For each identified species, the relative abundance of reads, in percentage, is shown in brackets. [1,4]A. d'Orbigny, 1835, p. [2] S.S. Berry, 1911, p. [3] C. A. Lesueur, 1821, 1821; [5] C. Linnaeus, 1800; [6] Férussac *in* d'Orbigny, 1826; [7] C.G. Ehrenberg, 1831, p. [8] J. Steenstrup, 1880, p. [9] J. Steenstrup, 1880.

Sample	Declared Species	Identified species (VSearch_99%)	Identified species (VSearch_97%)
DGAH	*Doryteuthis gahi*[1]	*Doryteuthis gahi* (100%)	*Doryteuthis gahi* (100%)
DGIG	*Dosidicus gigas*	*Dosidicus gigas* (100%)	*Dosidicus gigas* (100%)
DOPA	*Doryteuthis opalescens*[2]	*Doryteuthis opalescens* (99.8%)	*Doryteuthis opalescens* (100%)
DPEA	*Doryteuthis pealeii*[3]	*Doryteuthis pealeii* (99.8%)	*Doryteuthis pealeii* (99.9%)
IARG	*Illex argentinus*	*Illex argentinus* (99.6%)	Cephalopoda (95.1%); *Illex spp* (4.8%)
ICOI	*Illex coindetii*	*Illex spp* (99.5%)	*Illex spp* (100%)
IILL	*Illex illecebrosus*	*Illex argentinus* (99.9%)	Cephalopoda (95.2%); *Illex spp* (4.7%)
LVUL	*Loligo vulgaris*	Cephalopoda (99.2%)	*Loligo vulgaris* (100%)
SBER	*Sepia bertheloti*[4]	*Sepia bertheloti* (100%)	*Sepia bertheloti* (100%)
SOFF	*Sepia officinalis*[5]	*Sepia officinalis* (100%)	*Sepia officinalis* (100%)
SORB	*Sepia orbignyana*[6]	*Sepia orbignyana* (98.4%)	*Sepia orbignyana* (98.6%)
SPHA	*Sepia pharaonis*[7]	*Sepia pharaonis* (95.8%)	*Sepia pharaonis* (100%)
TPAC	*Todarodes pacificus*[8]	*Todarodes pacificus* (99.5%)	*Todarodes pacificus* (100%)
UDUV	*Urotheutis duvaucelii*[9]	*Urotheutis duvaucelii* (100%)	*Urotheutis duvaucelii* (100%)

were also problems with *Loligo vulgaris*, that was classified as Cephalopoda (taxonomic level Class) using 99% level. Lowering down the level of identity threshold to 97% solved the problem of *Loligo vulgaris* (Table 3). Not in the case of the species of the genus *Illex*, since lowering the identity threshold did not improve the results and the two species could not be differentiated (Table 3).

3.6. Commercial products

In total, 88.9% of the commercial products analysed showed that the species detected by genetic analysis was the one indicated in the label. Mislabelling occurred in 11.1% of the products, where the declared and detected species did not correspond. Additionally, 12.7% of the samples contained a mixture of species (considering another species present when more than 5% was detected by metabarcoding). In 87.30% of the products analysed, one species represented most of the reads (>99%), indicating that these products contained only one species.

The species level was achieved in most samples, demonstrating that both the genetic marker and the bioinformatic analysis were adequate and reliable for detecting the cephalopod species present in commercial products.

The labels of ring products fall into two categories:

a) The species is mentioned in the food name, such as in the case of non-battered rings labelled "Anillas the pota" and "chipiron", which are the Spanish commercial names for the species belonging to Ommastrephidae and *Loligo* genus, respectively.
b) The species is not mentioned in the food name, as in the case of battered rings, instead, the label shows "Anillas a la Romana", which refers more to the cooking technique than the cephalopod species. In some of these products, the commercial name of the species is present in a smaller font size, close to the food name.

Fig. 4A shows the percentage of reads for each of the main species identified by VSearch (99% of identity threshold) in each of the ring products analysed. The labels of non-battered rings (N = 5) indicated that species used were mostly *Illex argentinus* (80%) and *Dosidicus gigas* (20%, C1), and none of these samples were mislabelled (Table S2).

For the battered rings (N = 12), five products (38%) were of the "enharinado" type, meaning that only flour was used for coating. These samples were labelled with the word "chipirón" or "chipirones" (RE1–RE5). The products contained species from the family Loliginidae, although the currently accepted genus name according to World Register of Marine Species (WoRMS, n. d.) is *Uroteuthis*, not *Loligo*. In three of these products (RE1, RE2, and R3), a mixture of two to four species was detected, while the other two products (RE4 and RE5) contained only one species, *Doryteuthis gahi* (Fig. 4A–Table S2).

According to the Spanish Ministry of Agriculture, Fisheries and Food (2023) legislation, the label "Loligo spp." indicates that any species of the genus *Loligo* may be present, with *Loligo vulgaris* being the most valued. However, in that document, species now classified within Uroteuthis genus are still referred to as *Loligo*. Therefore, the three products (RE1, RE2, and R3) were considered correctly labelled. In contrast, the two products (RE4 and RE5) containing *Doryteuthis gahi* were mislabelled, as the correct commercial name should be "Indian squid" and not just "squid".

In the remaining battered products (N = 7), *Illex argentinus* was detected in 100% of the samples analysed (Fig. 4A).

The overall mislabelling rate for ring-type products was 11.76% (2 out of 17 ring products).

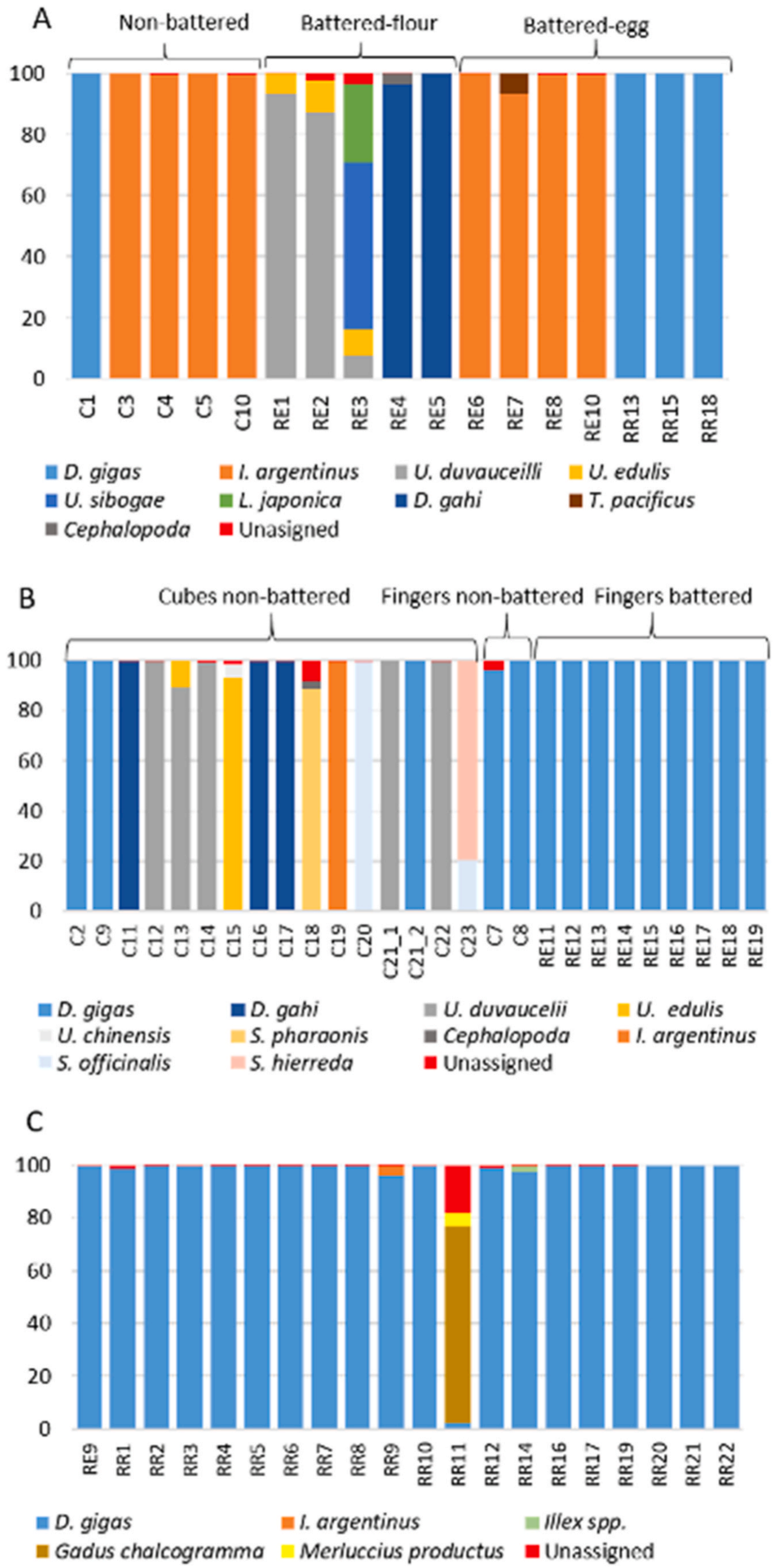
The pieces consisted of 26 samples, which contained two types of shapes: cubes and fingers of cephalopod tissues. Additionally, these pieces could be either non-battered or battered, resulting in type "c" and type "i" products. The variety of commercial names regarding species was higher than in the other products. We observed up to eight different commercial names for cephalopods; however, the most abundant was Jumbo Flying Squid (*Dosidicus gigas*), which accounted for 50% of the samples termed as pieces. This species was present in all the battered samples, while the non-battered samples were more diverse in terms of species.

Fig. 4B and Table S2 show the percentage of reads for each of the main species identified by VSearch (99% identity threshold) in each product. Most of the samples contained the species indicated on the product label, although there were some exceptions. Product C13 was labelled as chopped Indian squid, and the ingredients indicated the species as *Loligo duvaucelli* (an outdated name). In fact, 90% of the reads were assigned to *Uroteuthis duvaucelli*, which is not a mislabelling case since the commercial name was correct, although there were 10% of the reads which were identified as *Uroteuthis edulis*. Product C15 was labelled as Oriental squid, this commercial name corresponds to the species *Uroteuthis chinensis* (J.E. Gray, 1849), however, 93% of the reads were *Uroteuthis edulis* and only 5% were *Uroteuthis chinensis*, therefore we considered it a mislabelling case. Finally, product C23 was labelled as "Sepia" (in Spanish), which should correspond to the species *Sepia officinalis*. However, the sample contained a mixture of *Sepia officinalis* (20.6% of the reads) and *Sepia hierredda* (M. Rang, 1837) (79.3%), indicating a mislabelling case.

Considering the two cases of mislabelling, the rate for this category of products was of 7.7% (2 out of 26 products).

In the case of formed products (N = 20), we have found that commercial names are very diverse, and the term "ring" is usually avoided. Fig. 4C and Table S2 show the percentage of reads for each of the main species identified by VSearch (99% of identity threshold) in these products. All these samples fall in the category i) CN 1605. All but one contained only *Dosidicus gigas*. That sample, RR11, was made from fish, as indicated in the ingredient list as "fish protein". The sequencing results showed the presence of two fish species of the order Gadiformes in RR11: *Gadus chalcogramma* (74.6% of the reads) and *Merluccius productus* (5.3% of the reads). Additionally, 2% of the reads were from *D. gigas*, which was indicated by the company with the "product may contain molluscs" on the label.

Two samples (RR12 and RR16) were labelled as Argentine shortfin squid but actually contained *Dosidicus gigas*. Besides, sample RR20 was



(caption on next page)

Fig. 4. Species identification in cephalopod-based products using the VSearch classifier (99% similarity threshold).
(A) Ring-shaped products: percentage of reads assigned to each species. Products are grouped as non-battered, battered with flour, and battered with egg. (B) Pieces products: percentage of reads assigned to each species. Groups include cubes (non-battered), fingers (non-battered), and fingers (battered). (C) Formed products: percentage of reads assigned to each species.

labelled as squid (Loligo spp.) but *D. gigas* was detected instead. The resulting mislabelling rate for this category was of 15% (3 out of 20 products).

4. Discussion

Although historical and cultural aspects have influenced globally distributed and locally exploited cephalopod fisheries, the consumption of cephalopods and, consequently, their fisheries have experienced a global increase in the last 50 years (Ainsworth et al., 2022). These changes in consumption have promoted the search for new fishing areas and the global trade of new species of this type of seafood product.

Spain is one of the eight countries that dominate the global trade of cephalopods, as reflected by a significant dedicated fishery and transformation industries, which produce seafood products for both domestic and foreign markets (Ospina-Alvarez et al., 2022). In fact, Spain is one of the major importers and exporters of seafood products in the world (FAO, 2024), with significant domestic consumption of molluscs, amounting to 41,000 tons in 2023 (Spanish Ministry of AgricultureFishingand Food, 2024).

Cephalopods from national fisheries are usually marketed fresh and unprocessed in local markets and supermarkets. However, frozen cephalopods (both unprocessed and processed) are increasingly becoming popular, not only in Spain but also in other European countries (Ospina-Alvarez et al., 2022). They are sold as convenience seafood preferred by consumers who cannot afford the time to buy and cook fresh cephalopods or the price often associated with them.

4.1. Globalization and sustainability of cephalopod fisheries

It is widely accepted that the processing and marketing of seafood products have been globalized in the last decades (Kelling et al., 2023). Companies producing processed cephalopods must source the raw material from distant waters, either by their own high seas fleet or by purchasing the raw material in international markets. In some cases, these companies use a vertical integration approach and maintain a high level of interconnections and networks around the world. These companies considered "keystone actors" due to their size and revenues, may significantly influence the sustainability of the marine ecosystems they exploit (Österblom et al., 2015).

We have found that the presence of cephalopod species in the products available in the Spanish market reflects the importance of these species in the global figures of cephalopod captures (recorded landings) reported in SOFIA 2024; FAO, 2024). The highest landings in 2022 were of *Dosidicus gigas* with 1076 thousand tons and *Illex argentinus* with 396 thousand tons, while data for other species of Loliginidae and Ommastrephidae are aggregated and amounted to 877 thousand tons.

Although cephalopods are becoming an increasingly important type of seafood in global trade (FAO, 2024), there is strong concern about the status of their stocks, some of which are poorly known and therefore at risk of inadequate management practices (Arkhipkin et al., 2021). We detected that in 54% of the products analysed in the Spanish market, Jumbo flying squid (*D. gigas*) was present, while Argentine squid (*I. argentinus*) was present in 19% of the products. Both belong to the Ommastrephidae family; thus, this family was present in 73% of the products analysed in this work. Species of the Loliginidae family were only present in 22% of the products, and European squid (*L. vulgaris*) was not detected in any of the products analysed. This indicates that the Spanish industry is obtaining raw materials mainly from the Pacific Ocean (*D. gigas*) and the Southwest Atlantic (*I. argentinus*). In the case of *D. gigas*, the species can be targeted by fleets of different countries (Shi et al., 2020), with little knowledge about the practices employed (i.e., type of fishing gear).

In our study, *D. gigas* appeared in most of the products that fall into category "i," which means they do not have the obligation to indicate the fishing gear category or the geographic origin on the label. In other cases, i.e., products within category "c," the information provided is only generic, giving more than one fishing gear category, such as "hooks and lines" and/or "trawls," or more than one origin, such as FAO 51 and 52, or FAO 61 and 71. Consumers are therefore misinformed about the sustainability of these products and are not provided with important information to make informed purchasing choices (Lorusso et al., 2024; Morris et al., 2024).

4.2. Commercial names and species diversity

Another issue that we have found is related to commercial names. In a group of products that are rather similar and include a particular group of species, there is a significant diversity of commercial names and, in some products, even of species. It is particularly striking the number of names used for formed products made of pieces of cephalopods. In 19 products, we observed 9 different commercial names, while most of them contained just *D. gigas*. This can be explained by the circumstantial presence of that species as a raw material for these products, probably due to the abundance of that species in previous years. However, these commercial names do not link with any particular species, allowing the raw material to be changed depending on availability and prices in the global market without the need to change commercial names.

We have also found the presence of different Loliginidae species in the analysed products, such as *Uroteuthis sibogae* (W. Adam, 1954), *Loliolus japonica* (Hoyle, 1885), *Uroteuthis edulis* (W.E. Hoyle, 1885), and *Uroteuthis duvaucelii* (A. d'Orbigny, 1835), originating from distant fisheries but marketed under the same commercial name "chipiron" or "calamar" in the Spanish market. Another issue is the use, in some of these cases of the plural "chipirones," which is not included in current legislation; therefore, some products were misusing this designation.

4.3. Mislabelling of squid products

In this study, we have used primers to amplify a shorter fragment of the universal 16S rDNA marker. The reason for this is double, in one hand we have used just the variable region of the larger fragment (Chapela et al., 2002), and in the other this fragment is particularly advantageous for next-generation sequencing (NGS) platforms such as Illumina, which require relatively small insert sizes for optimal performance. Several recent metabarcoding studies have adopted these primers for seafood authentication (Andronache et al., 2025; Mottola et al., 2024). While COI (~650 bp) is the standard for DNA barcoding, its length and primer universality issues limit amplification success in thermally processed products where DNA degradation is common. The chosen 16S region balances amplification success with taxonomic resolution, making it appropriate for the objectives of this study.

Amplicon sequencing using HTPS is an emerging approach for identifying multiple species and ingredients in processed products (Lorusso et al., 2024). Despite the need for further development, particularly in streamlining bioinformatic pipelines and improving database curation, this methodology shows strong potential for detecting undeclared species and allergens (Giusti, Armani, & Sotelo, 2017). Accurate taxonomic assignment relies on the integrity of genetic data, yet previous studies have reported inconsistencies in public databases, even those requiring complete specimen and geographic origin information such as BOL (Cheng et al., 2023). Additionally, incomplete reference datasets remain a major limitation, as many species are either unknown or have not been genotyped (Teixeira et al., 2025).

However, we found some problems with the identification of the genus *Illex* using the amplicon sequencing using HTPS approach, which are more related to their taxonomical status rather than the technique itself. In fact, the identification of the species *I. coindetii*, *I. illecebrosus*, and *I. argentinus* is not simple using morphometry, and several variables should be used to differentiate them (Martinez et al., 2002). This problem has impacted the genetic identification of the species of the genus *Illex* using the COI DNA marker, probably due to previous morphological misidentification issues of the samples used to obtain the genetic data (Carlini et al., 2006). Besides, Yokobori et al., 2004, have reported duplication events in some mtDNA genes in some cephalopods (*Octopus vulgaris*, *Todarodes pacificus* and *Watasenia scintillans*), such as COI that might jeopardize the identification of species using this marker. Additionally, some authors have described that the identification of some cephalopod species using 16S rRNA is not possible due to the very low interspecific variability among them (Wakabayashi et al., 2012). Paiva et al. (2024) have also pointed out the difficulties of identifying some cryptic cephalopod species, like the *Illex* sp. mentioned above, due to few informative morphological taxonomical characters.

The overall species mislabelling rate in our study (11.1%) was lower than that reported in other studies. For instance, Pardo et al. (2018) found a 60% mislabelling rate for squid in mass-catering establishments across four EU countries, although their analysis was based on only five squid samples. Giusti et al. (2023), in a meta-analysis of the Italian seafood market, reported mislabelling rates of 42.2% for *Loligo vulgaris* and 26.1% for *Sepia officinalis*, both significantly higher than the rate observed in our study. Similarly, Giagkazoglou et al. (2024) reported an average mislabelling rate of 40% for cephalopod products in Greece, which increased to 67% in fresh products and 23% for frozen products.

In our study, mislabelling rates differed significantly by product type: rings showed the highest rate (29.4%), mainly due to the incorrect use of the commercial name “chipirón”; pieces had a rate of 7.7% and formed products 10%. Part of this issue can be attributed to the Spanish list of commercial names, which is confusing and ambiguous, particularly for highly valued cephalopod species such as *L. vulgaris*. This situation is similar to findings in Canada, where ambiguous commercial names contributed to high mislabelling rates (Morris et al., 2024). Moreover, in some countries, such as China, species names are not mandatory for processed squid products, and the commercial designation is simply “squid” (Shi et al., 2020). In that case, the mislabelling rate was 0%, because all three species identified in dried squid products (*Dosidicus gigas*, *Illex argentinus*, *Todarodes pacificus*) are commercially considered squid. Likewise, Willette and Joaquin (2026) found no mislabelling (0%) in squid products in Los Angeles (CA, USA), even though they identified ten different squid species, all of which can legally be labelled as “squid” under US FDA guidelines. These differences highlight that mislabelling rates can vary depending on product type (mainly due to differences in the level of specificity required for labelling, with highly processed products often requiring less detail), as well as country and year.

4.4. Mislabelling and IUU fisheries

Mislabelling can result from unintended errors but also to hide illegal practices. It is suggested that fisheries in the Indian Ocean are suffering from a rampant increase in unregulated squid fisheries (830% increase). The lack of regulations in these areas has led to unsustainable squid production and ecological impacts on the ecosystem (World Wildlife Fund [WWF], 2020; Arkhipkin et al., 2023). A significant portion of the squid caught by these unregulated fisheries is transhipped and sent to other countries, where they can enter the global supply chain. Since Spain is one of the major importers of squid, both for domestic consumers and the seafood processing industry, which also exports these products, it is possible that some of the marketed products we have analysed might contain cephalopods originating from these unregulated fisheries. This strongly supports the need to include and control, as much as possible, the information in the labels of category “i” products, including species, geographic origin and fishing gear.

4.5. Mislabelling and consumers health

Regarding other categories of information, such as the need to indicate the presence of allergens, in this case, mollusc, we observed that in 41% of the analysed products, there was no indication of the word mollusc on the label. In some of them, just the commercial name of the species was in bold or underlined. This leaves the sensitive consumer responsible for knowing that the species indicated on the label is a mollusc and therefore a potential allergen for them.

5. Conclusions

Ensuring proper traceability and accurate labelling is fundamental for consumer protection, market transparency, and the sustainable management of marine cephalopod resources. Our study demonstrates that current practices for processed squid products (CN 1605) often fall short of these objectives. We identified critical gaps in essential information, including the geographic origin of raw materials, the presence of mixed species, incomplete allergen declarations, and the use of overly generic or ambiguous commercial names. These shortcomings not only mislead consumers but also may obscure the sustainability status of fisheries and hinder informed purchasing decisions.

The detection of species mixtures and mislabelling, although lower than in some previous studies, highlights the complexity of global seafood supply chains and the limitations of existing regulatory frameworks. In particular, the absence of mandatory origin and gear information for processed products prevents consumers from assessing the environmental impact of their choices and creates opportunities for products derived from unregulated or IUU fisheries to enter the market. This situation undermines efforts to promote responsible consumption and fair trade.

Our findings also underscore the importance of adopting advanced molecular tools, such as amplicon sequencing using HTPS, to monitor species composition in highly processed products. While this technology requires further refinement, especially in bioinformatic pipelines and reference database curation, it offers a powerful approach to detect undeclared species and allergens, thereby supporting compliance and enforcement.

Strengthening labelling regulations to ensure complete and precise information, i.e. by covering species identity, origin, and allergen declarations, is imperative. Such measures would enhance consumer trust, improve traceability, and contribute to the sustainability of cephalopod fisheries. Ultimately, transparent labelling is not merely a regulatory requirement but a cornerstone of ethical seafood trade and informed consumer choice.

CRediT authorship contribution statement

Carmen G. Sotelo: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Ana Sanchez:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Begoña Correa:** Writing – review & editing, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Marta Perez Testa:** Writing – review & editing, Methodology, Formal analysis, Data curation. **Ricardo I. Perez-Martín:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Authors acknowledge the bioinformatic support provided by Marta M. Colmenero (UCM, Madrid) and thank the support of this work by contract Number CSIC BDC 20238142.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foodcont.2026.112028.

Data availability

Data will be made available on request.

References

Adam, W. (1954). Cephalopoda. Partie III. IV. Cephalopodes a l'exclusion des genres *Sepia, Sepiella* et *Sepioteuthis*. Siboga Expedition. *The Monograph, 55*(c), 123–193.
Ainsworth, G. B., Pita, P., Garcia-Rodrigues, J., Pita, C., Roumbedakis, K., Fonseca, T., Castelo, D., Longo, C., Power, A. M., Pierce, G. J., & Villasante, S. (2022). Disentangling global market drivers for cephalopods to foster transformations towards sustainable seafood systems. *People and Nature, 5*, 508–528. https://doi.org/10.1002/pan3.10442
Andrews, S. (2010). FastQC: A quality control tool for high throughput sequence data. http://www.bioinformatics.babraham.ac.uk/projects/fastqc/.
Andronache, J., Cichna-Markl, M., Dobrovolny, S., & Hochegger, R. (2025). Development of a DNA metabarcoding method for the identification of crustaceans (Malacostraca) and cephalopods (Coleoidea) in processed foods. *Foods, 14*(9), 1549. https://doi.org/10.3390/foods14091549
Arkhipkin, A. I., Hendrickson, L. C., Payá, I., Pierce, G. J., Roa-Ureta, R. H., Robin, J. P., & Winter, A. (2021). Stock assessment and management of cephalopods: Advances and challenges for short-lived fishery resources. *ICES Journal of Marine Science*. https://doi.org/10.1093/icesjms/fsaa038, 78(2), 714–730.
Arkhipkin, A. I., Nigmatullin, C. M., Parkyn, D. C., Winter, A., & Csirke, J. (2023). High seas fisheries: The achilles' heel of major straddling squid resources. *Reviews in Fish Biology and Fisheries, 33*(2), 453–474. https://doi.org/10.1007/s11160-022-09733-8
Barrett, C. J., Barry, P., MacLeod, E., Stott, S., Vieira, R., & Laptikhovsky, V. (2022). The importance of cephalopods in the diet of fish on the northwest European shelf. *ICES Journal of Marine Science, 79*, 1675–1686. https://doi.org/10.1093/icesjms/fsac086
Berry, S. S. (1911). Preliminary notices of some new Pacific cephalopods. *Proceedings of the United States National Museum, 40*(1838), 589–592. https://doi.org/10.5479/si.00963801.1838.589
Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J, … Caporaso, J. G. (2019). Reproducible, interactive, scalable and extensible microbiome data science using Qiime2. *Nature Biotechnology, 37*, 852–857. https://doi.org/10.1038/s41587-019-0209-9
Borit, M., & Olsen, P. (2020). *Beyond regulatory compliance. Seafood traceability benefits and success cases (FAO fisheries and aquaculture circular no. 1197)*. FAO. https://doi.org/10.4060/ca9550en
Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016). DADA2: High-resolution sample inference from illumina amplicon data. *Nature Methods, 13*, 581–583. https://doi.org/10.1038/nmeth.3869
Carlini, D. B., Kunkle, L. K., & Vecchione, M. (2006). A molecular systematic evaluation of the squid genus illex (Cephalopoda: Ommastrephidae) in the North Atlantic Ocean and Mediterranean Sea. *Molecular Phylogenetics and Evolution, 41*(2), 496–502. https://doi.org/10.1016/j.ympev.2006.05.011
Castellanos, Z. J. A. de (1960). Una nueva especie de calamar Argentino, Ommastrephes argentinus sp. *Nov. (Mollusca, Cephalopoda). Neotropica, 6*(20), 55–58.
Chapela, M. J., Sotelo, C. G., Calo-Mata, P., Pérez-Martín, R. I., Rehbein, H., Hold, G. L., Quinteiro, J., Rey-Méndez, M., Rosa, C., & Santos, A. T. (2002). Identification of cephalopod species (Ommastrephidae and Loliginidae) in seafood products by forensically informative nucleotide sequencing (FINS). *Journal of Food Science, 67*(5), 1672–1676. https://doi.org/10.1111/j.1365-2621.2002.tb08703.x
Cheng, Z., Li, Q., Deng, J., Liu, Q., & Huang, X. (2023). The devil is in the details: Problems in DNA barcoding practices indicated by systematic evaluation of insect barcodes. *Frontiers in Ecology and Evolution, 11*, Article 1149839. https://doi.org/10.3389/fevo.2023.1149839
D'Amico, P., Armani, A., Gianfaldoni, D., & Guidi, A. (2016). New provisions for the labelling of fishery and aquaculture products: Difficulties in the implementation of regulation (EU)n.1379/2013. *Marine Policy, 71*, 147–156. https://doi.org/10.1016/j.marpol.2016.05.026
De la Chesnais, T., Fulton, E. A., Tracey, S. R., & Pecl, G. T. (2019). The ecological role of cephalopods and their representation in ecosystem models. *Reviews in Fish Biology and Fisheries, 29*(2), 313–334. https://doi.org/10.1007/s11160-019-09554-2
Ehrenberg, C. G. (1831). Cephalopoda in mare rubro viventia. In P. C. Hemprich, & C. G. Ehrenberg (Eds.), *Symbolae Physicae, seu Icones et Descriptiones Corporum Naturalium Novorium aut Minus Cognitorum. quae ex itineribus per Libyan Aegyptum Nubiam Dongalan Siriam Arabian et Habessiniam* (Vol. 4, p. 6). Pars Zoologica.. unnumbered pages.
European Market Observatory for Fisheries and Aquaculture Products. (2025). *EUMOFA data* https://eumofa.eu/data.
European Union. (2011). Regulation (EU) no 1169/2011 of the european parliament and of the council of 25 October 2011 on the provision of food information to consumers. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32011R1169.
European Union. (2013). Regulation (EU) no 1379/2013 of the european parliament and of the council of 11 December 2013 on the common organization of the markets in fishery and aquaculture products. https://eur-lex.europa.eu/legal-content/EN/TXT/?uri=CELEX:32013R1379.
FAO. (2024). The state of world fisheries and aquaculture 2024: Blue transformation in action. https://openknowledge.fao.org/server/api/core/bitstreams/f985caed-cc7a-457e-8107-7ce16c6ef209/content.
FAO GLOBEFISH Highlights. (2023). *International markets for fisheries and aquaculture products*. Rome: GLOBEFISH Highlights. https://doi.org/10.4060/cc7781en. Second issue 2023, with January–December 2022 Statistics.
Fernandes, T. J. R., Amaral, J. S., & Mafra, I. (2020). DNA barcode markers applied to seafood authentication: An updated review. *Critical Reviews in Food Science and Nutrition, 61*(22), 3904–3935. https://doi.org/10.1080/10408398.2020.1811200
Filonzi, L., Ardenghi, A., Rontani, P. M., Voccia, A., Ferrari, C., Papa, R., Bellin, N., & Nonnis Marzano, F. (2023). Mole cular barcoding: A tool to guarantee correct seafood labelling and quality and preserve the conservation of endangered species. *Foods, 12*, 2420. https://doi.org/10.3390/foods12122420
Giagkazoglou, Z., Loukovitis, D., Gubili, C., Chatziplis, D., Symeonidis, A., & Imsiridou, A. (2024). Untangling the cephalopod market: Authentication of seafood products in Greece with DNA-Barcoding. *Food Control, 163*. https://doi.org/10.1016/j.foodcont.2024.110523. Article 110523.
Giusti, A., Armani, A., & Sotelo, C. G. (2017). Advances in the analysis of complex food matrices: Species identification in surimi-based products using next generation sequencing technologies. *PLoS One, 12*(10), Article e0185586. https://doi.org/10.1371/journal.pone.0185586
Giusti, A., Mallogi, C., Tinacci, L., Nucera, D., & Armani, A. (2023). Mislabelling in seafood products sold on the Italian market: A systematic review and meta-analysis. *Food Control, 145*. https://doi.org/10.1016/j.foodcont.2022.109395. Article 109395.
Giusti, A., Tinacci, L., Sotelo, C. G., Marchetti, M., Guidi, A., Zheng, W., & Armani, A. (2017). Seafood identification in multispecies products: Assessment of 16S rRNA, cytb, and COI universal primers' efficiency as a preliminary analytical step for setting up metabarcoding next-generation sequencing techniques. *Journal of Agricultural and Food Chemistry, 65*(13), 2660–2670. https://doi.org/10.1021/acs.jafc.6b05641
Gleadall, I. G., Moustahfid, H., Sauer, W. H. H., Ababouch, L., Arkhipkin, A. I., … Tadanori, T. (2024). Towards global traceability for sustainable cephalopod seafood. *Marine Biology, 171*(44). https://doi.org/10.1007/s00227-023-04300-6
Gray, J. E. (1849). *C"atalogue of the Mollusca in the Collection of the British Museum. Part I. Cephalopoda Artepedia* (pp. 1–164). Printed by order of the Trustees of the British Museum, London.
Helyar, S. J., Lloyd, H. A. D., De Bruyn, M., Leake, J., Bennett, N., & Carvalho, G. R. (2014). Fish product mislabelling: Failings of traceability in the production chain and implications for illegal unreported and unregulated (IUU) fishing. *PLoS One, 9*(6), Article e98691. https://doi.org/10.1371/journal.pone.0098691
Hoyle, W. E. (1885). Diagnoses of new species of Cephalopoda collected during the Cruise H.M.S. 'Challenger'. Part II. The Decapoda. *Annals and Magazine of Natural History. Series, 5*(16), 181–203.
Hunsicker, M. E., Essington, T. E., Watson, R., & Sumaila, U. R. (2010). The contribution of cephalopods to global marine fisheries: Can we have our squid and eat them too? *Fish and Fisheries, 11*, 421–438. https://doi.org/10.1111/j.1467-2979.2010.00369.x
Kelling, I., Carrigan, M., & Johnson, A. F. (2023). Transforming the seafood supply system: Challenges and strategies for resilience. *Food Security, 15*(6), 1585–1591. https://doi.org/10.1007/s12571-023-01400-5
Klapper, R., Velasco, A., Döring, M., Schröder, U., Sotelo, C. G., Brinks, E., & Muñoz-Colmenero, M. (2023). A next-generation sequencing approach for the detection of mixed species in canned tuna. *Food Chemistry X, 17*. https://doi.org/10.1016/j.fochx.2023.100560. Article 100560.
Kroetz, K., Luquec, G. M., Gephartd, J. A., Jardinee, S. L., Leeb, S. L., Chicojay Moore, K., Cole, C., Steinkruger, A., & Donlanc, C. J. (2020). Consequences of seafood mislabeling for marine populations and fisheries management. *Proceedings of the National Academy of Sciences, 117*, 30318–30323. https://doi.org/10.1073/pnas.2003741117
Lamarck, J. B. (1800). Extrait d'un mémoire sur le genre de la Séche, du Calmar et Poulpe, vulgairement nommés, Polypes de Mer. *Bulletin des Sciences, par la Société Philomatique de Paris, 2*(5), 129–131.
Lesueur, C. A. (1821). Descriptions of several new species of cuttlefish. *Journal of the Academy of Natural Sciences of Philadelphia, 2*(1), 86–101.
Linnaeus, C. (1800). *Systema Naturae* (10th ed.). Laurentius Salvius.
Lishchenko, F., Perales-Raya, C., Barrett, C., Oesterwind, D., Power, A. M., Larivain, A., … Pierce, G. J. (2021). A review of recent studies on the life history and ecology of European cephalopods with emphasis on species with the greatest commercial

fishery and culture potential. *Fisheries Research, 236*. https://doi.org/10.1016/j.fishres.2020.105847. Article 105847.

Lorusso, L., Shum, P., Piredda, R., Mottola, A., Maiello, G., Cartledge, E. L., & Mariani, S. (2024). Mismanagement and poor transparency in the European processed seafood supply revealed by DNA metabarcoding. *Food Research International, 194*. https://doi.org/10.1016/j.foodres.2024.114901. Article 114901.

Martinez, P., Sanjuan, A., & Guerra, A. (2002). Identification of *Illex coindetii, I. illecebrosus* and *I. argentinus* (Cephalopoda: Ommastrephidae) throughout the Atlantic Ocean; by body and beak characters. *Marine Biology, 141*, 131–143. https://doi.org/10.1007/s00227-002-0796-7

Morris, M. R. J., Summers, M. M., Kwan, M., Mee, J. A., & Rogers, S. M. (2024). Mislabelled and ambiguous market names in invertebrate and finfish seafood conceal species of conservation concern in Calgary, Alberta, Canada. *PeerJ*. https://doi.org/10.7717/peerj.18113. Article 12:e18113.

Mottola, A., Piredda, R., Lorusso, L., Ranieri, L., Intermite, C., Barresi, C., Galli, C., & Di Pinto, A. (2024). Decoding seafood: Multi-marker metabarcoding for authenticating processed seafood. *Foods, 13*(15), 2382. https://doi.org/10.3390/foods13152382

National Statistics Institute. (2023). Nomenclátor: Población del padrón continuo por unidad poblacional a 1 de enero. https://www.ine.es/nomen2/index.do?accion=busquedaAvanzada&entidad_amb=no&codProv=36&codMuni=57&codEC=0&codES=0&codNUC=0&denominacion_op=like&denominacion_txt=&L=0.

Orbigny, A. d (1826). Tableau méthodique de la classe de Céphalopodes précédé d'une Introduction, par M. de Férussac. *Annales des Sciences Naturelles. Séries, 1*(7), 95–169.

Orbigny, A. d (1835). Tome premier. Texte. In A. E. de Férussac, & A. d'Orbigny (Eds.), *Histoire Naturelle Générale et Particulière Céphalopodes Acétabuliferes Vivants et Fossiles*. J. B. Balliere.

Ospina-Alvarez, A., de Juan, S., Pita, P., Ainsworth, G. B., Matos, F. L., Pita, C., & Villasante, S. (2022). A network analysis of global cephalopod trade. *Scientific Reports-Nature, 12*. https://doi.org/10.1038/s41598-021-03777-9. Article 322.

Österblom, H., Jouffray, J. B., Folke, C., Crona, B., Troell, M., Merrie, A., & Rockström, J. (2015). Transnational corporations as 'keystone actors' in marine ecosystems. *PLoS One, 10*(5), Article e0127533. https://doi.org/10.1371/journal.pone.0127533

Paiva, B. L., Rodrigues, A. E. S., Almeida, I. O. D. F., Silva, K. D. F., Haimovici, M., Markaida, U., Charvet, P., Faria, V. V., Batista, B. B., Tomás, A. R. G, Rodrigues-Filho, L. F. S, Ready, J. S., & Luna-Sales, J. B. (2024). Molecular identification of whole squids and calamari at fairs and markets in regions of Latin America. *Scientific Reports, 14*(1), 1–12. https://doi.org/10.1038/s41598-024-81134-2

Paolacci, S., Mendes, R., Klapper, R., Velasco, A., Ramilo-Fernandez, G., … Sotelo, C. G. (2021). Labels on seafood products in different European countries and their compliance to EU legislation. *Marine Policy, 134*. https://doi.org/10.1016/j.marpol.2021.104810. Article 104810.

Pardo, M. A., Jimenez, E., Vidarsson, J. R., Olafsson, K., Olafsdottir, G., Daníelsdóttir, A. K., & Perez-Villarreal, B. (2018). DNA barcoding revealing mislabelling of seafood in European mass catering. *Food Control, 92*, 7–16. https://doi.org/10.1016/j.foodcont.2018.04.044

Pérez-Lloréns, J. L., Acosta, Y., & Brun, F. G. (2021). Seafood in Mediterranean countries : A culinary journey through history. *International Journal of Gastronomy and Food Science, 26*, Article 100437. https://doi.org/10.1016/j.ijgfs.2021.100437

Rang, M. S. (1837). Documents pour servir à l'histoire naturelle des Céphalopodes crypyobranches. *Magasin de Zoologie, Mollusques, classe V, 7*, 1–77.

Robeson, M. S., O'Rourke, D. R., Kaehler, B. D., Ziemski, M., Dillon, M. R., Foster, J. T., & Bokulich, N. A. (2021). RESCRIPt: Reproducible sequence taxonomy reference database management. *PLoS Computational Biology, 17*(11), Article e1009581. https://doi.org/10.1371/journal.pcbi.1009581

Sales, J. B. L., Rodrigues-Filho, L. F. S., Haimovici, M., Sampaio, I., & Schneider, H. (2011). Molecular differentiation of the species of two squid families (Loliginidae and Ommastrephidae) based on a PCR study of the 5S rDNA gene. *Food Control, 22*, 96–98. https://doi.org/10.1016/j.foodcont.2010.06.011

Shi, R., Huang, M., Wang, J., He, C., Ying, X., Xiong, X., & Xiong, X. (2020). Molecular identification of dried squid products sold in China using DNA barcoding and SYBR green real time PCR. *Food Additives & Contaminants: Part A, 37*(7), 1061–1074. https://doi.org/10.1080/19440049.2020.1746411

Spanish Ministry of Agriculture, Fishing, and Food. (2023). *List of commercial names of fishery and aquaculture species admitted in Spain* (in Spanish) https://www.mapa.gob.es/en/pesca/temas/mercados-economiapesquera/listado-denominaciones-comerciales-anexo-unico-actualizado-a-marzo-de-2023_tcm38-645033.pdf.

Spanish Ministry of Agriculture, Fishing, and Food. (2024). *Report on food consumption in Spain 2023* (In Spanish). https://www.mapa.gob.es/es/alimentacion/temas/consumo-tendencias/informe_2023_alta_tcm30-685877.pdf

Steenstrup, J. (1880). De Ommatostrephagtige Blaeksprutter indbyrdes Forhold. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger, 1880*, 73–110.

Teixeira, M. A. L., Aylagas, E., Pearman, J. K., & Carvalho, S. (2025). Gaps and data ambiguities in DNA reference libraries: A limiting factor for molecular-based biodiversity assessments using annelids as a case study. *Ecology and Evolution, 15*(6), Article e71544. https://doi.org/10.1002/ece3.71544

Toxqui-Rodríguez, S., Naya-Català, F., Sitjà-Bobadilla, A., Piazzon, M. C., & Pérez-Sánchez, J. (2023). Fish microbiomics: Strengths and limitations of MinION sequencing of gilthead sea bream (*Sparus aurata*) intestinal microbiota. *Aquaculture, 569*. https://doi.org/10.1016/j.aquaculture.2023.739388. *Article* 739388.

Verany, J. B. (1839). Memoire sur six nouvelles espèces de Céphalopodes trouves dans la Mediterranee a Nice. *Memorie della Reale Accademia delle Scienze di Torino, (series 2), 1*, 91–98.

Wakabayashi, T., Suzuki, N., Sakai, M., Ichii, T., & Chow, S. (2012). Phylogenetic relationships among the family Ommastrephidae (Mollusca: Cephalopoda) inferred from two mitochondrial DNA gene sequences. *Marine Genomics, 7*, 11–16. https://doi.org/10.1016/j.margen.2012.04.005

Willette, D. A., & Joaquin, M. L. (2026). DNA barcoding and metabarcoding reveal labelling accuracy and species substitution in squid and surimi from Los Angeles markets. *Food Control, 181*. https://doi.org/10.1016/j.foodcont.2025111733. Article 111733.

World Register of Marine Species (n.d.). WoRMS. An authoritative classification and catalogue of marine names. https://www.marinespecies.org/index.php.

World Wildlife Fund. (2020). Unregulated fishing on the high seas of the Indian Ocean: The impacts on risks to and challenges for sustainable fishing and ocean health. https://www.wwf.eu/?1014116/Unregulated-fishing-on-the-high-seas-of-the-Indian-Ocean.

Yokobori, S., Fukuda, N., Nakamura, M., Aoyama, T., & Oshima, T. (2004). Long-term conservation of six duplicated structural genes in cephalopod mitochondrial genomes. *Molecular Biology and Evolution, 21*, 2034–2046. https://doi.org/10.1093/molbev/msh227