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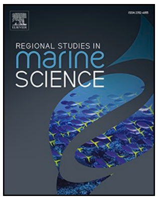

A comprehensive compilation of Iberian Medusozoan data: Diversity, ecology, and omics insights

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ABSTRACT

This study investigates the diversity and distribution of Medusozoa, a clade of the phylum Cnidaria, within the framework of the Iberian Peninsula and surrounding archipelagos. Medusozoa is notably recognized for encompassing jellyfish species with the capacity to exert detrimental ecological and socioeconomic impacts, this group of mostly marine organisms assumes a critical role in aquatic food webs and exhibits considerable biotechnological potential. A comprehensive dataset sourced from over 230 bibliographic references and public databases, comprising over 30,000 reports of Medusozoa in the Iberian region, reveals 593 species across the four medusozoan classes (549 hydrozoans, 37 scyphozoans, 5 staurozoans, and 2 cubozoans). Additionally, publicly available genomic, transcriptomic, and proteomic metadata from the phylum Cnidaria are incorporated. The analyses highlight Hydrozoa as the most frequently reported and diverse class in the Iberian region. Specifically, the order Leptothecata exhibits the highest diversity, while Siphonophorae stands out as the most documented with *Physalia physalis* emerging as the highest reported species. Spatial distribution patterns reveal that holoplanktonic species are more widespread and abundant than their benthic and meroplanktonic counterparts. Furthermore, medusozoans with a free-swimming life form display greater diversity and dispersal compared to sessile species. The Northeast Atlantic section of the region demonstrates greater medusozoan diversity compared to the Mediterranean. Key findings also include information into invasive and introduced species, bloom-forming organisms, and edible species. A sustained trend of discovering new species of Medusozoa over time was observed, underscoring untapped exploration potential in the Iberian region. The study reveals a clear limitation of omics data in cnidarians, particularly in the Medusozoa clade. This research provides an overall perspective on medusozoans in the Iberian region, underlining the importance of additional omics studies while highlighting growing interest in exploring the biotechnological potential of these organisms. This research serves as a valuable resource for future investigations, providing insights into underexplored species and those with greater ecological and socioeconomic importance.

1. Introduction

Medusozoans represent a predominantly marine clade of Cnidaria that comprises four classes: Hydrozoa (hydrozoans), Scyphozoa (true jellyfish), Cubozoa (box jellyfish), and Staurozoa (stalked jellyfish) (Fig. 1) (Marques and Collins, 2004, Daly et al., 2007). These invertebrates inhabit various marine environments, ranging from shallow coastal waters to deep-sea habitats (Benovic, 2004, Altuna, 2007, Moura et al., 2008, Lučić et al., 2009). Nonetheless, some species have been observed in non-marine ecosystems, such as estuaries, lakes, and rivers (Stefani et al., 2010, Wintzer et al., 2011, Amorim et al., 2018, Morales et al., 2018). These organisms play critical roles in aquatic

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ecosystems and food webs, preying on planktonic organisms, crustaceans, and small fishes, while also serving as prey for sea turtles, fish, sea slugs, and birds (Doyle et al., 2014). Moreover, they can act as hosts for a variety of symbiotic organisms, including algae (Newkirk et al., 2018), bacteria (Kramar et al., 2019), bryozoans (Altuna, 2016), crustaceans (Gonçalves et al., 2016), and dinoflagellates (Montgomery and Kremer, 1995).

Hydrozoa, the most diverse class in Medusozoa, comprises over 3700 species, consisting predominantly of small organisms, although certain hydroids within the Siphonophora order can remarkably reach over 40 m long (Dunn, 2009). Hydrozoans are primarily marine, yet some species are euryhaline, and inhabit brackish and freshwater environments (Folino-Rorem and Renken, 2018). In most cases, their life cycle begins with the formation of a planula larva, that develops into a sessile polyp, which, through asexual reproduction, forms a colony (Boero et al., 1992). The colony asexually produces medusae when a free-medusa stage is present. In the absence of this stage, the medusa transforms into a fixed sporosac. The cycle ends with the fusion of gametes and the formation of a zygote, which develops into a new planula larva (Miglietta et al., 2009). Multiple variations exist and are well described in Piraino et al. (2004). Species from Anthoathecata, Leptothecata, and Limnomedusae orders often display meroplanktonic behavior, asexually producing jellyfish from the colonial hydroid stage. In contrast, the Actinulida, Narcomedusae, and Trachymedusae orders are holoplanktonic, lacking a sessile benthic stage. The order Siphonophorae comprises colonial, highly polymorphic, holoplanktonic jellyfish with polypoid and medusoid zooids (Uye and Brodeur, 2017).

According to the World Register of Marine Species (WoRMS, 2023), the class Scyphozoa includes about 240 marine species distributed in three orders (Coronatae, Rhizostomeae, Semaeostomeae). Often referred to as "true jellyfish", they are known to cause blooms with adverse effects on fisheries, aquaculture, and tourism (Purcell et al., 2001, Bosch-Belmar et al., 2017, Fuentes et al., 2018, Avian and Ramšak, 2021). Despite this, only 49 species have had their life cycles described, while the complete life cycle of most scyphozoans yet to be described (Jarms, 2010). Scyphozoans can exhibit either a meroplanktonic or a holoplanktonic life cycle (Holst et al., 2007). Meroplanktonic species alternate between asexual polyps and sexual medusae stages, with medusae being more dominant and longer-lived (Collins, 2002). The cycle begins with medusae releasing gametes for external fertilization. The fertilized eggs develop into planula larvae, that settle on the substrate to become scyphistomae polyps. Trough asexual reproduction, they produce ephyrae by strobilation, which then mature into adult medusae (Collins, 2002, Helm, 2018). In contrast, holoplanktonic scyphozoans remain in the medusa planktonic state throughout their entire life cycle. They develop directly from fertilized eggs to planula larvae, which metamorphose into ephyrae or actinulae-like stages (Helm, 2018).

The class Cubozoa comprises 50 species of marine box jellyfish (WoRMS, 2023). These marine, pelagic, metagenetic species, typically found in coastal warm waters, are remarkably known for their visual capacities (complex eyes) and extreme toxicity, posing a threat to human health (Bentlage et al., 2010, Kingsford and Mooney, 2014, Straehler-Pohl and Gul, 2017, Avian and Ramšak, 2021). The life cycles of cubozoans resemble those of scyphozoans, except they do not release ephyrae into the water. Instead, the entire scyphistoma metamorphoses into an ephyra, which then detaches from the substrate and develops into an adult medusa (Kingsford and Mooney, 2014). However, there are notable exceptions such as incomplete metamorphosis, swimming secondary polyps, or monodisc strobilation (Straehler-Pohl and Jarms, 2005, Toshino et al., 2015, Courtney et al., 2016, Underwood et al., 2018).

The class Staurozoa includes the stalked jellyfish and comprises about 49 species (WoRMS, 2023). Staurozoans are benthic animals found in shallow temperate waters (Miranda et al., 2016a, 2018). These invertebrates also display a metagenetic life cycle with some remarkable changes as they present stauropolyps that metamorphose into non-free swimming stauromedusae that remain attached to the substrate by a basal peduncle (Miranda et al., 2010, Miranda and Collins, 2019).

Medusozoans have gained increasing attention mainly due to the growing global awareness of jellyfish blooms and their significant impacts in key areas. These blooms adversely affect fisheries by damaging or obstructing fishing equipment, resulting in reduced catches (Bosch-Belmar et al., 2020). In aquaculture, the invasion of jellyfish into the cultures poses threats to fish and causes damage to facility infrastructures (Clinton et al., 2021). Additionally, in industries such as desalination plants and power stations, jellyfish can clog intake pipe systems, leading to increased operational and maintenance costs (Baliarsingh et al., 2020, Lin et al., 2023). Furthermore, the proliferation of stinging jellyfish in bathing areas negatively impacts tourism, deterring tourists and impacting local businesses (Ghermandi et al., 2015, Ruiz-Frau, 2023). On the other hand, jellyfish aquaculture has gained

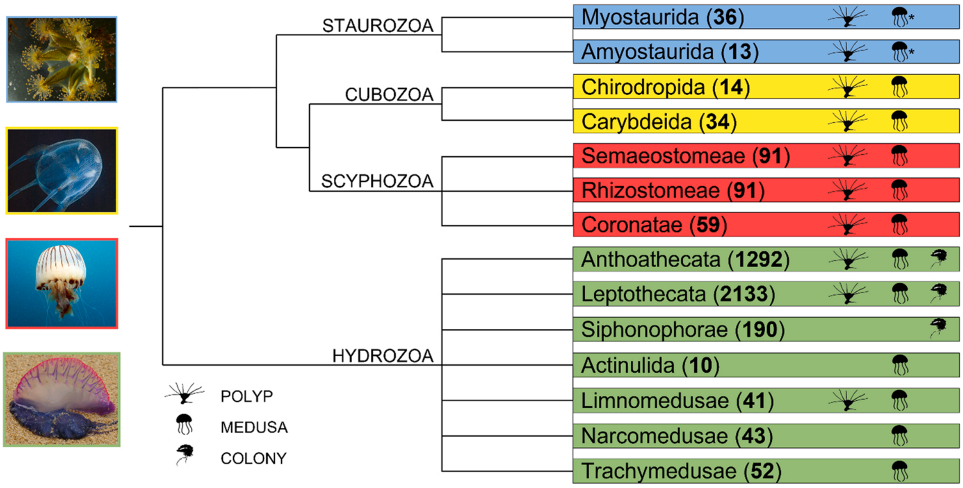

Fig. 1. Phylogeny of the clade Medusozoa. The four classes of Medusozoa: Staurozoa (blue outline), Cubozoa (yellow), Scyphozoa (red), and Hydrozoa (green), with the life forms present in each order (suborder, in the case of Staurozoa). In parenthesis: the total number of species of each order (suborder, in the case of Staurozoa); asterisk: the sessile stauromedusae. Image credits (with colorful outlines): blue – licensed by HE Westlake under the CC BY-SA 4.0, source Wikimedia Commons (https://bit.ly/3jHfW9U); yellow – licensed by Seascapeza under the CC BY-SA 3.0, source Wikimedia Commons (https://bit.ly/3bhOYkF); red – licensed by Christophe Quintin under the CC BY-NC 2.0, source flickr (https://bit.ly/3BvLAO5); green –licensed by Biusch under the CC BY-SA 3.0, source Wikimedia Commons (https://bit.ly/3Emo2wU).

interest aiming the prospect of bioactive compounds (De Domenico et al., 2019, Duarte et al., 2021), used as food source, for human consumption (Amaral et al., 2018) and aquafeed (Costa et al., 2019), and for aquaria and research (Purcell et al., 2013, Leal et al., 2018).

The application of omics technologies has greatly enhanced the understanding of the biology and evolution of medusozoans (Kayal et al., 2018, Moura et al., 2022). Omics information can help identify the causes of jellyfish abundance and invasions (Dawson et al., 2015), explore and identify new genes and compounds (Felician et al., 2019, Nong et al., 2020, Dong et al., 2021), search the evolution of developmental pathways and cell differentiation (Lim et al., 2014, Matsumoto et al., 2019), and to investigate the potential of venom proteins (Choudhary et al., 2018, Li et al., 2020).

The study of Medusozoans, although limited by the irregularity of their occurrence (Boero et al., 2008), has provided a wealth of information on their diversity in the Iberian Peninsula and surrounding archipelagos. However, data regarding medusozoans from this region is dispersed across numerous publications, including the studies by Medel and López-González (1996), Cantero and Carrascosa (2002), Altuna (2015), and Gueroun et al. (2021). To address this issue, a comprehensive review conducted on the diversity of Medusozoa in the entire Iberian region, including Portugal, Spain, Azores, Madeira, and Canary Islands, is presented, extending the work previously initiated by Rodrigues et al. (2020). This research includes medusozoan reports in the Iberian region, integrated with genomic, transcriptomic, and proteomic metadata for the phylum Cnidaria, shedding light on the medusozoan biogeography and ecology, and emphasizing the need for further omics studies.

2. Methods

2.1. Diversity and distribution data

To assess Medusozoa diversity in the Iberian Peninsula and its surrounding archipelagos, an extensive literature review was conducted and complemented by data obtained from publicly accessible databases, resulting in the compilation of the publicly available medusozoan reports.

The study area is in the southwestern region of Europe, where the Northeast Atlantic Ocean and the Mediterranean Sea converge (24°35'N - 46°52'N, 35°35'W - 06°18'E), including the Exclusive Economic Zones (EEZs) of Portugal (with the EEZs of Azores and Madeira archipelagos) and Spain (with the EEZ of Canary Islands). Additionally, the study area also includes the minor Spanish territories in North Africa, such as the two autonomous cities, Ceuta and Melilla, and the "Plazas de Soberanía" (Alhucemas Islands, Chafarinas Islands, and Peñón de Vélez de la Gomera) (Fig. 2). Throughout this work, mainland Portugal and Spain will be referred as Portugal and Spain, respectively, and the entire study area as the "Iberian region".

When compiling the reports of Medusozoa, only records from the EEZs above mentioned were considered. Data were gathered from scientific literature, including articles, books, reports, and theses, published between 1829 and 2023 (see Supplementary material references). Data retrieval from Google Scholar involved systematically using the nomenclature of each of the 593 species found. Subsequently, the literature retrieved were examined to determine the presence of each species within the EEZs considered. Search results were not constrained by time or language, and only the first two pages results were considered, as subsequent pages did not provide relevant information. To expand the data compilation, three online databases, namely Global Biodiversity Information Facility (GBIF.org, 2023), iNaturalist.org (iNaturalist, 2023), and Ocean Biodiversity Information System (OBIS, 2023), were accessed to retrieve data on medusozoan reports within the area of study (last retrieved in October 2023). To ensure reliability and relevance, data was manually curated. Redundant data was removed to prevent duplication and only records containing at least the genus-level identification and the year of the record were retained. For iNaturalist records, a "research grade" data quality level was required and observations with "private" coordinates were excluded. Additionally, reports of species that could not be confirmed in existing scientific literature were included and labeled as such in the datasheet for future considerations.

Taxonomic data were cross-checked in the WoRMS for accuracy and validation. Currently accepted nomenclature was used for invalid species names, and entries with "cf." qualifiers indicating uncertain identifications were recorded at the genus level. Species entries identified at the genus level were only included in the tally and analysis of species diversity if that genus had no other representatives in the collected data. This criterion applies consistently across all comparisons of species diversity counts, including those between different EEZs, the

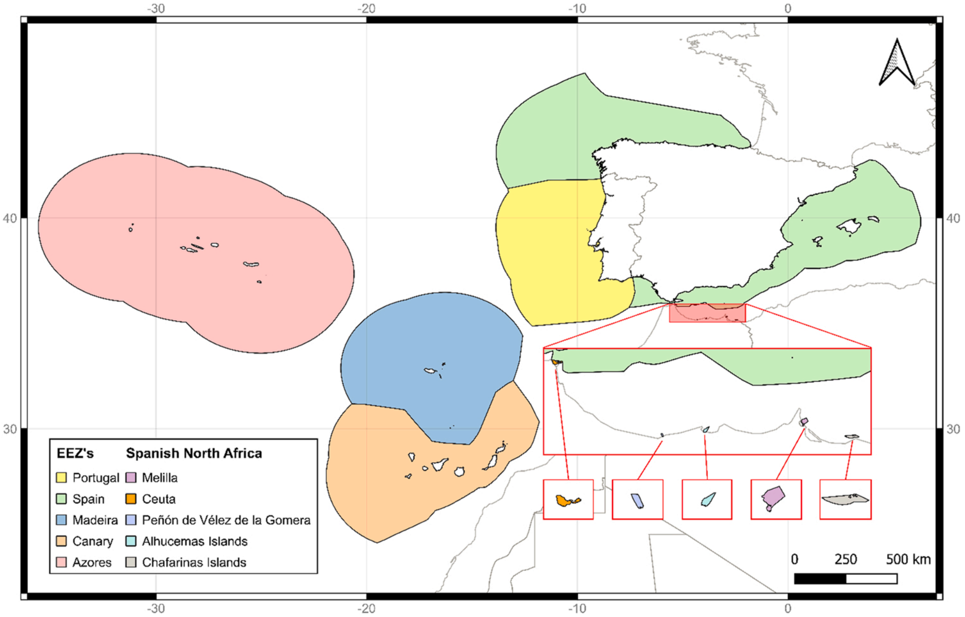

Fig. 2. Study area. The Iberian region encompassing the Iberian Peninsula with the exclusive economic zones (EEZ's) of Continental Portugal and Spain, and the surrounding archipelagos of Macaronesia with the EEZ's of Azores, Madeira, and the Canary Islands.

Mediterranean and Atlantic areas, and so on. Disputed species, non-marine species, and those with temporary nomenclature were included for future consideration. Data analysis (*e.g.*, species counting and percentage calculations) were performed using an Excel spreadsheet. Life history information was obtained from bibliographical research, with particular attention paid to the works of Bouillon and Schuchert for Hydrozoa (Bouillon et al., 2006, Schuchert, 2006, 2007, 2008a, 2008b, 2009, 2010), Jarms and Morandini for Scyphozoa (Jarms and Morandini, 2019), Jarms and Straehler-Pohl for Cubozoa (Straehler-Pohl and Jarms, 2005, 2011, Straehler-Pohl et al., 2017), and Miranda for Staurozoa (Miranda et al., 2012, 2016a, 2018, 2023). For analytical purposes, scyphozoan species lacking disclosed details about their life cycle were tentatively categorized as meroplanktonic. Information about the natural environment of each species (marine, brackish, freshwater) was retrieved from WoRMS (WoRMS, 2023).

Distribution maps for medusozoans in the Iberian region were created using the QGIS 3.28.2 software (QGIS.org, 2023). EEZ shapefiles for the study area were retrieved from Marineregions.org (Flanders Marine Institute, 2023). Heatmap layers were generated with a radius of 1 map unit, layer rendering blending mode set to “Multiply”, and the remaining settings kept as default.

Non-marine species were excluded from the analysis comparing species distribution between the Atlantic and Mediterranean regions, as they are not present in either. Nevertheless, a separate distribution map for non-marine species was produced (Fig. B1).

Species flagged as invasive or introduced were identified using the Global Invasive Species Database (GISD) (Invasive Species Specialist Group ISSG, 2023), and the Global Register of Introduced and Invasive Species (GRIIS) catalogue (Pagad et al., 2022).

2.2. Medusozoan reports datasheet description

The Medusozoan reports datasheet compiles public data on Medusozoa in the Iberian region, organized into columns. The "recordOrigin" column specifies the data source, with "referenceID" serving as the record identifier. For database records, it corresponds to the original occurrence id. The "refYear" column indicates the publication year for literature records. Date details are in “year”, “month”, and “day” columns, while location information includes “latitude”, “longitude”, "location", "location2" and "location3". When available, reports coordinates are presented in decimal degrees format (WGS84) in the “latitude” and “longitude” columns. If not available, approximate coordinates from Google Maps were used, retaining descriptive site data in the “location3” column. The “location” column categorizes reports by EEZ, and “location2” labels them as from the Mediterranean Sea, Northeast Atlantic Ocean, or non-marine area. Taxonomic data is columns “class”, “subclass”, “order”, “suborder”, “family”, “genus”, and “species”. Species life history details are in "lifeCycle", "lifeForms," and "isFree-swim". The "lifeCycle" column categorizes species as holoplanktonic, meroplanktonic, or benthic. "lifeForms" column provides information on each species main life forms, and "isFree-swim" indicates if a species has a free-swimming life form. Data on the species’ natural environment is in columns labeled “isMarine”, “isBrackish”, and “isFresh”.

2.3. Omics data

Transcriptomic and genomic data were retrieved from the National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) (Leinonen et al., 2011), encompassing all cnidarian entries. The data were manually curated, categorized by class, and refined by assay type, selectively including RNA-sequencing (RNA-seq) for transcriptomes, as well as whole-genome amplification (WGA) and sequencing (WGS) for genomes.

Simultaneously, comprehensive proteomic metadata were compiled from major repositories such as ProteomeXchange (Deutsch et al., 2023), PRIDE (Perez-Riverol et al., 2022), MassIVE (Center for Computational Mass Spectrometry, 2023), iProX (Ma et al., 2019), and UniProt Proteome (The UniProt Consortium, 2023). Additionally, a thorough literature review was conducted to identify and incorporate additional proteomic studies on Medusozoa not available in any repository.

3. Results

3.1. Diversity and distribution data

The investigation compiled a total of 233 studies and public data from GBIF, iNaturalist, and OBIS databases, resulting in a datasheet of public reports of medusozoans in the Iberian region (Table A1). Additionally, a checklist of the reported medusozoan species is provided (Table B1). Upon the acceptance of this manuscript, any data that is currently unavailable on GBIF will be uploaded and made accessible through the platform.

The compilation identified 30,121 reports, uncovering 593 medusozoan species from all four classes in the Iberian region. Hydrozoa dominates with 549 species and 26,390 reports, followed by Scyphozoa (37 species, 3680 records), Staurozoa (five species, 17 records), and Cubozoa (two species, 34 records) (Fig. 3). The total medusozoan diversity of the region encompasses 290 genera, 117 families, and 12 orders (Table 1). Leptothecata is the most specious order, and Siphonophorae is the most frequently observed order (Fig. 4), with *Physalia physalis* (Linnaeus, 1758) being the most reported species (Table B2).

The only reported non-marine species in this study belong to class Hydrozoa, totaling six species and 1795 records, mainly from *Hydra* spp. in Spain. Marine species are distributed in both the Northeast Atlantic Sea area and the Mediterranean Sea area. The Northeast Atlantic has 21,756 records, including 537 species (314 exclusive), while the Mediterranean Sea has 6570 reports, with 273 species (50 exclusive, 223 shared). Of the reported medusozoans, 40% display a benthic life cycle strategy, 32% are holoplanktonic, and 28% are meroplanktonic. Additionally, 59% of all registered species have a free-swimming form in their life cycle, while the remaining are exclusively sessile. Medusozoans are documented along nearly the entire coastline of the study area, including all minor Spanish territories in North Africa, except for the Alhucemas Islands and Peñón de Vélez de la Gomera (Fig. 5). Notably, the public records of Medusozoa are concentrated in the coastal area of Portugal, the Spanish Valencian coast, and the central group of the Azores (Fig. B2). A significant concentration of reports is observed in the Northwest of the Spain EEZ. The distribution pattern indicates that species with a free-swimming life cycle stage are more widespread across the Iberian region, while sessile species are mostly concentrated in coastal areas (Fig. B3). The number of publicly available sightings of medusozoans is increasing exponentially, and there is no decrease in the discovery of new species in recent times (Fig. 6).

The EEZ of Portugal has 10,104 records, documenting 229 species, 143 genera, 72 families, and 11 orders. The region has the largest number of staurozoan species, with three species recorded. Most records in Portugal’s EEZ are of holoplanktonic species with a free-swimming life stage. Leptothecata is the most species-rich order, while Siphonophorae has the highest number of occurrence records. *Muggiaea atlantica* Cunningham, 1892 is the most frequently recorded hydrozoan in Portugal, and *Catostylus tagi* (Haeckel, 1869) is the most recorded scyphozoan.

Spain’s EEZ has 13,088 records, hosting 423 species, 234 genera, 72 families, and representatives from all 12 orders, surpassing other regions in diversity, especially in hydrozoans and scyphozoans. It is the area of the Iberian region with the highest density of medusozoan species, with most records pertaining to holoplanktonic species with a free-swimming life stage. *Velella velella* (Linnaeus, 1758) is the most frequently recorded hydrozoan, and *Pelagia noctiluca* (Forsskål, 1775) is the most

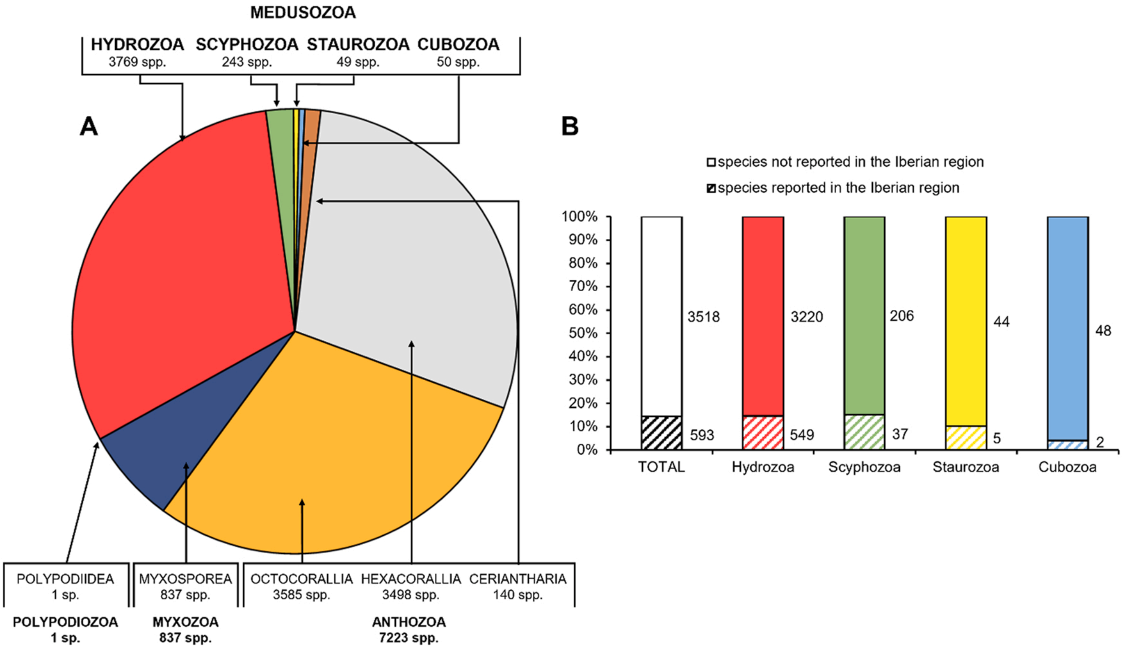

Fig. 3. Schematic representation of the global and regional diversity of Medusozoa. A: General diversity of each Cnidaria class. (source: WoRMS Database accessed in October 2023) B: Global and regional diversity of Medusozoa in which the striped portions of each bar represent the species present in the Iberian region.

documented scyphozoan.

The Azores EEZ boasts 4892 records, cataloging 264 species, 154 genera, 68 families, and eight orders, with a prevalence of benthic species. Notably, it has the lowest medusozoan species density among the examined areas.

The EEZ of Madeira has the fewest records, with only 692 reports, and it is the least diverse area in the Iberian region, documenting 161 species across 106 genera, 52 families, and eight orders. Reports in this area are mainly from holoplanktonic species with a free-swimming life form and benthic species.

The Canary EEZ, with 1345 records, features 232 species, 145 genera, 71 families, and 11 orders, with most of the records documenting holoplanktonic species with a free-swimming life stage.

In the Azores, Madeira, and Canary EEZs, *P. physalis* emerges as the dominant hydrozoan, while *P. noctiluca* stands out as the most common scyphozoan.

Furthermore, a comprehensive compilation of the most frequently reported hydrozoan and scyphozoan species in both the overall region and individual EEZs has been provided (Table B2). In addition, a list of reported invasive and introduced medusozoan species is presented (Table 2), along with compiled data on documented bloom-forming species (Table 3), and a gathered list of recorded edible species (Table 4). These tables serve as valuable references for a better understanding of the ecological dynamics of these organisms within the context of the Iberian region and shedding light on their ecological and socioeconomic potential.

3.1.1. *Class hydrozoa*

The Iberian region accounts for 549 hydrozoan species across 261 genera, 96 families, and seven orders. Spain's EEZ boasts the highest hydrozoan diversity with 394 species, followed by Azores (246), Canary (213), Portugal (205), and Madeira (152). The average number of species per order is 78, with Leptothecata emerging as the most speciose order in all the EEZs, boasting 240 species belonging to 95 genera, and *Lensia* Totton, 1932 as the most speciose genus with 19 species. Notably, Leptothecata dominates in Azores and Madeira EEZ's, while Siphonophorae prevails in the other EEZs. Actinulida is exclusive to Spain, with the remaining orders represented in all areas of the Iberian region. Approximately 57% of documented hydrozoans have a free-swimming life stage, and over 80% are colonial or present a colonial phase. Moreover, more than 62% are holoplanktonic. *Lensia* is the most frequently registered genus, and *P. physalis* is the most documented species in the public Iberian region records.

Introduced hydrozoan species in Portugal comprise *Blackfordia virginica* Mayer, 1910, *Cordylophora caspia* (Pallas, 1771), and *Craspedacusta sowerbii* Lankester, 1880 in brackish and freshwater environments, and *Gonionemus vertens* Agassiz, 1862, *Kirchenpaueria halecioides* (Alder, 1859), *Maeotias marginata* (Modeer, 1791), and *Tubularia indivisa* Linnaeus, 1758 in marine habitats (Marchante et al., 2020). In Spain, including the Canary Islands, the introduced hydrozoan species are *C. caspia* in freshwater environments, and *Tridentata marginata* (Kirchenpauer, 1864) in marine ecosystems (Dana et al., 2022). None of the reported hydrozoans is considered invasive. The distribution heatmap of hydrozoan public records aligns closely with the total distribution of medusozoans, encompassing almost 88% of total medusozoan reports (Fig. 7A). Reports of hydrozoans in the Iberian region are higher in the spring and summer months and lower in the autumn and winter months (Fig. B4).

3.1.2. *Class scyphozoa*

In the study region, there are 37 species of Scyphozoa belonging to 22 genera, 15 families, and three orders. Spain's EEZ holds the highest scyphozoan diversity with 26 species, followed by Portugal (20), Azores (18), Canary (17), and Madeira (9). On average, each order contains 12 species, with Coronatae being the most speciose with 17 species belonging to six genera, and *Nausithoe* Kölliker, 1853 as the leading genus with eight species. Remarkably, the predominant scyphozoan order displays significant variation across different EEZs. Rhizostomeae overwhelmingly dominates in Portugal, shares dominance with Semaeostomeae in Spain, is absent in the Azores and Madeira EEZs, and sees Semaeostomeae as the dominant order in the Canary EEZ. *P. noctiluca*, is the most frequently recorded scyphozoan species, while the Australian spotted jellyfish *Phyllorhiza punctata* von Lendenfeld, 1884 is the only invasive species recorded in the Iberian region. The distribution heatmap of scyphozoan public occurrences in the Iberian region shows a hotspot in the central area of the Portuguese coast and on the Spanish Valencian and Catalan coasts (Fig. 7B). Scyphozoan reports show they start to increase in the beginning of spring until they reach a maximum

Table 1
Medusozoan diversity in the Iberian Peninsula and Islands.

	Iberian region	*Portugal*	*Spain*	*Azores*	*Madeira*	*Canary*
EEZ Area (km^2)	2736,391	315,501	561,763	960,421	452,796	445,910
EEZ Species density (species/km^2)	2.167×10^{-4}	7.258×10^{-4}	7.530×10^{-4}	2.749×10^{-4}	3.556×10^{-4}	5.203×10^{-4}
Number of species						
All	593	229	423	264	161	232
Hydrozoa	549	205	394	246	152	213
Scyphozoa	37	20	26	18	9	17
Staurozoa	5	3	2	0	0	1
Cubozoa	2	1	1	0	0	1
Number of genera						
All	290	143	234	154	106	145
Hydrozoa	261	127	213	145	100	133
Scyphozoa	22	12	18	9	6	10
Staurozoa	5	3	2	0	0	1
Cubozoa	2	1	1	0	0	1
Range species per genus	1–19	1–8	1–17	1–12	1–12	1–7
Max. representative	*Lensia*	*Aglaophenia / Lensia*	*Lensia*	*Lensia*	*Lensia*	*Aglaophenia*
Number of families						
All	117	72	100	68	52	71
Hydrozoa	96	58	83	61	46	60
Scyphozoa	15	10	14	7	6	9
Staurozoa	4	3	2	0	0	1
Cubozoa	2	1	1	0	0	1
Range genera per family	1–12	1–8	1–10	1–10	1–7	1–11
Max. representative	Rhopalonematidae	Diphyidae	Rhopalonematidae / Sertulariidae	Rhopalonematidae	Diphyidae	Rhopalonematidae
Range species per family	1–35	1–17	1–30	1–23	1–22	1–15
Max. representative	Diphyidae	Campanulariidae / Diphyidae	Diphyidae	Diphyidae	Diphyidae	Rhopalonematidae
Number of orders						
All	12	11	12	8	8	11
Hydrozoa	7	6	7	6	6	6
Scyphozoa	3	3	3	2	2	3
Staurozoa	1	1	1	0	0	1
Cubozoa	1	1	1	0	0	1
Range family per order	1–34	1–22	1–29	1–23	1–17	1–19
Max. representative	Anthoathecata	Leptothecata	Leptothecata	Leptothecata	Anthoathecata	Anthoathecata, Leptothecata
Range genera per order	1–95	1–54	1–79	1–55	1–40	1–46
Max. representative	Leptothecata	Leptothecata	Leptothecata	Leptothecata	Leptothecata	Leptothecata
Range species per order	1–240	1–106	1–174	1–116	1–76	1–86
Max. representative	Leptothecata	Leptothecata	Leptothecata	Leptothecata	Leptothecata	Leptothecata
Life cycle						
Holoplanktonic (%)	192 (32%)	57 (25%)	131 (31%)	111 (42%)	61 (38%)	98 (42%)
Meroplanktonic (%)	164 (28%)	67 (29%)	119 (28%)	54 (20%)	29 (18%)	57 (25%)
Benthic (%)	237 (40%)	105 (46%)	173 (41%)	99 (38%)	71 (44%)	77 (33%)
Free-swimming?						
Yes (%)	352 (59%)	122 (53%)	246 (58%)	165 (63%)	90 (56%)	155 (67%)
No (%)	241 (41%)	107 (47%)	177 (42%)	99 (37%)	71 (44%)	77 (33%)

in the warm August summer.

3.1.3. Class staurozoa

The Iberian region contains five staurozoans from the Stauromedusae order, distributed among four genera and three families. Notable sightings include *Calvadosia campanulata* (Lamouroux, 1815) in Portugal (Setúbal) and Spain (Southern Bay of Biscay) (Da Cunha, 1944, Altuna, 2015), *Depastrum cyathiforme* (M. Sars, 1846) in the Canary Islands (Lanzarote) (Haeckel, 1880), *Haliclystus auricula* James-Clark, 1863 in Portugal (Porto and Viana do Castelo) (Nobre, 1903, Da Cunha, 1944), *Lipkea ruspoliana* Vogt, 1886 in Portugal (Arrábida Natural Park) (Miranda et al., 2023), and *Stylocoronella riedli* Salvini-Plawen, 1966 in Spain (Southern Bay of Biscay) (Besteiro and Urgorri, 1988, Altuna, 2015).

3.1.4. Class Cubozoa

Two cubozoan species of the order Carybdeida were documented in the study area, rendering Chirodropida the sole unrepresented medusozoan order in the region. *Carybdea marsupialis* (Linnaeus, 1758) was reported in Portugal (Nobre, 1931) and Spain (Bordehore et al., 2011, Acevedo et al., 2013, 2019, Rubio Gómez and Gutiérrez-Hernández, 2020, Rodríguez-García et al., 2021), while *Copula sivickisi* (Stiasny, 1926) was reported in the Canary Archipelago (Moro et al., 2020).

3.2. Omics data

The comprehensive examination of Cnidaria data gathered from repositories such as NCBI SRA, ProteomeXchange, PRIDE, MassIVE, iProX, and UniProt Proteome, as well as a literature review focused specifically on medusozoan proteomic studies (until November 2023), unveiled interesting insights. Among the vast phylum Cnidaria, only about 650 out of the approximately 12,100 species have publicly available genomic (WGA, WGS), transcriptomic (RNA-Seq) (Table A2), or proteomic data (Table A3). Notably, only 20% of these belong to the Medusozoa clade, comprising 87 hydrozoans, 26 scyphozoans, nine cubozoans, and eight staurozoans, totaling 130 species. Remarkably, nearly half of these medusozoan species were reported in the Iberian region, encompassing 53 hydrozoans, 12 scyphozoans, two staurozoans and two cubozoans. Noteworthy representatives such as the scyphozoans *Chrysaora fuscescens* Brandt, 1835, and *Chrysaora quinquecirrha*

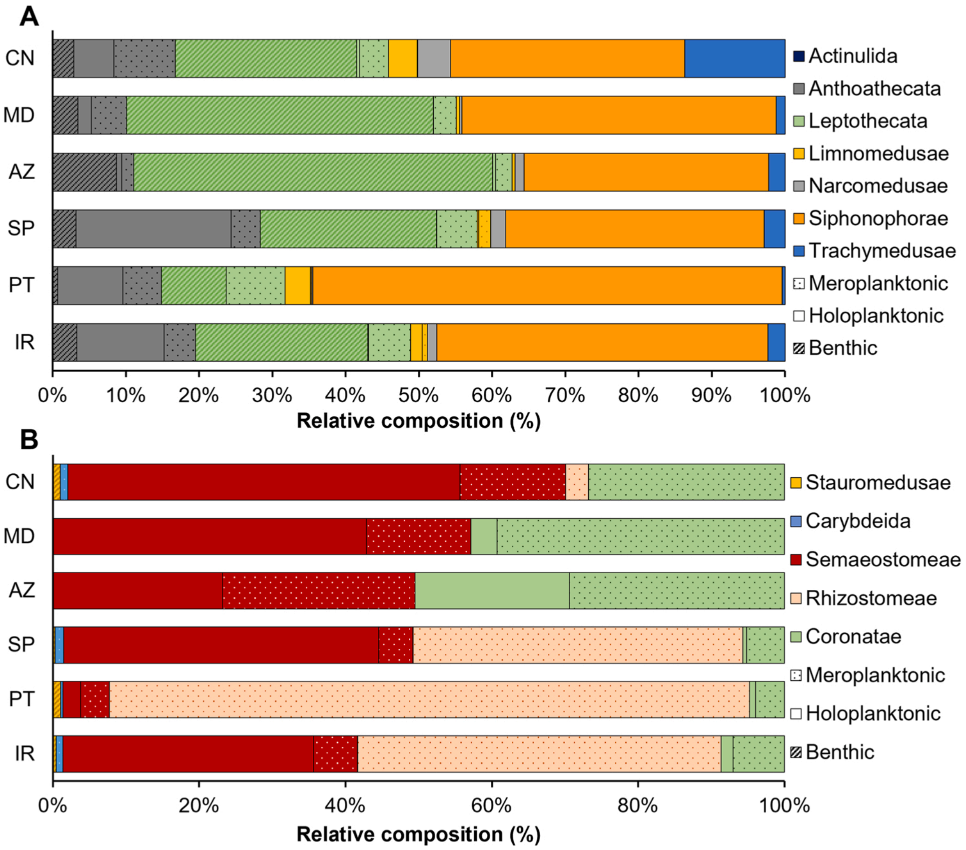

Fig. 4. Iberian region relative percentage (%) composition of medusozoan reports by order. A: Hydrozoa; B: Scyphozoa, Cubozoa, and Staurozoa. IR: Iberian region; PT: Portugal; SP: Spain; AZ: Azores; MD: Madeira; CN: Canary Islands.

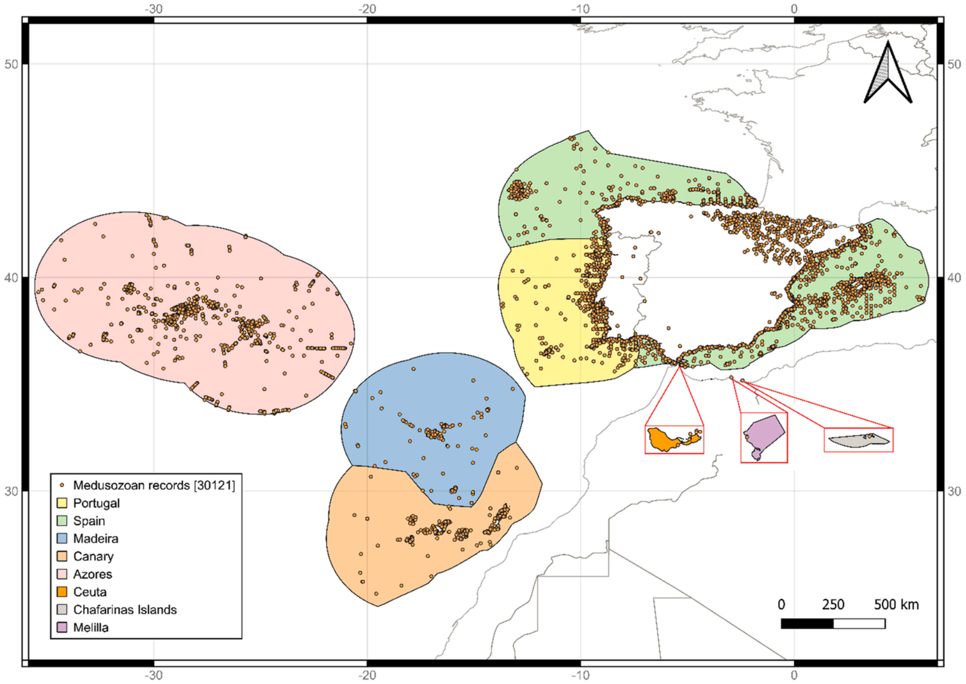

Fig. 5. Distribution of medusozoans in the Iberian region. The points represent the reports available in Table A1.

(Desor, 1848), and the hydrozoans *Clytia hemisphaerica* (Linnaeus, 1767), and *H. vulgaris*, are particularly distinguished for having all three types of omics data publicly accessible. Within the Anthozoa class, over 77% of genomic, transcriptomic, and proteomic data in the repositories originate from the last five years. This trend is even more pronounced for Medusozoa, (over 87%), indicating a growing interest in employing

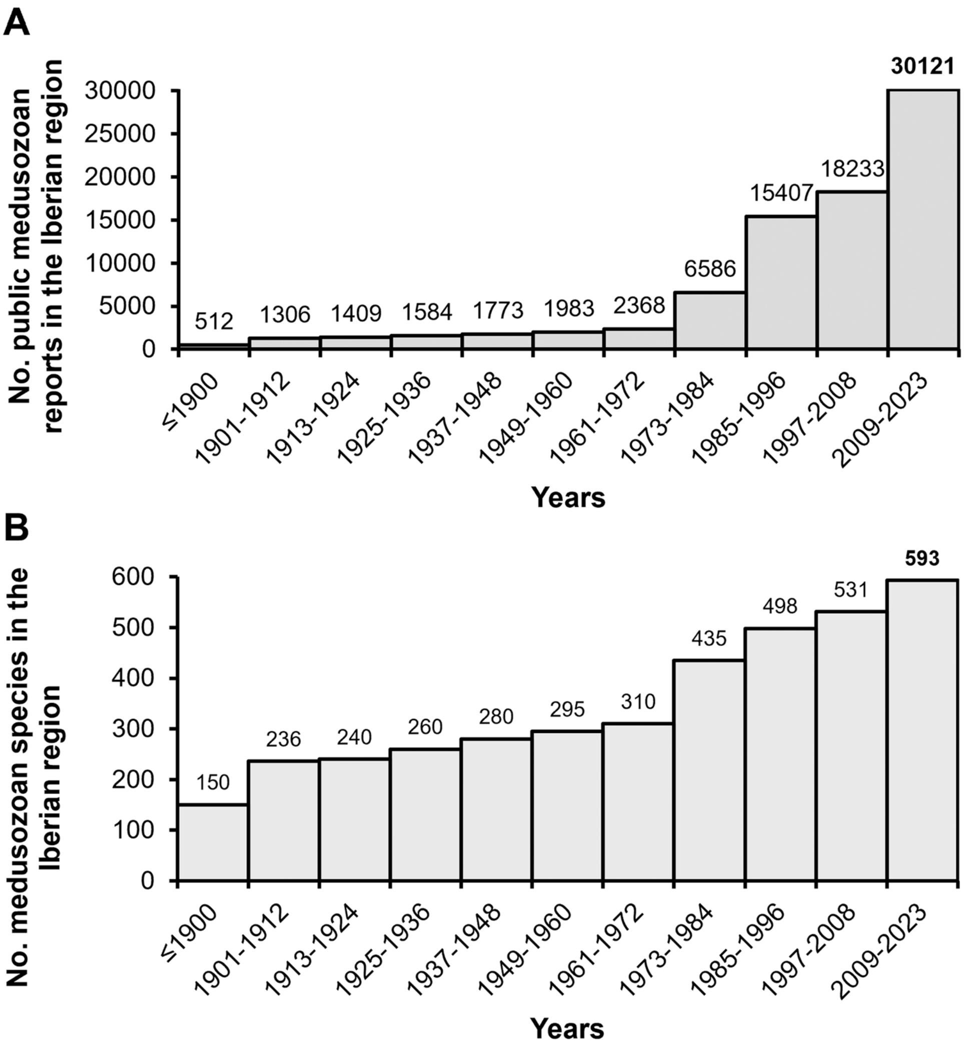

Fig. 6. Medusozoans reported in the Iberian region over the years. A: Cumulative number of public reports of medusozoans in the Iberian region; B: Cumulative number of medusozoan species in the Iberian region.

Table 2
Medusozoans with invasive and introduced status reported in the Iberian region.

Taxonomy	*Portugal*	*Spain*	*Azores*
Hydrozoa			
Order Anthoathecata			
Cordylophora caspia (Pallas, 1771)	X	X	
Ectopleura crocea (Agassiz, 1862)			X
Tubularia indivisa Linnaeus, 1758	X		X
Order Leptothecata			
Blackfordia virginica Mayer, 1910	X		X
Kirchenpaueria halecioides (Alder, 1859)	X		X
Tridentata marginata (Kirchenpauer, 1864)		X	
Order Limnomedusae			
Craspedacusta sowerbii Lankester, 1880	X		X
Gonionemus vertens A. Agassiz, 1862	X		
Maeotias marginata (Modeer, 1791)	X		
Scyphozoa			
Order Rhizostomeae			
*Phyllorhiza punctata** von Lendenfeld, 1884		X	

* it is the only species with invasive status

omics approaches to study these organisms. Many studies have employed various specimens or pooled tissues for the extraction of DNA, RNA or proteins from cnidarians. A broad array of tissues and structures, such as acrorhagi, bell margin, body wall, branch, gonad, head, nectosome, oral arm, siphosome, tentacle, umbrella, and zooid, have been used for genetic material extraction. Notably, the extensive use of nematocysts should be highlighted, as much research on Cnidaria is particularly focused on studying their venoms and toxins (Leung et al., 2020, Guo et al., 2022, Hernández-Elizárraga et al., 2022).

4. Discussion

4.1. Medusozoan diversity and distribution in the Iberian region: key findings and considerations

In biodiversity studies, the nature of compiled data plays a crucial role in result analysis. This study focuses on Medusozoa reports in the Iberian region, documented through sightings and samplings. Medusozoan sightings are influenced by organism size, morphology, and other visual characteristics, where smaller or more transparent organisms pose challenges in their detection (Boero et al., 2008, González-Duarte et al., 2023). Depth in the water column is also a factor to consider, as organisms from deeper waters may be less observable compared to those closer to the surface. Yet, diminished visibility in deeper waters does not necessarily signify lower organism abundance (Raskoff, 2010). In some cases, the use of Remotely Operated Vehicles (ROVs) can help surpass this limitation (Wenneck et al., 2008). Sampling methods including dredges, trawl nets, and plankton nets, present additional challenges. Indeed, various sampling methods demonstrate selectivity towards distinct animal groups (Hosia et al., 2017). Dredges and trawl nets are

Table 3
Medusozoans with worldwide reports of blooms in the Iberian region.

Taxonomy	*Location*	*Reference*
Class Cubozoa		
Order Carybdeida		
Carybdea marsupialis (Linnaeus, 1758)	Denia, Spain	Bordehore et al., 2011
Copula sivickisi (Stiasny, 1926)	Shirahama, Japan	Morandini et al., 2014
Class Hydrozoa		
Order Anthoathecata		
Velella velella (Linnaeus, 1758)	Northern California Current, USA	Zeman et al., 2018
Order Leptothecata		
Aequorea pensilis (Haeckel, 1879)	North Arabian Sea, Pakistan	Gul and Gravili, 2013
Staurostoma mertensii (Brandt, 1834)	Bay of Fundy, Grand Manan Island, Canada	Young and Hagadorn, 2020
Order Limnomedusae		
*Gonionemus vertens** A. Agassiz, 1862	Berre Lagoon, France	Marchessaux et al., 2017
Olindias muelleri Haeckel, 1879	Aegean Sea, Çeşme Peninsula, Turkey	Aytan et al., 2019
Order Siphonophorae		
Apolemia uvaria (Lesueur, 1815)	Norwegian waters, Norway	Båmstedt et al., 1998
Physalia physalis (Linnaeus, 1758)	Mediterranean Sea	Boero, 2013
Class Scyphozoa		
Order Coronatae		
Linuche unguiculata (Swartz, 1788)	Karujeu Island, Solomon Islands	Fossette et al., 2012
Nausithoe punctata Kölliker, 1853	East China Sea, Northeast Taiwan	Tseng et al., 2015
Periphylla periphylla (Péron & Lesueur, 1810)	Trondheimsfjord, Norway	Tiller et al., 2015
Order Rhizostomeae		
Cotylorhiza tuberculata (Macri, 1778)	Northern Adriatic Sea	Kogovšek et al., 2010
*Phyllorhiza punctata** von Lendenfeld, 1884	Southern Brazil, Brazil	Haddad and Nogueira Júnior, 2006
Rhizostoma pulmo (Macri, 1778)	Northern Adriatic Sea	Kogovšek et al., 2010
Order Semaeostomeae		
Aurelia aurita (Linnaeus, 1758)	Northern Yellow Sea, China	Dong et al., 2012
Aurelia solida Browne, 1905	Gulf of Trieste, Croatia	Kramar et al., 2019
Chrysaora fuscescens Brandt, 1835	Northern California Current, USA	Suchman and Brodeur, 2005
Chrysaora hysoscella (Linnaeus, 1767)	Gulf of Trieste, Italy	Del Negro et al., 1992
Chrysaora quinquecirrha (Desor, 1848)	Chesapeake Bay, USA	Decker et al., 2007
Cyanea capillata (Linnaeus, 1758)	Yangtze Estuary, China	Xian et al., 2005
Discomedusa lobata Claus, 1877	Iran and Croatia	Purcell et al., 2015
Drymonema dalmatinum Haeckel, 1880	Puerto Rico	Williams et al., 2001
Mawia benovici (Piraino et al., 2014)	Gulf of Trieste, Italy	Avian et al., 2016
Pelagia noctiluca (Forsskål, 1775)	Strait of Messina, Italy	Milisenda et al., 2018

better suited for benthic medusozoans (Ríos et al., 2022), while plankton nets, designed for planktonic medusozoans, may yield varied results influenced by mesh size (Nogueira Júnior et al., 2015, Tosetto et al., 2019).

4.1.1. *Diversity*

Table 4
Edible jellyfish species recorded in the Iberian region.

Scyphozoa	*References*
Order Coronatae	
Periphylla periphylla (Péron & Lesueur, 1810)	Wang, 2007
Order Rhizostomeae	
Catostylus tagi (Haeckel, 1869)	Raposo et al., 2018
Cotylorhiza tuberculata (Macri, 1778)	Brotz et al., 2017
*Phyllorhiza punctata** von Lendenfeld, 1884	Coleman et al., 1990; Kailola et al., 1993
*Rhizostoma luteum** (Quoy & Gaimard, 1827)	Edelist et al., 2021
Rhizostoma pulmo (Macri, 1778)	Ozer and Celikkale, 2001; Torri et al., 2020
Stomolophus meleagris Agassiz, 1860	Hsieh et al., 2001; López-Martinez and Álvarez-Tello, 2013; Brotz et al., 2017
Order Semaeostomeae	
Aurelia aurita (Linnaeus, 1758)	Pedersen, 2016
*Chrysaora hysoscella** (Linnaeus, 1767)	Edelist et al., 2021
*Cyanea capillata** (Linnaeus, 1758)	Edelist et al., 2021
Pelagia noctiluca (Forsskål, 1775)	Armani et al., 2013

* Species not consumed by humans on a large scale but with potential for commercial fishery

Hydrozoans take the lead in the Iberian region, particularly with the prevalence of the dominant Siphonophora order, a trend consistent with their recognition as the most speciose class in the clade (WoRMS, 2023). This aligns with findings from Hosia et al. (2017), who studied gelatinous organisms in the northern Mid-Atlantic Ridge from Iceland to the Azores, confirming siphonophores as the most abundant species in that region.

The highest reported medusozoan species is the Portuguese man-of-war, *P. physalis*. Known for its high toxicity and potent stinging capabilities, this species is easily recognized by local communities due to awareness campaigns, and its distinctive features such as vibrant colors, large tentacles, and a sizable pneumatophore, as well as for frequently washing up on beaches (Munro et al., 2019, GelAvista, 2023). The reports are predominantly derived from human observations submitted on the accessed databases, which may help explain why this is the most reported species in the region.

Within Scyphozoa, the order Coronatae, which is the least speciose order, exhibited the highest species richness in the region. The predominant scyphozoan order varied a lot between EEZs. Interestingly, the EEZs of Azores and Madeira archipelagos did not present any Rhizostomeae, contradicting the supposed distribution of *C. tagi* (Scyphozoa, Rhizostomeae) from the Tagus estuary to the African coast (Cornelius et al., 2001). Currently, the predominantly meroplanktonic nature of scyphozoans is challenged solely by the holoplanktonic *Pelagia* and *Periphylla*, lacking a polyp stage in their life cycle (Jarms, 2010). However, comprehensive knowledge of scyphozoan life cycles remains limited, with only about 50 out of nearly 250 species having fully described life cycles (Jarms, 2010, Jarms and Morandini, 2019). In this study, scyphozoan species with undisclosed life cycle details were provisionally classified as meroplanktonic for analytical purposes. Yet, a more thorough understanding requires additional data, especially from deep-sea species that can have different life cycle features (Morandini, personal communication). Among the scyphozoan genus documented in the region, *Atolla* Haeckel, 1880, *Discomedusa* Claus, 1877, *Mawia* Avian et al., 2016, *Paraphyllina* Maas, 1903, *Periphyllopsis* Vanhöffen, 1902, and *Poralia* Vanhöffen, 1902 have only their free-swimming stage described, with their complete life cycles yet to be documented.

The study region observes five staurozoan species, which may appear limited in number but represent 10% of the class's diversity. The absence of recorded staurozoans in the Azores and Madeira is likely due to limited investigations on this group. Global distribution patterns, concentrated in mid-latitudes, suggest the unlikelihood of staurozoan absence in both archipelagos (Miranda et al., 2018). Scarcity of scientific research locally and globally, contributes to the limited available

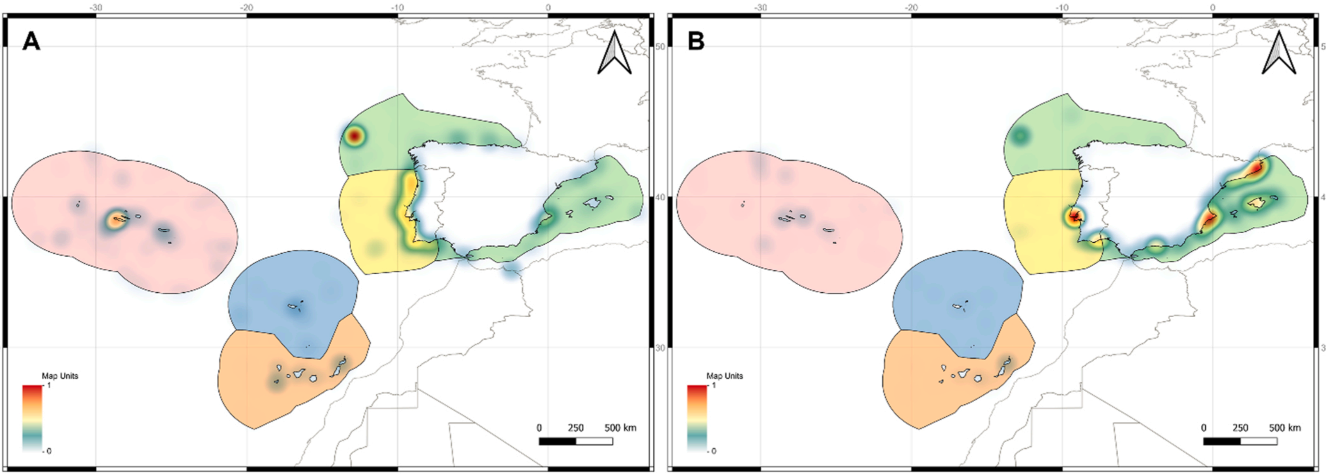

Fig. 7. Heatmaps of Medusozoa distribution in the Iberian region. A: Hydrozoa. B: Scyphozoa. Heatmaps represent the marine reports available in Table A1.

information on this taxonomic group. Notable exceptions are the publications by Miranda et al. (2010, 2012, 2016a, 2016b, 2017a, 2017b, 2018, 2023), Miranda and Collins (2019).

Limited data on Cubozoa in the Iberian region comprises two species: *C. marsupialis*, reported throughout the Mediterranean and considered native (Gueroun et al., 2015, Acevedo, 2016), and *C. sivickisi*, recently reported in the Canary (Moro et al., 2020). The latter report raises questions given the absence of other Iberian reports and misidentifications observed in previous studies mistaking other cubozoan species for *C. marsupialis* (Acevedo, 2016). On the other hand, Schlaefer et al. (2020) propose *C. sivickisi* as a cosmopolitan species, supporting its presence in the Mediterranean Sea. The absence of cubozoans and staurozoans in the Azores and Madeira archipelagos aligns with Gueroun et al. (2021), who also observed no cubozoan records in the Macaronesia region, of which the Azores and Madeira archipelagos are a part.

This research extends the data compilation initiated by Rodrigues et al. (2020), originally focused solely on Portugal. The current analysis reveals a substantial increase of 135 species reported in Portugal, encompassing mainland Portugal, Azores, and Madeira, rising from 272 in Rodrigues et al. (2020) to 407 in the present study. This expansion is attributed to the use of GBIF, iNaturalist and OBIS data, along with an expansion of the literature volume revisited, especially older publications predating the 1960 s. It is important to acknowledge that certain species likely no longer inhabit the region, possibly facing local extinctions. This assumption is supported by the absence of recent reports for several species documented in the past, such as *Atolla bairdii* Fewkes, 1886 (Maas, 1904, Broch, 1913), *Atolla verrillii* Fewkes, 1886 (Vanhöffen, 1902, Broch, 1913), *D. cyathiforme* (Haeckel, 1880), *Nausithoe rubra* Vanhöffen, 1902 (Ranson, 1945), and *Zygophylax pinnata* (G. O. Sars, 1874) (Pictet and Bedot, 1900). Conversely, it is equally or more plausible that other species may inhabit the area but have not yet been recorded. In fact, comparing the gathered results to other diversity studies provides an intriguing perspective. Gravili et al. (2015a) reported 115 non-siphonophore hydrozoan species in the Mediterranean Salento Peninsula, while the present study identified around 200 from Mediterranean records. Additionally, Bouillon et al. (2004) documented 457 hydrozoan species in the entire Mediterranean, whereas the current investigation found 549, with 256 belonging to Mediterranean reports. When accounting temporal evolution, following Gravili et al. (2015b) consideration, and focusing on species reported in the last decade, the total number of medusozoan species in the Iberian region decreases to 226, with less than 7000 records.

4.2. Distribution

Medusozoans in the Iberian region concentrate mainly along the coasts of Portugal and Spain, and in the Azores central group, with a notable concentration of records in the Northwest of Spain's EEZ. This "hotspot" is explained by a substantial number of Siphonophora records from the OBIS database, specifically sourced from the National Oceanography Centre Southampton dataset "Discovery Collections Midwater Database" (Pugh, 2000), reflecting extensive sample campaigns during *Discovery* sailings. This illustrates the importance of analytical caution. While compiled reports may not precisely reflect the actual prevalence of Medusozoa in the study area, the commendable effort acknowledges data limitations. To enhance diversity and distribution analysis, obtaining additional data through monitoring programs, such as the Portuguese GelAvista program, a citizen science project monitoring gelatinous organisms (GelAvista, 2023), and the CIESM JellyWatch Program, dedicated to recording jellyfish outbreaks across the Mediterranean Sea (CIESM, 2020) is crucial.

Results show that holoplanktonic medusozoans are more widely distributed and abundant than benthic and meroplankton species in the Iberian region (Fig. B5). This pattern aligns with the distribution of pelagic medusozoans and ctenophores in Macaronesia (Gueroun et al., 2021) and global patterns of medusozoan distribution and abundance (Boosten et al., 2023). These results confirm global trends indicating benthic and meroplanktonic medusozoans primarily found in coastal waters, while holoplanktonic species exhibit no specific preference for coastal or open waters (Boosten et al., 2023). The observed medusozoans diversity by life cycle showed higher diversity of benthic species, followed by holoplanktonic, and meroplanktonic. These results partially contradict the global trend that suggests that benthic species are indeed the highest diverse, but holoplanktonic species are typically less diverse than meroplankton (Gibbons et al., 2010). The importance of addressing the gaps in the current understanding of medusozoan life cycles becomes evident, as new knowledge can potentially alter observed trends.

The higher diversity of medusozoans in the Northeast Atlantic Ocean compared to the Mediterranean Sea can be attributed to several factors. For example, the Strait of Gibraltar, a narrow passage connecting the two seas, plays a crucial role in shaping water flow dynamics. The denser and saltier Atlantic waters form a surface layer that flows over the Mediterranean waters, while a subsurface current flows out of the Strait and into the Atlantic, with the latter having a lesser impact on the volume of water exchanged. (Margirier et al., 2020). The Northeast Atlantic Ocean, with its larger size, complex oceanographic regime, and enhanced connectivity to other waters, may provide a more diverse ecosystem with a wider range of habitats for medusozoans to thrive. In contrast, the Mediterranean Sea is a more stable and predictable environment, characterized by less niche differentiation and fewer nutrients that may limit the diversity of medusozoans (Powley et al., 2017). Additionally, human activities such as fishing, pollution, and coastal development may have greater impacts on the semi-enclosed Mediterranean Sea than in the wide-open Northeast Atlantic Ocean, leading to reduced global diversity of medusozoans.

There is a significant scarcity of information worldwide concerning the nature - whether native, introduced, or invasive - of medusozoan species, and the Iberian region is no exception. The GISD (2023) recognizes only one medusozoan species as invasive, the white spotted jellyfish *P. punctata*. The GRIIS catalogue (2022) provides further insights into invasive and introduced medusozoans in the Iberian region. However, recent sightings of *P. punctata* along the southwestern Atlantic coast of Spain (Enrique-Navarro and Prieto, 2020), have yet to be included. Additionally, the GRIIS acknowledges the rhizostomeae *Rhopilema nomadica* Galil et al., 1990 in its checklist for Spain as an introduced species, but despite extensive data compilation efforts, the occurrence of this species in the Iberian region could not be confirmed.

4.3. Omics disparity in Cnidaria: unraveling Anthozoa's wealth and Medusozoa's potential for bioprospection of natural compounds

The analysis of cnidarian omics metadata collected various repositories and literature, highlights a significant disparity between Anthozoa and Medusozoa, the two primary clades of the phylum. Approximately 80% of available omics data pertains to Anthozoa (Fig. B6), resulting in four times the amount of information available for Medusozoa. This aligns with the prevalent focus on bioprospecting for natural products within the Cnidaria phylum. Cnidaria stands as the second most extensively explored group of marine invertebrates in the search for novel natural products (Datta et al., 2015, Carroll et al., 2019), with most of these natural products being sourced from benthic Anthozoan species (Mariottini and Grice, 2016). This imbalance may be due the easier access to samples from anthozoans compared to medusozoans. Moreover, the available information on Cnidaria is concentrated on a few species, with the top seven cnidarian species holding over half of the total omics data of the phylum. These include anthozoans *Nematostella vectensis* Stephenson, 1935 and four species of *Acropora* Oken, 1815, along with the hydrozoan *H. vulgaris*. Notably, *H. vulgaris* constitutes approximately 60% of the total Medusozoa data, primarily due to its status as a model organism.

Genomes annotation is crucial for functional gene identification and protein characterization, aiding in metagenomics, transcriptomic, and proteomics studies. However, the annotated genomes from Cnidaria are limited to 33 from Anthozoa, six from Hydrozoa, and three from Myxozoa. Remarkably, there is an absence of annotated genomes from Scyphozoa, emphasizing the insufficient attention that jellyfish has received in omics studies despite the recent increasing interest. Most of the medusozoan omics data has been generated in the past five years, with a predominant focus on venom studies. The main objective of such studies is to identify and characterize the molecular structure, function, and mode of action of toxins. This information serves valuable purposes, including comparative analyses, exploration of bioactive compounds, and the development of more effective treatments for jellyfish stings in humans (Jaimes-Becerra et al., 2017, Choudhary et al., 2019, Wang et al., 2019, Riyas et al., 2021). Furthermore, omics studies can aid unravel the evolutionary and phylogenetic relationships of Medusozoans, shed light on their developmental processes and mechanisms of gene regulation, and provide insights into host-microbiota interactions (Lommel et al., 2018, Mortzfeld et al., 2018, Koch and Grimmelikhuijzen, 2019, Matsumoto et al., 2019, Rathje et al., 2020). Omics projects focusing on underexplored species holds promise for significant advancements in bioprospecting natural compounds with numerous relevant biotechnological applications (Chandhini and Rejish Kumar, 2019, Merquiol et al., 2019).

Exploring the omics of Cnidaria, with its rich diversity, involves extracting genetic material from various tissue types. The choice depends on the inherent characteristics of the organisms and the study objectives. Extract genetic material from small or low-cell content organisms, such as rich in water gelatinous medusozoans, can be challenging (Frazão and Antunes, 2016). Often, a collective pool of specimens or tissues is used to concentrate samples, addressing biological heterogeneity and enhancing quality control (Ames et al., 2016). Moreover, studies may encompass organisms at different life stages, providing a holistic understanding of the genetic landscape across developmental phases (Brekhman et al., 2015). Some investigations focus on organisms or tissues under distinct laboratory conditions, offering insights into the impact of environmental variables on genetic expression (Cziesielski et al., 2018). Other research may analyze specific tissues or structures to achieve their objectives (Ponce et al., 2016, Lommel et al., 2018). This versatility of omics studies ensures the alignment of research objectives and the characteristics of the organism under study.

5. Conclusion

Information on Medusozoa in the Iberian region is spread across more than 200 publications and thousands of reports available in public databases. This investigation brings together all this vast information in a collective dataset, comprising over 30,000 records of 593 Medusozoa species across four classes along with omics metadata covering the phylum Cnidaria. Addresses the challenge of dispersed and varied data formats, presenting a valuable preliminary resource for researchers and stakeholders.

Key findings from our comprehensive analysis shed light on critical aspects of medusozoan species, including the most prevalent with each class, those reaching highest abundances in specific EEZs, invasive and introduced species, bloom-forming organisms, and edible species. A sustained trend of discovering new Medusozoa species over time was observed in the examination, underscoring the untapped potential for further exploration in the region.

The surge in available omics data in recent years reflects a growing interest in unlocking the biotechnological potential of Cnidaria, and Medusozoa in particular. Although limited, studies have explored a range of topics, including analysis of novel toxins and other non-toxin compounds, evolutionary and phylogenetic relationships, developmental processes, gene regulation, and microbiome investigations. Additional data would be needed to obtain a more accurate view of Cnidaria in the Iberian context. As future work, it would be interesting to add Anthozoa data compiled from the literature, and integrate data from monitoring programs, such as citizen science initiatives.

This comprehensive compilation of data on medusozoan diversity and omics research establishes a sturdy groundwork for future research. It aids in pinpointing less-explored target organisms and underscores the pivotal role of certain species in the environment, society, and economy.

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Ethical statement

The authors confirm that they have permission for the use of all software in this review. Citations to appropriate and relevant literature are used throughout.

CRediT authorship contribution statement

Paulo A. V. Borges: Writing – review & editing. **Agostinho Antunes:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Daniela Almeida:** Writing – review & editing. **Francisco A. Guardiola:** Writing – review & editing. **Tomás Rodrigues:** Writing – original draft, Conceptualization.

Declaration of Competing Interest

The authors have no conflicts of interest to declare that are relevant to the content of this article. All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript. The authors have no financial or proprietary interests in any material discussed in this article.

Data availability

No data was used for the research described in the article.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.rsma.2024.103462.

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