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Studio delle foreste di idroidi e comunità associate nel Mar Mediterraneo con focus su una foresta di *Eudendrium racemosus* nello Stretto di Messina

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Abstract

This thesis examines the environmental role of hydrozoans (Hydrozoa) with regard to their ecological functions, trophic interactions, and symbiotic relationships within marine ecosystems in the Mediterranean Sea. Hydrozoans are highly diverse organisms and their remarkable phenotypic plasticity, coupled with undeniable biological complexity, makes them essential for the preservation of biodiversity and the functioning of benthic habitats (Bouillon, et al., 2006).

Focusing on the Mediterranean Sea ecosystem, the subject of this research, hydrozoans account for approximately 10% of global species. Yet, despite their numerical relevance, they remain relatively understudied compared to other components of marine fauna (Gravili et al., 2013). To address this gap, a systematic review of the literature was conducted, analyzing the geographical distribution, life cycles, trophic strategies, and symbiotic relationships of over 200 Mediterranean hydrozoan species. This review revealed a limited number of studies on the hydrozoan microbiome, despite evidence that hydrozoans significantly influence benthic community structure. They achieve this dual role as predators and ecosystem engineers by creating complex three-dimensional habitats, such as "hydrozoan forests" (Di Camillo, et al., 2006).

Building on these findings, the final section of this thesis focuses on the hydrozoan forest of *Eudendrium racemosum* located in the Strait of Messina. This area is of ecological interest due to its geographical uniqueness, characterized by strong currents and high biodiversity. Field research conducted along the Pellaro coast highlighted the importance of *E. racemosum* as a structural and functional element of the ecosystem, confirming literature findings regarding the role of hydrozoans in supporting biodiversity and benthic communities (Gravili, Boero, Alifano, & Stabili, 2012; Di Camillo, et al., 2012).

In light of the gaps identified in the scientific literature on hydrozoans and their microbiome, this thesis presents the first comprehensive investigation of the subject, examining their interactions not only with the surrounding environmental matrix but also with associated predators, particularly nudibranchs. To this end, the microbiomes of hydrozoans and three common nudibranch species associated with them (*Flabellina affinis*, *Cratena peregrina*, and *Dondice sp.*) were analyzed with the aim of describing the bacterial taxonomic composition of this holobiont and identifying similarities and differences in the acquisition of prokaryotic symbionts among the studied organisms and their surrounding environment. Currently, no data are available in the literature regarding the microbial community associated with these three Mediterranean nudibranch species.

The results demonstrate the co-occurrence of bacterial taxa specific to both nudibranchs and hydrozoans, as well as the influence of prokaryotic microorganisms from the surrounding environment, such as water and sediments. The findings further suggest that the hydrozoan-nudibranch complex acquires part of its microbiome through horizontal transmission from these environmental matrices. Additionally, specific bacterial taxa, unique to the microbiomes of hydrozoans and nudibranchs and absent from the surrounding environment, were identified, supporting mechanisms of vertical transmission of symbionts between hydrozoans and their associated nudibranchs.

Vertical transmission highlights the existence of a strong symbiotic relationship between benthic organisms and their associated fauna, contributing significantly to the understanding of microbial dynamics and marine biodiversity.

Beyond the findings of this research, which further underscore the potential of hydrozoans as environmental indicators and ideal models for studying the impacts of climate change on marine ecosystems, remains a need for further studies. This is particularly true for less explored regions in the scientific literature, such as the Calabrian coasts. Such research would help fill existing knowledge gaps regarding the ecology and trophic roles of hydrozoans within marine food webs. Concurrently, these investigations could open new avenues in pharmacology, given the biological and chemical diversity of hydrozoan holobionts and their potential applications in the development of novel drugs.

Summary

CHAPTER 1
INTRODUCTION

Cnidarians hold a foundational role in evolutionary biology as basal metazoans and are ecologically significant as predators, prey, and structure-builders (Goffredo & Dubinsky, 1998; Santos, et al., 2020).

They represent the most primitive metazoans from a biological perspective, making the understanding of their evolution crucial for studying the origins of animals (Feng, et al., 2023). Consequently, the phylogeny of Cnidarians has been a subject of debate for decades and remains unresolved for certain taxa (McFadden, van Ofwegen, & Quattrini, 2022; Kayal, et al., 2017). Investigating the origins and evolutionary history of the phylum Cnidaria reveals the foundations of their ecological success. However, key mechanisms driving the emergence and diversification of important traits—such as symbiosis, colonial body structures, complex life cycles, and the evolution of cnidocytes—are still areas of ongoing debate. Nevertheless, a generally accepted Cnidarian phylogeny, supported by morphological evidence, evolutionary traits, and molecular data, has been established (Daly, et al., 2007a).

Through a phylogenetic analysis, Kayal et al. (2017) identified two major clades within the phylum: Medusozoa and Anthozoa. Medusozoa includes Cubozoa, Hydrozoa, and Scyphozoa, while Anthozoa encompasses Octocorallia and Hexacorallia. The researchers noted that the Medusozoa clade is supported by several morphological and molecular features, including the presence of stinging cells known as nematocysts and a subumbrellar cavity in the bell-shaped body of jellyfish (Kayal, et al., 2017). Within Medusozoa, Kayal et al. (2017) found that Cubozoa are a sister group to a clade comprising Hydrozoa and Scyphozoa. Furthermore, they suggest that the Anthozoa clade is defined by the presence of mesoglea, a gelatinous layer between the outer and inner cell layers, which is absent in other cnidarians. This clade is further subdivided into Octocorallia and Hexacorallia, which are differentiated by the number and arrangement of their tentacles and the presence or absence of an internal skeleton.

Although the phylogenetic relationships of Cnidarians are still debated, recent studies utilizing morphological, transcriptomic, and genomic data have made progress in unraveling this complex issue (Chang, Aeschbach, Duffy, & Czeisler, 2015; Kayal, et al., 2017). Despite some discrepancies across studies, a significant congruence has emerged in the evolutionary reconstructions of cnidarian lineages, underscoring the importance of large genomic datasets and expanded taxonomic sampling to address evolutionary questions (Young & Gillung, 2019).

As previously mentioned, attempting to reach a conclusion about their evolutionary process, it seems likely that all Cnidarians evolved from an ancestral, solitary, non-symbiotic polyp with stinging cells and a planula larva, lacking a medusa stage. Traits such as symbiosis, coloniality, and the development (or loss) of a medusa stage have independently arisen during Cnidarian evolution (Technau & Steele, 2011).

Hydrozoans represent a highly diverse and complex class of organisms with varied life cycle patterns and morphological traits (Daly, et al., 2007; Goffredo & Dubinsky, 1998; Khalturin, Shinzato, Khalturina, Hamada, & Fujie, 2019). They play a crucial role as predators in aquatic ecosystems, influencing habitat dynamics and community structure. Their presence, abundance, and diversity can serve as indicators of ecosystem health. Research on hydrozoans may lead to the development of new tools and technologies in marine biology and medicine, as these organisms produce compounds with potential antitumor and antibiotic properties (Goffredo & Dubinsky, 1998; Santos, et al., 2020).

The challenges in understanding their evolutionary history and relationships remain significant, but ongoing research and technological advancements will undoubtedly provide further insight into these fascinating organisms.

1.1 Hydroids

Hydrozoans are predatory invertebrates that inhabit various aquatic ecosystems, including freshwater, brackish, and marine environments (Daly, et al., 2007). Although freshwater hydrozoan species have been identified, the majority are marine in origin. In fact, according to Daly et al. (2007), approximately 3500 species of hydrozoans have been documented, with about 100 freshwater species currently known (Daly, et al., 2007). Hydrozoans belong to the phylum Cnidaria, alongside corals, jellyfish, and sea anemones, and represent the most basal clade of cnidarians. Based on combined molecular and morphological data, the group is considered paraphyletic, comprising four major evolutionary lineages: Hydroidolina, Trachylina, Staurozoa, and Cubozoa (Kayal, et al., 2018).

Hydrozoans exhibit complex life cycles that occur in both pelagic and benthic environments (Bryant & Arehart, 2019). Pelagic hydrozoans include hydromedusae (the sexual phase) and species belonging to the order Siphonophora, which form large polymorphic colonies. Benthic hydrozoans consist of solitary or colonial hydroids as well as meiobenthic hydrozoans (Daly, et al., 2007).

While “hydrozoans” is the correct term to refer to the entire class, which includes a wide range of marine species such as hydromedusae and hydroids, the term “hydroids” refers to a specific subgroup. Hydroids represent a particular phase in

the life cycle of hydrozoans, where they form colonies that are fixed to a substrate, composed of polyps. In the following discussion, the term “hydroids” will be used because the focus is often on the fixed colonial polyp forms, i.e., hydroids, rather than the entire class of hydrozoans, which also includes other forms such as medusae (Watson, 2024).

The reproductive strategies of hydroids are diverse and intricate. They are known to reproduce both asexually and sexually (Danko, Schaible, Pijanowska, & Danko, 2018). Asexual reproduction in hydrozoans occurs in benthic environments through processes such as budding, stolons, and fragmentation. In contrast, sexual reproduction involves the release of gametes, which, following fertilization, develop into planula larvae that ultimately metamorphose into benthic hydrozoans (Fernandez, Collins, Gittenberger, & Roy, 2020; Leclère, Copley, Momose, & Houliston, 2016). An in-depth description of hydroids’ life cycles is reported in paragraph 1.3.

Hydrozoans are filter-feeding predators and, as such, they ingest a variety of organisms, including bacteria, phytoplankton, fish larvae, crustaceans, epibenthic creatures, and dissolved organic matter. For example, *Eudendrium racemosum* (Cavolini, 1785) preys on numerous taxa, including copepods, nematodes, gastropods, bivalves, and polychaetes (Cavolini, 1785).

Similarly, *Perarella schneideri* (Motz-Kossowska, 1905) inflicts damage on and destroys its colonies through trophic interactions that adversely affect *Schizoporella* (Hinks, 1877) colonies, which serve as their substrate, rendering them vulnerable to microbial infections. This case exemplifies a cleptocommensal strategy where the hydrozoan exploits organic material gathered by the bryozoan’s lophophore and is subsequently exploited by halacarid mites (Bavestrello, et al., 2000).

Coma et al. (1995) provide the first evidence of a hydrozoan species (*Campanularia everta*; (Clark, 1877) whose diet is primarily composed of suspended particulate organic matter (POM) (Coma, Ribes, Zabala, & Gili, 1998). Furthermore, although hydrozoans have traditionally been regarded as carnivorous, it has been observed that *Obelia dichotoma* (Linneaus, 1758), found in the Arctic Kongsfjorden, shows consumption rates of fecal pellets, organic matter, and microalgae that are comparable to or even exceed those of zooplankton. Such findings suggest that hydrozoans may not only be carnivorous but also omnivorous, with prey items other than zooplankton, such as fecal pellets, phytoplankton, and benthic microalgae, playing a significant role in their gastrovascular cavities. This omnivorous feeding strategy, with a preference for small particles, is consistent with the feeding habits of the planktonic stage of *Obelia* species (Orejas, Rossi, Peralba Marcó, & García, 2012).

Some hydrozoan species host symbiotic algae that assist in nutrient fixation. In particular, the relationships between hydrozoans and diatoms are predominantly trophic. The diatoms living in the confined space between the hydrothecae and polyps form specific associations with their hydrozoan hosts. In return for the limited space they share with the hydrozoan species, the diatoms receive both protection and nutrients derived from the hydrozoans' metabolism. Furthermore, they benefit from sunlight that penetrates through the transparent thecae, reaching the diatom layer and facilitating their photosynthesis (Di Camillo, Betti, Bo, & Martinelli, Contribution to the understanding of seasonal cycle of Aurelia aurita (Cnidaria: Scyphozoa) scyphopolyps in the Northern Adriatic Sea, 2010).

When present in large quantities, hydrozoans are regarded as some of the most significant predators in both benthic and planktonic communities (Bouillon, Gravili, Gili, & Boero, 2006).

In benthic environments, they are among the first metazoans to colonize new substrates and, as previously noted, serve as hosts for other species, thereby creating additional conditions for subsequent colonization. Substrate preference varies among different hydrozoan species, and such preferences influence their growth, survival, and reproductive strategies. Hydrozoans are also capable of establishing symbiotic relationships with a wide range of marine phyla. While they are pioneering species that quickly settle on previously uncolonized substrates, they can also establish themselves as epibionts when outcompeted by more efficient competitors (Boero, 1984; Riedl, 1966; Puce, Bavestrello, Di Camillo, & Boero, 2007). For instance, hydrozoans are cnidarians that form symbiotic associations with various marine groups. While many exhibit generalist substrate preferences, some, such as *Halocoryne epizoica* (Hadzi, 1917), show more specific associations, being closely linked to a single bryozoan species (Pantos & Bythell, 2010). The ability to settle on/in the tissues or on the skeletal structure so flying organisms, allows hydroids to form new ecological niches at low degree of competition. It leads to the evolution of taxa specialized in symbiosis with a particular phylum and it offers wide possibilities of speciation (Bavestrello, 2008).

The benthic habitats of hydrozoans exhibit considerable diversity, ranging from estuaries to deep-sea trenches. They are found on rocky and sandy bottoms, on macroalgae, and on various epifaunal and in faunal substrates. Some species form colonial structures such as tubes and mats, while others develop as solitary individuals (Gili & Hughes, 1995). Benthic hydrozoans are recognized for their crucial role within their habitats, as they significantly enhance the biodiversity and ecological dynamics of benthic ecosystems (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017).

Hydrozoans are known for their sudden “meadows” or “forests” of exceptional abundance (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017), and an increase in their numbers is typically detrimental to the ecosystem, as they consume ichthyoplankton and small zooplankton, acting as predators and competitors of fish, fish eggs, and fish larvae (Soto, Sanvicente-Añorve, & Espinosa-Fuentes, 2006). Consequently, understanding the ecology and life history of hydrozoans is crucial, given their role as key components in aquatic ecosystems and their significant impact on the food web, making it essential from a biological and evolutionary perspective (Savoca, Fresco, Alesci, Capillo, & Spanò, 2022).

The morphological diversity of hydrozoans is reflected in their ability to fulfill various ecological roles and their adaptability to a wide range of environmental conditions. Some species can tolerate high or low water flow rates, deep or shallow environments, and different salinities (Bouillon, Gravili, Gili, & Boero, 2006).

Certain hydrozoans play a crucial role in nutrient cycling and energy transfer within ecosystems. For instance, *Lytocarpia myriophyllum* (Linneaus, 1758) functions as an ecosystem engineer by creating habitats with stable edaphic conditions. This results in a buffering zone that mitigates fluctuations in environmental parameters compared to the surrounding terrestrial and aquatic environments. *L. myriophyllum* is also vital for sediment stabilization and influences local biodiversity through its intricate root-like system. Hydrozoans belonging to the family Aglaopheniidae, including *L. myriophyllum*, capture suspended organic particles, although their capture rate is lower than that of carnivorous hydrozoans. Sediments colonized by *L. myriophyllum* exhibit lower organic loads compared to adjacent uncovered sediments, indicating a selective feeding on freshly produced organic matter. The filtering activity of *L. myriophyllum* not only affects the quantity of organic matter in the sediment but also its nutritional quality by selectively intercepting sinking particles. Additionally, the root-like system of *L. myriophyllum* also impacts the nutritional quality of the organic matter in the underlying sediments.

Hydroids are recognized for their considerable phenotypic plasticity, which allows them to adjust to varying environmental pressures and conditions (Pazzaglia, Reusch, Terlizzi, Marín-Guirao, & Procaccini, 2021). Certain species can endure significant fluctuations in salinity, while others can adapt to both high and low water flow rates. This blend of extensive genetic variability and phenotypic adaptability positions hydroids as effective indicators of environmental changes.

Anthropogenic factors, such as pollution, overfishing, and climate change, negatively affect hydroid populations (Bouillon, Gravili, Gili, & Boero, 2006). For instance, climate change leads to shifts in species distribution, with some species moving towards cooler regions or deeper waters to avoid higher temperatures.

Similarly, pollution hampers the growth and survival of hydroids due to the accumulation of contaminants in their tissues.

Understanding the ecology and biology of hydroids is therefore valuable for managing and protecting aquatic ecosystems, particularly in response to anthropogenic stressors and global changes.

1.2 Distribution

The distribution of animal species in marine environments is influenced by a variety of factors, including currents, temperature, salinity, sediment type, productivity, and biotic interactions within the ecosystem (Bertness, Leonard, Levine, & Bruno, 1999). Research suggests that species diversity decreases with increasing latitude, as species are constrained by their thermal tolerances (Hiddink & Hofstede, 2008). Similarly, the variety of species is affected by tidal regimes, which shape the distribution of intertidal organisms along vertical gradients. Additionally, environmental changes, such as ocean acidification and global warming, alter species distribution patterns and impact the functioning and diversity of marine ecosystems (Hoegh-Guldberg & Bruno, 2010).

Like other marine invertebrates, hydroids are globally distributed with uneven patterns due to their dispersal behaviors and environmental variability. They inhabit a wide range of aquatic environments, including freshwater, brackish, and marine habitats, with distribution patterns varying by region and species. For instance, hydroid diversity is higher in tropical and subtropical regions, with high densities observed in coral reef ecosystems. In contrast, their distribution in polar environments is more restricted due to extreme environmental conditions, such as low water temperatures and limited food availability, which impact their colonization potential (Gori, et al., 2013). Research indicates that hydroids are distributed across 232 ecoregions (Miranda, Fernandez, Genzano, & Peña Cantero, 2021), forming part of the new classification system for coastal and shelf area planning, Marine Ecoregions Of the World (MEOW) (Spalding, et al., 2007).

Fernandez et al. (2020) examined the functional traits of hydrozoans in relation to environmental conditions across various biogeographic regions. The researchers found that, particularly in high-energy environments, hydrozoan colonies tend to be smaller and more complex compared to those found in low-energy settings. Additionally, hydrozoans inhabiting environments with significant seasonal variability in temperature and productivity exhibit higher reproductive output, although their growth rates are slower compared to those in more stable environments (Fernandez, Collins, Gittenberger, & Roy, 2020).

Regarding the Mediterranean Sea, it is renowned for its rich biodiversity, hosting approximately 13200 species, including 229 hydrozoans (Coll, et al., 2010; Gravili, Di Camillo, Piraino, & Boero, 2013). Only a small portion of the hydrozoan fauna, about 8%, shows Indo-Pacific characteristics and is predominantly found in the eastern Mediterranean, likely having arrived from the Red Sea via the Suez Canal. Acclimatized Lessepsian species have become so numerous that a separate biogeographical province has been established for this part of the basin. In contrast, the western Mediterranean exhibits biological and biodiversity affinities with the Atlantic (Galil, 2008). Chapter 2 of this thesis provides a detailed overview of hydrozoans in the Mediterranean Sea. Understanding the ecology and distribution of hydrozoans is closely linked to biogeographical and environmental factors, such as ocean currents, water temperature, and salinity. Further research and monitoring are needed to better understand the global distribution patterns of these organisms, which would aid in predicting the impacts of environmental changes and developing effective conservation strategies (Coll, Pennino, Steenbeek, Sole, & Bellido, 2019).

1.3 Life cycle

The basic life cycle of hydroids features a relatively long-lived diploid polyp stage that produces jellyfish by asexual budding. Jellyfish are motile, short-lived and the sexual stage produces gametes by meiosis. The developing embryo usually produces a planula that swims or crawls towards a suitable substrate to metamorphose into the polyp stage. There is a debate about the terminology of these different phases. One view is that the planula is a prolonged gastrula, the polyp stage should be regarded as the larval stage, and the medusa is the adult stage. The alternative view is that the planula is the larva, the long-lived polyp stage the adult, and the jellyfish simply short-term vehicles for the gonads, which evolved later to circumvent the increased mortality of the polyp stage (Gili & Hughes, 1995; Lechable, Jan, Duchene, & Uveira, 2020).

The term “polyp” is used both to describe the stage (hydroid is the polyp stage) and as a collective name for the different types of “polyps” on hydroids. Each hydroid colony includes several hydrants (feeding polyps), gonangia (reproductive polyps), and, in some species, specialized polyps including dactylozoids and pneumatophores (Gili & Hughes, 1995). There are many different variations of the basic polyp-jellyfish-planula life cycle model, illustrating the evolutionary and developmental plasticity of hydroids (Hyman, The polyclad flatworms of the Atlantic Coast of the United States and Canada, 1940; Naumov, 1960).

The most obvious change is the loss of a free-swimming jellyfish in about half of the species whose life cycle is known (Naumov, 1960; Boero, Bouillon, & Danovaro, 1987; Bouillon, Boero, & Fraschetti, 1991).

Hydroids are aquatic animals that possess a unique life cycle, consisting of multiple developmental stages, including both sexual and asexual reproduction mechanisms. The first phase of the life cycle involves the planula larva, which is a free-swimming stage that disperses the organism. Once the planula settles onto a substrate, it undergoes metamorphosis and transforms into a sessile polyp. During the strobilation process, the polyp produces one or more medusae, which are small, disk-shaped organisms that bud off from the polyp. These medusae are responsible for the sexual, free-swimming phase of the life cycle. Once mature, the medusae release gametes, leading to fertilization and the formation of planula larvae. The larvae are then ready to settle down and start the life cycle again (Marques & Collins, 2004; Fernandez, Collins, Gittenberger, & Roy, 2020).

A different example of sexual reproduction can be seen in the feather hydroid *Nemertesia antennina* (Linneaus, 1758), where male and female polyps produce sperm and eggs, respectively. When the sperm and egg meet, fertilization occurs, and the resulting zygote undergoes metamorphosis, becoming a planktonic larva that settles on the seabed and transforms into a new polyp (Gili & Hughes, 1995).

Hydroids have also several mechanisms of asexual reproduction, including budding and fragmentation. In budding, the parent polyp generates a small bud, which separates and develops into an independent polyp, such as in freshwater hydras, like *Hydra vulgaris* (Pallas, 1766). Fragmentation occurs when a small fragment of a hydroid, such as the fire coral *Millepora alcicornis* (Linnaeus, 1758), breaks off and develops into a new colony independently. This process is crucial for the coral colonies' survival when they suffer damage to their structures (Boero, 1984).

The hydrozoan *Eudendrium racemosum* (Cavolini, 1785) uses a specific form of asexual reproduction called stoloniferous budding. In this mechanism, a horizontal stolon develops new polyps in a line, allowing them to reproduce both sexually and asexually and enhance their adaptability in various environments.

The colonial hydroid *Obelia dichotoma*'s (Linneaus, 1758) life cycle involves a planula larva that develops into a polyp. This polyp generates multiple buds that develop into elongated, chain-like hydrocladia, which contain multiple polyps that generate medusae through the process of strobilation. The mature medusae release gametes, leading to fertilization and the creation of planula larvae that are ready to start the life cycle all over again (Boero, Balduzzi, Bavestrello, Caffa, & Cattaneo-Vietti, 1986).

The life cycle of the hydroid *Bougainvillia muscus* (Hodge, 1863) includes an oblate polyp phase and a heavily reduced medusa phase. The polyp phase generates several branches that bear a small number of gonophores (medusa buds) that develop into small, disk-shaped medusae. These tiny medusae mature and release gametes, leading to fertilization and the creation of a planula larvae that metamorphoses into a new polyp colony (Boero, Balduzzi, Bavestrello, Caffa, & Cattaneo-Vietti, 1986).

The above-mentioned examples represent just few cases of hydroids' life cycle but are enough to give an idea of their incredible adaptability to environmental factors such as temperature, food availability, and predation by adopting diverse morphologies and reproductive strategies. Other particular cases show how some hydroids reduce their medusa phase and reproduce asexually by budding new polyps under low food availability conditions. Some hydroids increase their asexual reproduction in favorable conditions, such as increased food availability or reduced predation, forming dense mats or colonies anchored to rocky substrates (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017; Gili & Hughes, 1995).

1.4 Hydroid forests

Hydroids, as already mentioned, are key components of zoobenthic communities, with growth patterns which remember the ones of higher plants due to their modular organization, asexually reproductive potential, and phenotypic plasticity (Tanasovici, Dias, Kitahara, & Vieira, 2022). They can survive unfavorable conditions by entering a dormant state, making them adaptable to a wide range of environmental scenarios. Hydroids form three-dimensional forests and establish both trophic and non-trophic relationships with various organisms, from viruses to vertebrates.

The Hydrozoa colonies exhibit diverse growth forms, including uniserial and multiserial patterns (Bouillon, Gravili, Gili, & Boero, 2006). Uniserial colonies, also called "runners," do not form large assemblages, while multiserial colonies perform lateral and distal growth and have the potential to form large assemblages, similar to trees (Patzkowsky, 1988). Philopatric colonies can produce genetically identical colonies, called ramets, that together form a genet, comprising genetically identical ramets (Patzkowsky, 1988).

Small polyp hydroids grow on organisms or primary substrates and act as habitats for other species, while larger colonies form substrate for other organisms and can form forests comparable to those of algae or gorgonians, enhancing local biodiversity (Ponti, Gutierrez, Ruti, & Dell'Aquila, 2014; Valisano, Notari, Mori, & Cerrano, 2016; Gori, et al., 2020; Zelli, et al., 2020). Hydroid ecology needs

further exploration to understand their ecological role and potential to enhance local biodiversity in aquatic ecosystems (Tanasovici, Dias, Kitahara, & Vieira, 2022).

Hydroids, in fact, can change the geological habitat features by affecting water movement, light penetration, and providing settling space, shelter or food to other species. Hydroid forests release planulae, medusoids, or medusae that contribute to benthopelagic coupling and affect biogeochemical cycles (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017). These features give hydroids high plasticity, resulting in potentially unlimited growth and adaptation of their shape, growth strategies, trophic behavior, and reproductive strategies, among other features, to different environmental conditions (Boero, 1984; Gili & Hughes, 1995; Bouillon, Gravili, Gili, & Boero, 2006).

Despite their crucial ecological role, hydroids are often underestimated in the classification of habitats and benthic communities research, mainly due to the lack of hydroid specialists in the definition of habitats, coupled with insufficient quantitative data (Becerro, 2008). Moreover, field activities in favorable seasons dominated by algae lead to the underappreciation of hydroids and their importance in structuring benthic communities (Tanasovici, Dias, Kitahara, & Vieira, 2022).

1.5 Interspecific relations

Hydroids establish a range of symbiotic relationships with various organisms, making them versatile hosts and epibionts (Puce, Bavestrello, Di Camillo, & Boero, 2007). These colonies provide microhabitats exploited by a diversity of organisms. Organic matter trapped by hydroid colonies supports detritus-feeding communities, while inorganic matter under hydrorhiza can be used by organisms like amphipods for burrow-building (Bavestrello, 2008).

The perisarc, a hydroid's exoskeleton composed of polysaccharides and proteins, can host a wide range of protists and prokaryotes, including *Vibrio* species, which are known to be chitinolytic (Di Camillo, et al., 2012). Epibiotic microorganisms have been observed using electron microscopy and cultivation techniques on different hydroid species and within the same colony (Gorelova, Kosevich, Baulina, & Fedorenko, 2009; Di Camillo, et al., 2012). Few bacteria have been reported living on the epidermis of hydrozoans such as green Hydra, with gram-negative, rod-shaped bacteria found along the margin of the ectodermal cells (Chang & Huang, 2014).

Instead, several species of hydrozoans host bacteria within their tissues. In *Hydra circumcincta* (Schulze, 1914), spirochetes are located extracellularly and within vacuoles of epithelial muscle cells. The gastrodermis of some strains of *Hydra viridissima* (Pallas, 1766) contains bacterial vesicles associated with cells

containing the symbiotic green alga *Chlorella sp*. (Guiry & Guiry, 2024). Nine species of bacteria are discovered living inside the epidermal cells of the hydrozoan *Tubularia indivisa* (Linneaus, 1758), leading to the hypothesis of their involvement in cnidarian toxin production (Schuett & Doepke, 2010; Di Camillo, et al., 2012).

Hydroids enhance biodiversity by providing complex three-dimensional microhabitats for the settlement and survival of other organisms. Large hydroids provide surfaces for a wide range of taxa (Bremec, Guglielmetti, & Irigoyen, 2008). Hydroid colonies as (*Amphisbetia operculate* (Linneaus, 1758), *Plumularia setacea* (Linneaus, 1758), *Symplectoscyphus subdichotomus* (Kirchenpauer, 1884) can also be a primary substrate for the recruitment of other invertebrates, including mussel and scallop spats (Bremec et al., 2008).

Some large forest-forming hydroids such as *Millepora spp*. (Linneaus, 1758) and *Pachyrhynchia cuppressina* (Kirchenpauer, 1884) host zooxanthellae which potentially contribute to their success by obtaining nutrition from autotrophic sources. Stylasterid corals enhance habitat complexity by providing refuge, food, and a substrate for different sessile and vagile invertebrates (Braga-Henriques, Tavares, & Costa, 2011; Salvati, Angiolillo, Bo, & Bavestrello, 2010).

1.6 Trophic ecology

Hydroids use trophic strategies to optimize their reproductive effort, with their reproductive period overlapping, at least partially, with increased food intake and maximum colony size (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017). They form large colonies and forests only where there is food availability to support their development (Gili & Coma, 1998) and can resist excessive growth when present in dense aggregations by feeding on approaching larvae of competitors (Sutherland & Karlson, 1977).

Hydroids use different trophic strategies, ranging from passive to active feeding and mixotrophy, depending on the species. Active filter feeders use microcurrents to attract food particles towards the mouth, while passive filter feeders extend their tentacles and wait for prey (Miglietta, Della Tommasa, Denitto, & Gravili, 2000). Specific studies have found that small polyps mainly eat small foods such as protists, while large polyps capture larger prey such as crustaceans (Miglietta, Della Tommasa, Denitto, & Gravili, 2000).

Experimental studies have shown that hydroids can exploit large amounts of sexton and contribute to controlling the secondary production in coastal waters (Gili & Coma, 1998; Gili & Hughes, 1995). Hydroids feed on a range of prey, including zooplanktonic preys, eggs, meiobenthic larvae, phytoplankton, bacteria, and detritus, and vary their prey composition and predation rates based on various

factors such as hydroid species, prey size, and environmental conditions (Coma, Ribes, Zabala, & Gili, 1998). However, the total carbon intake of hydroid species is comparable to that of other suspension feeders (Gili & Coma, 1998). Certain species, such as *Lytocarpia myriophyllum* (Linneaus, 1758), could remove large amounts of seston due to their high number of feeding polyps (Cerrano, et al., 2019).

Hydroids have been observed to resist overgrowth when present in dense aggregations (forests), contributing to the proposal of the inhibition model as one of the modes of community development (Connell & Slatyer, 1977; Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017). Trophic strategies are adopted by hydroids to optimize their reproductive effort, with some species, such as *Eudendrium*, producing planulae that settle directly in the vicinity of the mother colony (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017). Reproductive strategies play a crucial role in the maintenance of perennial hydroid forests, with extensive colonies displaying a combination of reproductive mechanisms. These strategies include both sexual and asexual reproduction, which contribute to the resilience and stability of hydroid populations over time, strategy of planulae and old colonies that regenerate from the resting stolon's (Boero, Balduzzi, Bavestrello, Caffa, & Cattaneo-Vietti, 1986).

Hydroids play a crucial role in the trophic structure of marine ecosystems by exerting significant control over secondary production in coastal waters. However, their ecological role and potential for enhancing local biodiversity in aquatic ecosystems remain underappreciated, necessitating further research into hydroid ecology (Miglietta, Della Tommasa, Denitto, & Gravili, 2000).

1.7 Hydroids Strait of Messina

The Strait of Messina is a narrow channel that connects the Ionian Sea with the Tyrrhenian Sea, separating the Italian mainland from the island of Sicily. Biologically, it serves as a crucial exchange zone for water masses and nutrients between different regions, making it a renowned area for biodiversity, not only within the Strait itself but also throughout the central Mediterranean Sea (Cucco, et al., 2016; Spanò & De Domenico, 2017).

The Strait of Messina features a distinctive underwater profile resembling a mountain, with slopes varying from the Sicilian to the Calabrian coasts. Additionally, the physical and chemical parameters of the Ionian and Tyrrhenian basins that converge in the area differ significantly, leading to strong currents generated by fluctuations in surface water levels during tidal changes (Ridente, Martorelli, Bosman, & Chiocci, 2014). The hydrodynamic characteristics of the

Strait are also linked to geological parameters, including its structure and intense tectonic activity. This combination of factors influences not only sediment distribution but also the unique benthic ecosystem present in the region (Spanò & De Domenico, 2017).

Specifically, the northern section of the Strait is characterized by the Valley of Scilla, a wide and deep depression that becomes less steep as it approaches the Tyrrhenian Sea. In contrast, the southern section contains the Messina Valley, a broad and irregular depression that transitions into a steep canyon (Messina Canyon) extending down to the Ionian Bathyal Plain. Over the centuries, the distinctive topography of the seafloor and the hydrodynamic conditions, combined with low water temperatures, have fostered numerous exclusive communities of Atlantic origin (Serpelloni & Burgmann, 2010).

The Strait of Messina is a notable area for observing species migration between the two basins. Its physical characteristics significantly affect the organisms residing there, creating a unique ecosystem in terms of biodiversity, biocoenosis, and species abundance. Given these factors, the Strait region has undergone extensive biological investigations and research (Spanò & De Domenico, 2017).

Numerous studies have examined marine ecology and biodiversity in the Strait of Messina. Castriota et al. (2017) investigated the composition, structure, and distribution of benthic communities in the shallow waters of the Strait, identifying a high diversity of species, including many endemics, that form complex and dynamic communities. The area also supports a significant diversity of hydroids, which serve as vital food sources for various pelagic and benthic organisms within the ecosystem of the Strait (Castriota, Falautano, Battaglia, & Maraventano, 2017).

Boero et al. (2003) conducted a study on hydroids in the Strait of Messina, revealing a high percentage of endemic species (Boero, Bouillon, Gravili, & Piraino, Who cares about the hydrozoa of the Mediterranean Sea? An essay on the zoogeography of inconspicuous groups., 2003). These hydroids have adapted to the unique physical and environmental conditions of the Strait, such as strong currents, salinity, and low turbidity. Consequently, they have become endemic species, although their distribution is influenced by local bathymetry, depth, water temperature, salinity, and currents (Bertolino, Boero, & Gravili, 2015).

1.8 Objectives

Due to the reasons described above, the organisms and the area of investigation have peculiarities that make their study interesting. These motivations have led to the orientation of research in this doctoral project on a forest of hydroids of *Eudendrium racemosus* found in the waters of the Strait of Messina, more precisely

along the coasts of Pellaro at a depth of approximately 20 meters and located 50 meters away from the coast.

Due to the vastness of the studied topic, it was chosen to first carry out a review on the state of the art of Mediterranean hydroids, to have a general overview of current knowledge and, above all, to identify the gaps that need to be filled on the subject. As reported, the acquired knowledge has oriented the research towards the investigation area of the Strait, which, compared to other areas of the Mediterranean Sea, has fewer studies on hydroids and on the study of the microbiome, biodiversity and trophic network associated with these organisms. As shown in the review, only two articles have been published on this topic in the Mediterranean Sea.

CHAPTER 2
MEDITERRANEAN HYDROIDS

2.1 Introduction

The Mediterranean basin's rich biodiversity is crucial for the region's ecological health and is also of global significance. It is home to numerous rare or endemic species that are found nowhere else in the world, making it a hotspot of biodiversity (Coll, et al., 2010).

The Mediterranean basin has a remarkable level of diversity when it comes to its hydrozoan species (Coll, et al., 2010; Gravili, Di Camillo, Piraino, & Boero, 2013). Despite covering only minimal fraction of the total surface area of the world's oceans (less than 0.8%), nearly 10% of all hydrozoan species can be found in this region (Bouillon, et al., 2006).

To better understand the ecological roles of these animals, a review of the current knowledge was conducted, focusing on their life cycles, trophic interactions, associated microbiome, and epibiotic relationships. The Mediterranean Sea is characterized by well-defined seasons, which lead to different ecological requirements and zoogeographical affinities for the fauna during the summer and winter months. This seasonality results in significant differences in the life cycles of hydroid species found in specific locations (Boero & Fresi, 1986). For instance, the study by Betti et al. (2017) provides new insights into the life cycles, zoogeography, and habitat preferences of a widespread hydrozoan, suggesting a close ecological relationship with seagrass ecosystems.

As in other marine ecosystems, Mediterranean hydroids play important roles in the transfer of energy through the food web, exhibiting a wide range of feeding strategies that are crucial not only to their own ecology but also to the broader Mediterranean food web. For example, the study by Cerrato et al. (2015) found that hydroids can significantly affect the biochemical composition of meiofauna, thereby impacting the Mediterranean's ecology and food web (Cerrano, Bianchelli, Di Camillo, Torsani, & Pusceddu, 2015).

The complex relationships between hydrozoans and microorganisms in marine environments have been investigated, as demonstrated by the research of Gravili et al. (2013) on the association between a luminous bacterium and the hydrozoan *Hydractinia echinata*. Gravili and collaborators discovered that the hydrozoan facilitates the growth of the bacterium by providing nutrients (Gravili, Boero, Alifano, & Stabili, 2012), while the bacterium supports the growth and reproduction

of the hydrozoan through the production of biofilm (Gravili, Di Camillo, Piraino, & Boero, 2013; Mergner, 1977).

In the Mediterranean basin, hydrozoans have also been found to support a variety of epibiotic organisms, including diatoms, bryozoans, and other invertebrates. Overall, the epibiotic relationships involving Mediterranean hydrozoans are complex and varied, impacting the organisms involved and the marine ecosystem in sometimes unexpected ways. The presence of epibiotic diatoms on *Eudendrium racemosum* has had numerous ecological implications for the hydrozoan, affecting its structural integrity, light interception, and overall fitness (Romagnoli, Totti, Accoroni, & De Stefano, 2014)

It is also important to consider that the Mediterranean basin represents a unique region with a high level of hydrozoan diversity, making the study and protection of its ecosystems beneficial both regionally and globally. In this regard, the study of hydrozoan life cycles, trophic ecology, and the evaluation of predator effects is crucial for understanding the role of hydrozoans in benthic-pelagic coupling (Di Camillo, et al., 2012).

To conclude this section, it is worth emphasizing that, in addition to the studies cited, numerous and diverse investigations on Mediterranean hydrozoans have been conducted, but they do not cover these organisms from a variety of research perspectives. The following review of the current literature on Mediterranean hydrozoans has been conducted to highlight the gaps in scientific knowledge of these animals.

2.2 Materials and methods

2.2.1 Search strategy

The Supplemental Material (SM, allegation1) was created following the guidelines proposed by the Collaboration for Environmental Evidence (CEE, 2022) and the Reporting standards for Systematic Evidence Syntheses (ROSES) (Haddaway, Macura, Whaley, & Pullin, 2018). CEE identifies a series of steps to follow in order to provide the quality standard and increased transparency and to allow reproducibility of the entire process (CEE, 2022). ROSES was specifically designed for environmental management and conservation studies as a checklist that addresses all relevant methodological information that should be reported in the SM (Haddaway, Macura, Whaley, & Pullin, 2018).

To identify the most appropriate database for literature data analysis, various search strings were tested. Initially, we conducted a scoping stage based on keywords such as “Hydroid” or “Hydrozoa” and “Mediterranean”. However, to

ensure comprehensive results, we modified our search by including the names of all Mediterranean basin regions. The final Title-Abstract-Keywords (TAK) search string used on Scopus and Web of Science was "Hydroid (or Hydrozoa) and Mediterranean (or Tyrrhenian or Adriatic or Ionian or Balearic or Aegean or Alboran or Marmara)".

The substrings used were broad enough to collect a large amount of literature, however limiting the results in line with the objective of the research. Finally, we specifically searched for scientific articles directly related to some of the projects focused on the study of specific Mediterranean hydroid species.

2.2.2 Database and searches

The Scopus and Web of Science platforms were utilized to gather scientific literature, as they were deemed reliable sources for acquiring information. Only indexed and peer-reviewed publications were considered to ensure the credibility of the data while non-indexed works were disregarded. It is noteworthy that only English literature was searched for and retained. Reviews and books were not included in the study, as they did not provide any additional information that was not already covered in the selected articles. The cited references were evaluated to identify any potential studies that were not included in the study's systematic mapping.

2.2.3 Exported results

Search results from Scopus and Web of Science were exported in .csv format along with all the literature information including abstract and keywords were manually added to a spreadsheet and all exported files were then loaded in the R environment (version 4.2.2; R Core Team, 2022) in RStudio (version 2022.12.0; RStudio Team, 2022) using the revtools package (Westgate, 2019).

Given that literature searches were conducted using various online tools, it is possible that the same publications may be listed multiple times. To address this issue, the DOI (Digital Object Identifier) was utilized to eliminate duplicates using the 'find_duplicates' function in the revtools package, thus creating a database of unique studies. Papers lacking a DOI were manually compared to eliminate duplicates as well. Additionally, relevant articles that fell outside of the search criteria were added manually to the final dataset.

2.2.4 Article screening and inclusion criteria

The systematic mapping involved a screening process that followed a series of selection criteria. In the first step, any scientific articles that did not pertain to benthic hydroids in the Mediterranean Sea were eliminated. This included studies on other organisms such as polychaetes and scyphozoans, as well as reviews and book chapters without new information. The second step involved categorizing the remaining studies based on their main topic, such as taxonomy, biogeographic distribution, siphonophores, ecology, alien species, fouling, and chemistry. In the third step, only ecological studies were retained, which were further classified based on the specific topic they addressed, including life cycle, trophism, symbiotic relationships between hydroids and associated fauna, microbiome and experimentation.

The final SM comprised 56 scientific publications that specifically focused on the ecology of benthic hydroids in the Mediterranean Sea. The screening process was carried out initially based on title and abstract reading, with subsequent steps involving the full-text analysis of the remaining studies.

Category variables	Data extracted		
(Bio)geographic	Latitude, longitude	site, country, area	depth
Hydroid studied	family	genus	species
Substrate	rocky, cave	artificial	animal/vegetable
literature	**Year published**		

Table 1. Variables, categories and data.

2.2.5 Data coding and analysis

The screening yielded the necessary information to create a data matrix for a clear overview of the biogeography of the studies conducted in the Mediterranean, including the geographic coordinates and bathymetry of sampling locations. Furthermore, the substrate type from which the organisms were retrieved was distinguished into rocky, sandy, detrital, artificial, animal, and vegetation categories. Information on the studied Mediterranean hydroid species was extracted, as well as the year of publication of the scientific article. For each category into which the ecological studies on Mediterranean hydroids were subdivided, the results reported in the published research were carefully studied and

compared in order to obtain a clear and comprehensive understanding of the current knowledge of Mediterranean hydroids. This process allowed us to identify gaps in our understanding and to proceed with further research in areas where knowledge is lacking.

2.3 RESULTS

2.3.1 Search results and screening

A total of 648 items were identified from online database searches, with 361 from Scopus and 287 from Web of Science, along with one added through personal research on the topic. After removing duplicates, a total of 360 articles remained. Following the first step of title and abstract screenings that excluded articles not focused on the study of Mediterranean hydroids, a total of 178 publications were included. Specifically, excluded articles were categorized into studies on polychaetes and scyphozoans, representing 24 and 40 studies, respectively, not conducted in the Mediterranean (39), out-of-topic studies (72), and reviews that did not provide new information (7). Articles focused on Mediterranean hydroids (178) were categorized based on the type of research conducted as follows: taxonomy (24 articles), planktonic phase (38), siphonophores (13), alien species (6), fouling (7), chemical approaches (8), biogeography (32), and ecological approach (56) (see Figure 1).

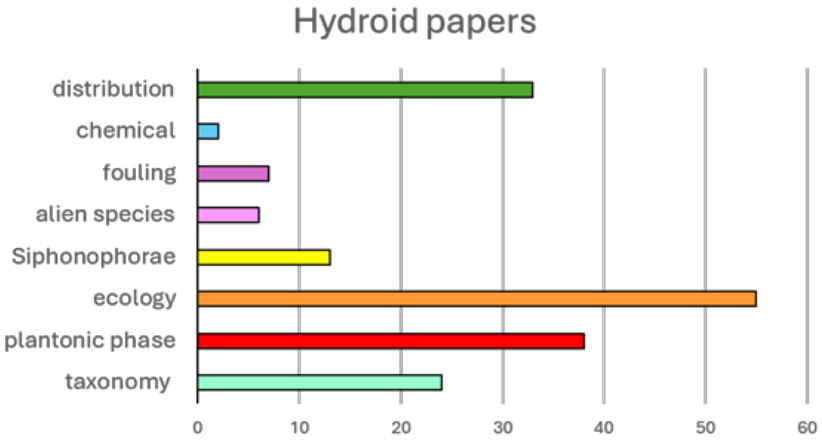


Figure 1. Categorization of the 178 studies on Mediterranean hydroids.

All remaining literature items were obtained (using the access provided by all coauthors' institutions), and full-text screening was subsequently conducted. Ultimately, 56 literature items were coded in the SM database, pertaining to the

study of Mediterranean hydroids from an ecological perspective. The selected articles were further categorized by topic, with 6 studies focused on experimentation, 5 on trophism, 6 on life cycle, 33 on symbiotic relationships, and 3 on the study of the microbiome associated with hydroids (Figure 2).

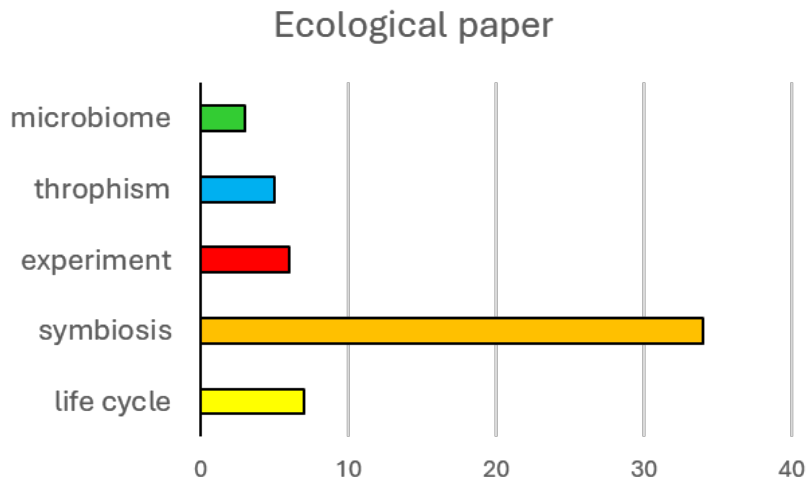


Figure 2. Ecological papers categorized by topic.

From the 56 selected studies, the biogeographic information was extracted through careful reading, allowing to obtain a clear picture of the areas in the Mediterranean where different hydroid species were collected and studied (see Figures 3). As shown on the map, the research was mainly concentrated along the Italian coasts, in particular, Apulia, Sicily, Campania, and Liguria. Other studies, mainly focused on symbiotic relationships between hydroids and other species, have also been conducted along the coasts of Spain, Tunisia, Croatia, Greece, and Turkey. As can be inferred from Figures 2 and 3, the majority of studies have been conducted on symbiotic relationships between hydroids and other organisms. It should be noted that only a single study was conducted along the Calabrian coasts, investigating symbiotic relationships with hydroids. Furthermore, no studies on microbiomes were conducted along the Calabrian coasts.

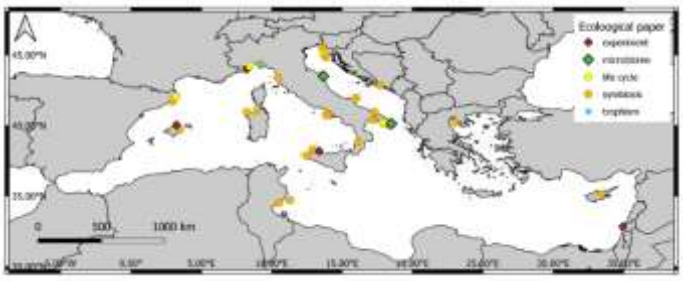


Figure 3. Geographic distribution of selected papers divided for specific topic.

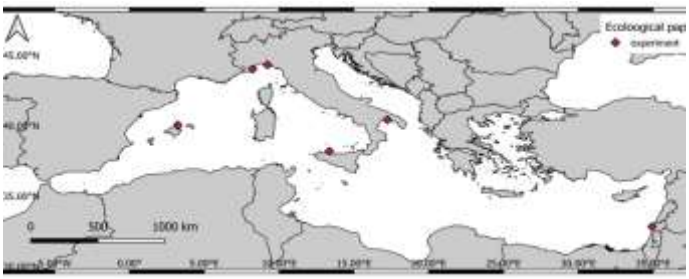


Figure 4a. Experiment.

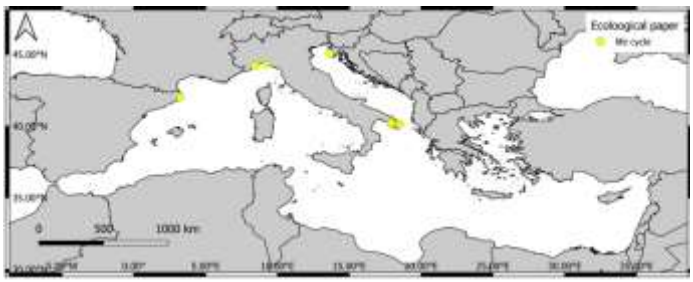


Figure 3b. Life cycle.

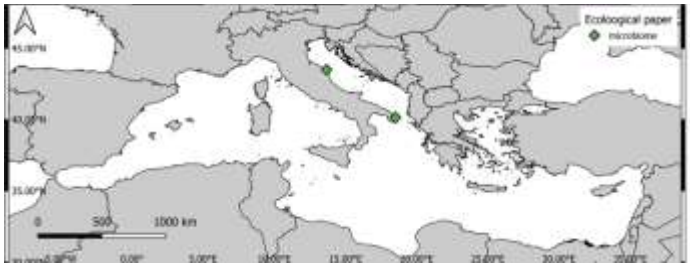


Figure 3c. Microbiome.

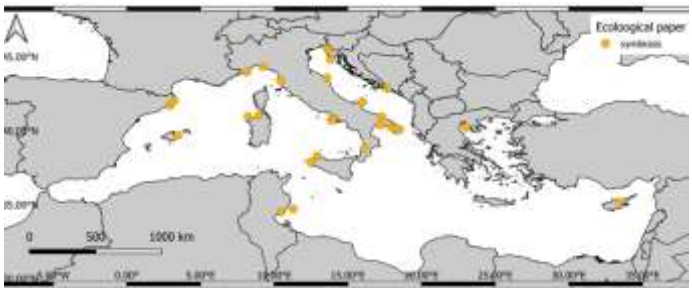


Figure 3d. Symbiosis.

Figure 3e. Trophism.

Based on the depth data extracted from the ecological studies on Mediterranean hydroids, it can be inferred that most of the samplings were carried out in the mesolittoral and infralittoral zones, with only one sampling occurring below the photic zone (Figure 4). The most used range is between 0 to 10 meters followed by 11 to 35 meters and the most common type of sampling was SCUBA diving.

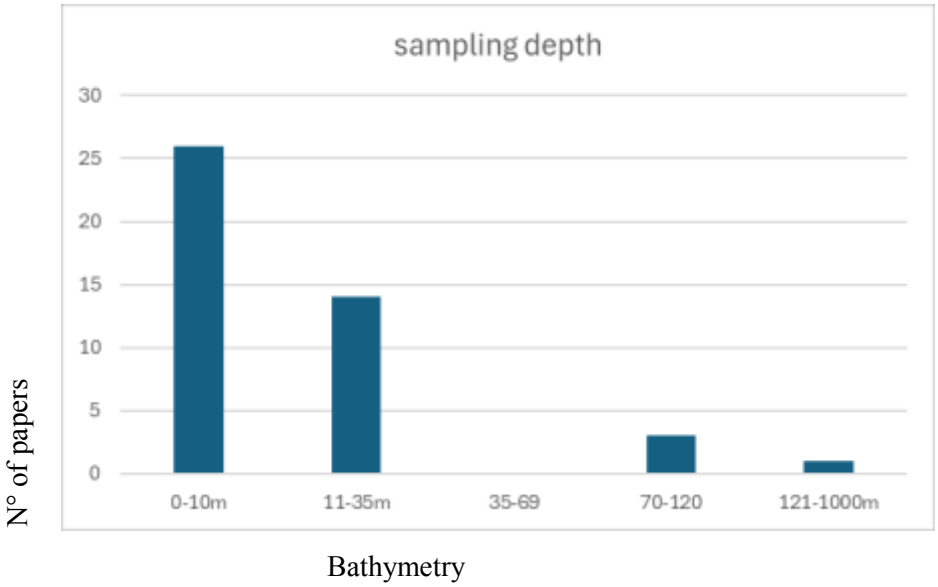


Figure 5. Categorization of ecological papers sampling depth based on.

The sampling of Mediterranean hydroids has been carried out on different types of substrates that have been categorized as rocky (7), detritic (1), artificial (9), and vegetal and animal with 20 and 9 published articles respectively (Figure 5).

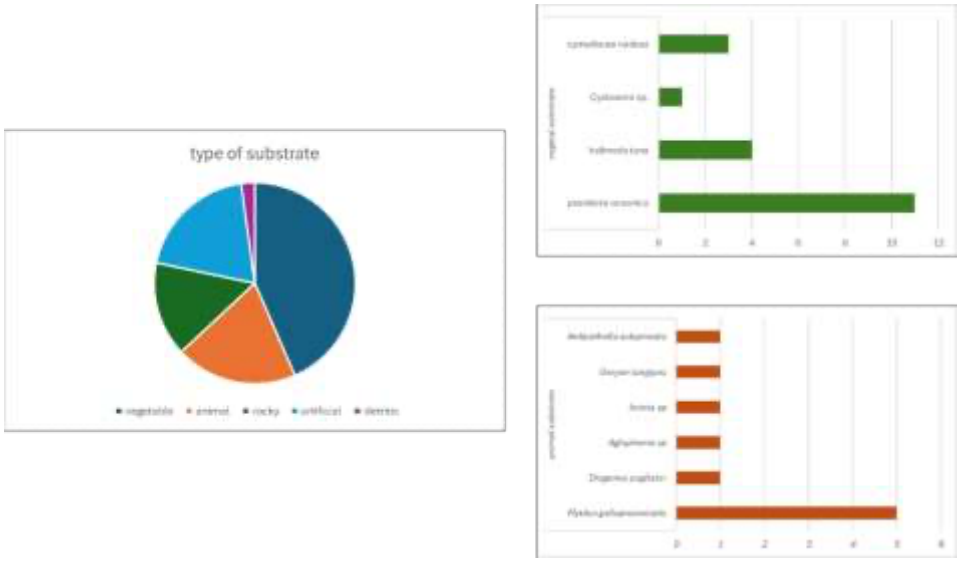
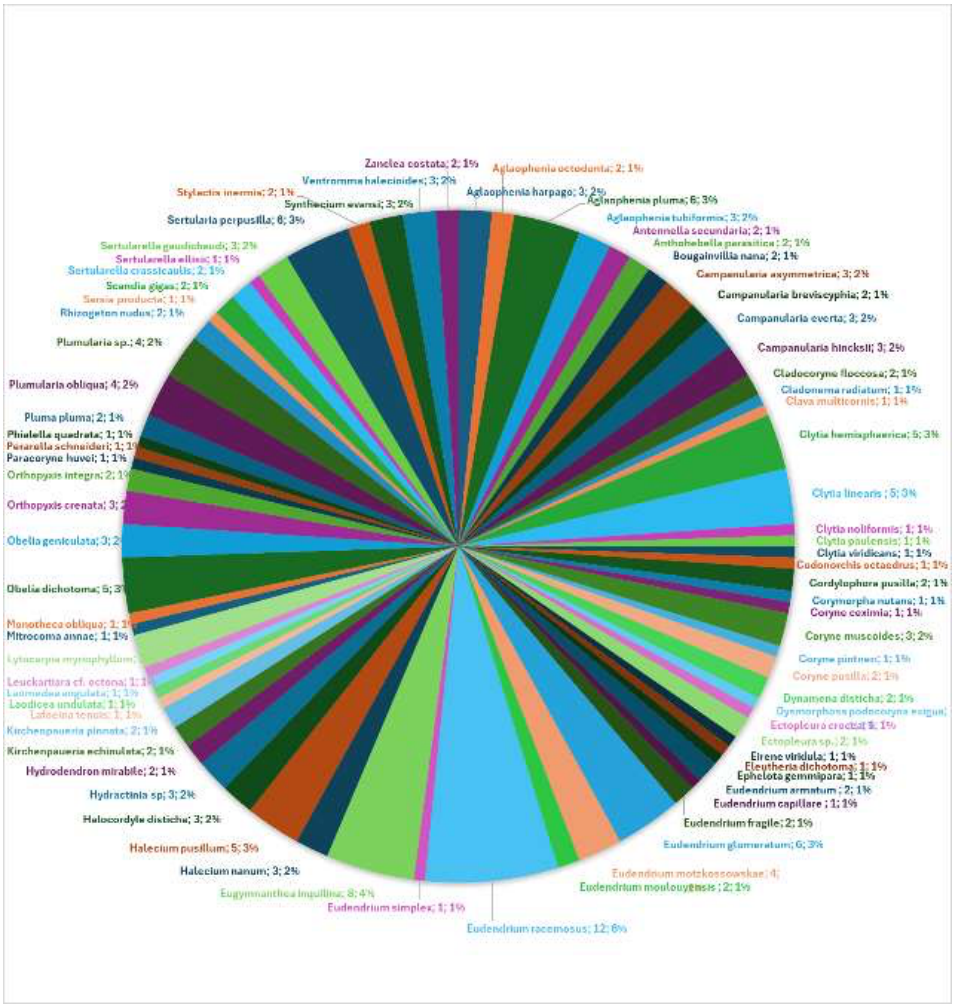


Figure 6. Type of different substrates where hydroids were collected from.

Special attention should be given to vegetal and animal substrates that have been further subdivided based on the species on which the hydroid was found. Most of the studies that have sampled these types of substrates belong to the category that deals with the study of symbiotic relationships between hydroids and other organisms. Regarding vegetal species, most research focuses on the epibiotic relationship between hydroids and *Posidonia oceanica* (11), followed by the substrate of *Halimeda tuna* (3), *Cymodocea nodosa* (4), and only two studies carried out on *Cystoseria sp*. The most studied animal substrate is *Mytilus galloprovincialis* (5), and it should be noted that publications regarding this species correspond to those studying *Eugymnanthea inquilina*, since the main topic of these studies investigating symbiotic relationships between these two species. The remaining studies with animal substrate investigate relationships with individual species and are single publications.

The extraction of information from articles dealing with the ecological aspect of Mediterranean hydroids allowed us to obtain the different studied species, reported in Figure 6. In the Mediterranean province most of the studies were focalised on single species, while the rest considered multi-species assemblages. The Figure 6

shows that the most studied species is *Eudendrium racemosus*, followed by *Eugymnanthea inquilina* most of them were studied in a single paper.



Species	N° of studies
Aglaophenia harpago	3
Aglaophenia octodonta	2
Aglaophenia pluma	6
Aglaophenia tubiformis	3
Antennella secundaria	2
Anthohebella parasitica	2
Bougainvillia nana	2
Campanularia asymmetrica	3
Campanularia breviscyphia	2
Campanularia everta	3
Campanularia hincksii	3
Cladocoryne floccosa	2
Cladonema radiatum	1
Clava multicornis	1
Clytia hemisphaerica	5
Clytia linearis	5
Clytia noliformis	1
Clytia paulensis	1
Clytia viridicans	1
Codonorchis octaedrus	1
Cordylophora pusilla	2
Corymorpha nutans	1
Coryne ceximia	1
Coryne muscoides	3
Coryne pintneri	1
Coryne pusilla	2
Dynamena disticha	2
Dysmorphosa podocoryna exigua	1
Ectopleura crocea	1
Ectopleura sp.	2
Eirene viridula	1
Eleutheria dichotoma	1
Ephelota gemmipara	1
Eudendrium armatum	2
Eudendrium capillare	1
Eudendrium fragile	2
Eudendrium glomeratum	6
Eudendrium motzkossowskae	4
Eudendrium moulouyensis	2
Eudendrium racemosus	12
Eudendrium simplex	1
Eugymnanthea inquilina	8
Halecium nanum	3
Halecium pusillum	5
Halocordyle disticha	3
Hydractinia sp	3
Hydrodendron mirabile	2
Kirchenpaueria echinulata	2
Kirchenpaueria pinnata	2

Species	N° of studies
Aglaophenia harpago	3
Lafoeina tenuis	1
Laodicea undulata	1
Laomedea angulata	1
Leuckartiara cf. octona	1
Lytocarpia myriophyllum	3
Mitrocoma annae	1
Monotheca obliqua	1
Obelia dichotoma	5
Obelia geniculata	3
Orthopyxis crenata	3
Orthopyxis integra	2
Paracoryne huvei	1
Perarella schneideri	1
Phialella quadrata	1
Pluma pluma	2
Plumularia obliqua	4
Plumularia sp.	4
Rhizogeton nudus	2
Sarsia producta	1
Scandia gigas	2
Sertularella crassicaulis	2
Sertularella ellisii	1
Sertularella gaudichaudi	3
Sertularia perpusilla	6
Stylactis inermis	2
Synthecium evansi	3
Ventromma halecioides	3
Zanclea costata	2

Figure 7. Studied species from ecological papers.

From the analysis of the publication dates of the 56 investigated articles, it can be observed that the first publication on Mediterranean hydroids dates back to 1973, while the latest one included in the review is from 2022. There is a peak of articles published between 2006 and 2008, and the highest number of articles published occurs in the year 2012 (Figure 7).

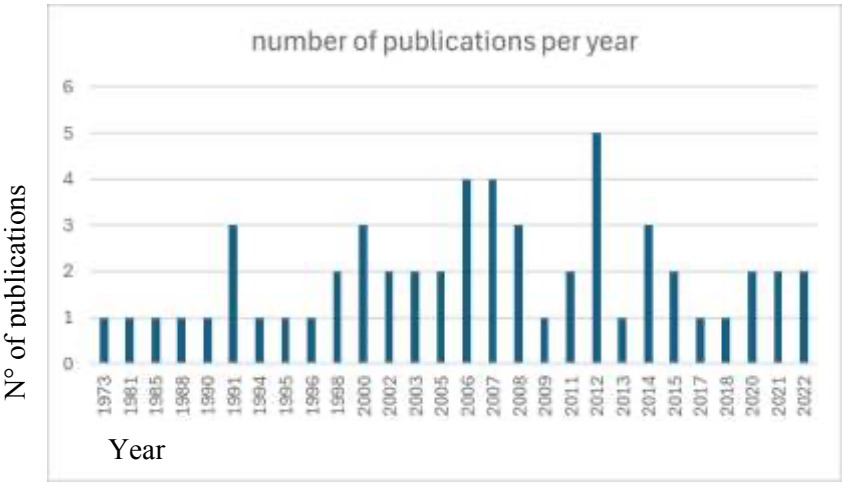


Figure 7. Number of publications per year 1973-2022 with ecological approach studied hydroids of Mediterranean Sea.

2.3.2 Microbiome

The microbiome of benthic hydroids in the Mediterranean Sea has been the focus of two articles analysing the presence of luminous bacteria on colonies of *C. linearis* and one investigated the association between *Ectopleura crocea* (a colonial hydroid distributed worldwide in temperate waters) and prokaryotic assemblages colonizing the hydranth surface. The studies were conducted in the Adriatic and Ionian Sea at depths ranging from 1 to 15 meters. The latest publication on the topic of hydroid microbiomes dates back to 2012 (Di Camillo, et al., 2012).

While several hydroid species have been shown to live with an associated microbial flora, the study by Di Camillo et al. in 2012 is the first to investigate the presence of bacteria on the hydroid's epidermis using a molecular approach combined with electron microscopy. Molecular analyses revealed that most of the observed prokaryotic diversity was within the domain of Bacteria, whereas Archaea accounted for a negligible fraction. This study is the first to report a stable association of bacteria with the epithelium of *E. crocea* species-specific (Di Camillo, et al., 2012).

The surface of many marine organisms is colonized by complex communities of microbes, yet our understanding of the diversity and role of host-associated microbes is still limited (Di Camillo, et al., 2012).

Hydroids use natural bioluminescence mainly for defensive or warning purposes, and the presence of luminous bacteria on hydroid colonies increases exogenous luminescence observed through fluorescence (Stabili, Gravili, Tredici,

Boero, & Alifano, 2011). Both studies that came out from the research about microbiome of Mediterranean hydroids had as topic association between luminous bacteria and Hydrozoa in the northern Ionian Sea. Stabili et al., 2011 sampled five groups each one consisting of about 300 *C. linearis* colonies, collected in July 2009 by SCUBA diving along the Otranto Channel (Ionian coast of Apulia, Italy). While Gravili et al. 2012 studied batches of colonies of 20 hydrozoans species (*Coryne muscoides, Eudendrium capillare, Amphinema dinema, Aglaophenia kirchenpaueri, Aglaophenia octodonta, Aglaophenia tubiformis, Antennella siliquosa, Halopteris diaphana, Ventromma halecioides, Hydranthea margarica, Monotheca obliqua, Plumularia setacea, Dynamena disticha, Sertularella ellisii, Sertularia perpusilla, Campanularia hincksi, Clytia hemisphaerica, Clytia hummelincki, Obelia dichotoma, Clytia linearis*) collected by SCUBA diving (directpicking) along the Ionian coast of Apulia, Italy. The study of Stabili et al., 2011 shows for the first time the presence of fluorescence on the chitinous exoskeleton of the common hydroid *C. linearis*, especially in the rings along the hydrocaulus and at the base of the hydrothecae. While the study of Gravili et al. (2012) has shown that the occurrence of luminous bacteria in investigated hydrozoan species could be related to the chitin localization and presence or absence of perisarc.

2.3.3 Trophism

In relation to the study of trophism in Mediterranean hydroids, the research identified five articles that analyzed its characteristics. While two studies were conducted in Spain, the remaining three pertain to the Italian regions of Liguria and Marche. According to the data reported in each article, sampling depths ranged from 0 to 70 meters. Specifically, the hydroid species examined in the five articles included *Eudendrium racemosus*, *Campanularia everta*, *Perarella schneideri*, and *Lytocarpia myriophyllum*. The sampling substrates encompassed rocky, vegetative made by *Halimeda tuna*, artificial, and detrital substrates. In the literature, the most recent publication on this topic dates back to 2015.

One of the studies analyzed, (Coma, Gili, & Zabala, 1995) conducted in Spain, reports that the diet of *Campanularia everta* includes a high proportion of amorphous POM, an innovative finding among hydroid species. These results highlight the capacity of hydroids to assimilate and consume large amounts of organic carbon, suggesting that they could be one of the most trophically active components of littoral benthic communities. Similarly, (Bavestrello, et al., 2000) demonstrated how *Perarella schneideri* exploits the organic material and confirmed the presence of cleptocommensalistic relationships between *Perarella schneideri* and caprellids. Moreover, the study conducted by Cerrano et al. (2015)

demonstrated that the presence of *L. myriophyllum* meadows enhances the quality of organic matter, meiofaunal abundance, and richness of meiofaunal taxa in the surrounding environment (Cerrano, Bianchelli, Di Camillo, Torsani, & Pusceddu, 2015).

Another study (Barange & Gili, 1988) conducted in Spain, reported that the predation of *Eudendrium racemosus* is non-selective and significantly depends on coastal pelagic plankton. *Eudendrium racemosum* captures prey items from three different sources, which may enhance its competitive ability for food resources in comparison to other benthic species. Similarly, (Di Camillo, et al., 2012) in the Adriatic Sea found that *E. racemosum* in the northern Adriatic Sea is not a selective feeder and can consume different types of food, including plankton, particles collected from suspended matter, and sediment. The study also demonstrated that the biomass of *E. racemosum* undergoes seasonal fluctuations, with high densities of polyps and colonies supported by the high abundance of larval bivalves during the summer and severe declines during the winter due to the decrease in pediveliger of mussels.

2.3.4 Life Cycle

Seven articles were selected on the topic of reproduction and life cycle of Mediterranean hydroids. All studies conducted sampling in Italy, including Apulia and Liguria, except for the oldest study, dating back to 1973, which was carried out in Croatia and the latest one 2017 in Slovenia. The sampling depths ranged from 0 to 38 meters. The studied hydroid species include *Corymorpha nutans, Campanularia everta, Coryne ceximia, Laodicea undulata, Obelia dichotoma, Bougainvillia nana,* and *Paracoryne huvei*. Sampling was conducted on a variety of substrates, including artificial, rocky, and animal substrates. Specifically, sampling from live organisms included the following species: *Aglophenia* sp., and *Ircinia* sp.

The Mediterranean Sea is host to a variety of hydrozoan species, each with its own unique life cycle adaptations and ecological impact. Svoboda (1973) studied the *Corymorpha nutans* polyps and found that they have a maximum lifespan of one season, with regeneration originating from injured or senile hydranths rather than a growth stage from a storage sprout. Coma et al. (1998), investigated the energy budget of *Campanularia everta*, highlighting its ability to adjust its energy expenditure according to periods of increased food availability, while also exhibiting the capacity to persist under unfavourable conditions. Puce et al., in 2003, described *Coryne eximia* as an example of a rare species capable of occasionally experiencing an explosive increase in abundance based on favourable

conditions, likely facilitated by the ability of degenerating medusae to function as floating resting stages. De Vito et al. (2006), studied *Laodicea undulata*, which is the most common species of Laodicea in the Mediterranean Sea and possesses a life cycle that allows it to regulate the production of larvae, polyps or jellyfish according to the most favourable time for each stage. Denitto et al. (2007), elevated var. nana of Bougainvillia to the status of a distinct species based on a unique taxonomic feature. Finally, Betti et al. (2017), shed light on the ecology of the poorly understood *Paracoryne huvei*, which may be eligible as a bioindicator of climate change due to its strict stenothermal feature and ability to take advantage of low salinity conditions following heavy rainfall periods.

2.3.5 Experimentation

Six studies were found that carry out experimentations on various Mediterranean hydroid species. The topics of experimentation include feeding of *Eudendrium racemosus*, hydroids as prey, hydroids as pioneer species, aquaculture, sterols, and serotonin research. Sampling was conducted mostly in Italy (Liguria, Sicily and Apulia), while one of the six studies conducted sampling in Spain and one in Israel. Sampling depths ranged from zero to 70 meters. The studied hydroid species from the Mediterranean region include *Eudendrium glomeratum, Pluma pluma, Eudendrium racemosus, and Pennaria disticha*. Organisms were collected from both rocky and artificial substrates. The most recent scientific article that conducted experimentation on Mediterranean hydroids was published in 2022 based on the conducted research.

The results of the experimentations studies on the hydroids of the Mediterranean, revealed that hydroids play a crucial role in benthic communities, affecting not only initial colonization but also the selection of biota through their bio-mineralogy (Bavestrello, 2008). In particular, it has been observed that *E. racemosum* planulae are influenced by the neurotransmitter serotonin during metamorphosis, while dopamine did not seem to affect their development (Zega, Pennati, Fanzago, & De Bernardi, 2007). Furthermore, the digestion of diatoms was found to be a key source of nutrition for many species, with *E. racemosum* displaying a highly efficient dual mode of digestion. This, along with their potential for rapid colonization and adaptation to changing conditions, makes hydroids significant players in the marine ecology of the Mediterranean (Gili, Covadonga, & Robson, 2008).

One species that Bosch-Belmar et al. (2022) studied was *Pennaria disticha*, which they found to be highly sensitive to increases in water temperature. As a habitat-former, *P. disticha* has the potential to modify microhabitats, affecting not only local biodiversity but also aquaculture facilities.

2.3.6 Symbiosis

The majority of the studies analyzed regarding hydroids in the Mediterranean Sea focused on the relationship between hydroids and marine organisms, including both plants and animals. Since these relationships vary in type, the 34 studies were selected and classified based on the specific association between the hydroid and the marine organism. This resulted in: 6 articles on fauna associated with hydroids, particularly addressing organisms such as diatoms, foraminifera, and coralline algae; 11 articles examining the epibiotic relationship between hydroids and *Posidonia oceanica*; 2 with *Cystoseira sp.*; 4 with *Cymodocea sp.*; 3 with *Halimeda tuna*; 5 with *Mytilus galloprovincialis*; 1 with *Diogenes pugilator*; 1 with *Geryon longipes*; and finally, 1 with *Ephelota gemmipara* (Figure 8).

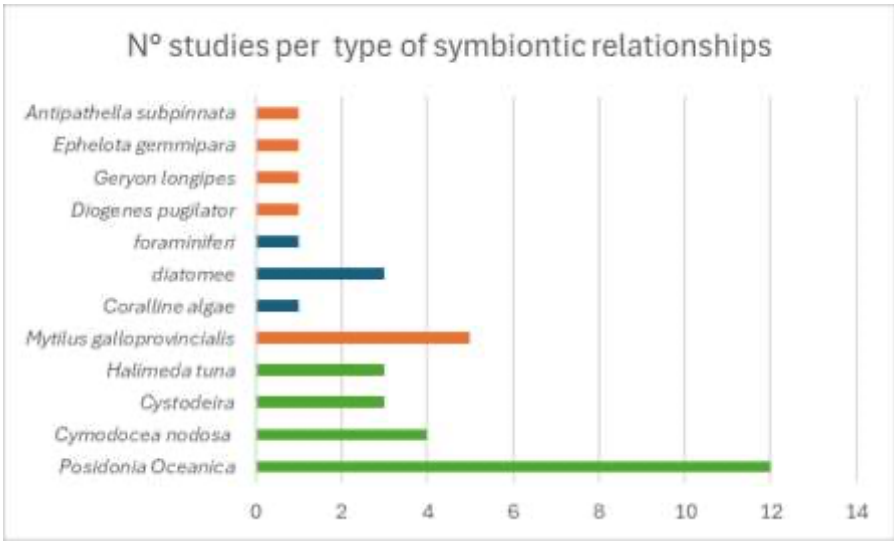


Figure 8. Number of studies per type of symbiotic relationships.

The 6 studies on fauna and Mediterranean hydroids refer to analyses conducted in various Italian regions, including Apulia, Sardinia, Liguria, Campania, and Sicily. Sampling occurred at different depths, ranging from 0 to 120 meters, covering various hydroid species such as *Eudendrium racemosus*, *Eudendrium armatum*, *Eudendrium glomeratum*, *Eudendrium moulouyensis*, *Ectopleura sp.*, *Clytia linearis*, *Campanularia hincksii*, *Synthecium evansi*, *Sertularella ellisii*, and *Aglaophenia tubiformis*. All analyzed samples were collected from rocky, animal, or artificial substrates: for animal substrates, organisms such as *Antipathella subpinnata*, *Paramuricea clavata*, *Paramuricea macrospina*, and *Eunicella cavolinii* were examined. The most recent article was published in 2014.

In particular, the research conducted by Di Camillo et al. (2005; 2006) and Romagnoli et al. (2007; 2014) emphasizes the specificity of the association between hydroids and diatoms. In this case, the hydroid host provides crucial nutrients and protection to the diatoms, but their distribution appears to be linked to the presence, composition, and even the color of the perisarc, in addition to the trophic conditions of the environment where the hydroid-diatom interaction takes place (Di Camillo, Puce, Romagnoli, Tazioli, & Totti, 2005). Furthermore, given the high concentration of algae near the polyps, Di Camillo et al. (2006) suggest that both benthic diatoms and coralline algae benefit from hydroids by utilizing the nutrients produced through their metabolism. The authors also observe that only a small number of samples (out of the 100 collected) typically host coralline algae, as not all hydroid species are suitable substrates. As a result, there appears to be a certain degree of specificity in the processes of epibiosis, primarily depending on the characteristics of the hydroids involved (Di Camillo, et al., 2006).

In the subsequent study by Romagnoli et al. (2007), the focus shifted to a diverse and complex community of microalgae distributed on the surface of the marine hydroid *Eudendrium racemosum*. As noted by the authors, these communities exhibit significant variability in response to seasonal changes, increasing in abundance and density during the winter months while decreasing in the summer. However, the ways in which these microalgae impact their host remain consistent, at least concerning the species observed by Romagnoli et al. (2007) associated with *E. racemosum*. Specifically, the diatoms exploit the catabolites produced by the hydroid's metabolism; thus, the life cycle of the diatoms that interact with the hydroid aligns with that of the host. Several species, including *Diatoma anceps*, *Licmophora reichardtii*, *Licmophora cf. dalmatica*, *Caloneis alpestris*, *Navicula cf. consentanea*, *Campylodiscus cf. clevei*, *Campylodiscus cf. decorus*, and *Campylodiscus cf. thuretii*, were first described through SEM analysis by Romagnoli et al. in 2014, enhancing the taxonomic knowledge and morphological data of the species associated with *E. racemosum* and providing additional insights into the biodiversity of the Mediterranean region.

Di Camillo (2008) identifies the presence of foraminifera as epibionts on *Eudendrium*, where they live by utilizing the food remnants expelled by the polyps, which serve as a source of organic nourishment for them. However, it appears that this relationship primarily benefits only the foraminifera, as analyses suggest that the hydroids derive no advantage from it. In fact, the presence of foraminifera on *Eudendrium* colonies is influenced solely by the relationship between the morphology of the test and the structure and size of the hydroid's branches (Di Camillo, Levorato, & Morigi, 2008).

The only study that examined the Mediterranean coast of Calabria is that conducted by Bo et al. (2011). This research documented for the first time the epibiotic relationship between a species of *Ectopleura* and anthozoan corals. The identification of *Ectopleura sp.* epibionts residing on *Antipathella subpinnata* represents the inaugural documentation of a tubulariid hydroid living in association with an antipatharian coral species. The authors propose that the hydroid's actinulae tend to attach themselves to substantial, upright anthozoan hosts, utilizing this strategy to avoid being dislodged and to increase their likelihood of survival.

- *Ep. Posidonia*

The eleven studies referencing *Posidonia oceanica* communities highlight that environmental factors, as well as biochemical ones, water movement, and anthropogenic activities play an important role in shaping and promoting epiphytic assemblages and their distribution. The characteristics that determine their presence, due to the wide variability that results at the ecological and biological levels, make epiphytic hydroids suitable for various biotopes, where they can persist in a stable manner. They are therefore excellent indicators for assessing the health status of the environment, as well as the *Posidonia* meadows and the associated fauna in general.

Regarding the distribution and adaptation of hydroid epiphytes on the leaves of *Posidonia*, significant insights come from the studies by Boero et al. (1981; 1985), which focused on the western Mediterranean. It has been observed that their distribution mainly occurs on the surface of the leaves: a co-evolutionary process according to Den Hartog (1973) that began around 5-6 million years ago, dating back to the first rise in sea levels after the Messinian crisis (Den Hartog & Polderman, 1975). Since *Posidonia* is a plant that thrives both in shallow waters and at greater depths, it can tolerate the physicochemical changes associated with these fluctuations, much like hydroids. Furthermore, as highlighted by Boero (1985), the topographical and temporal separation between *Posidonia* and hard substrates has facilitated the isolation of hydroid populations inhabiting *Posidonia* leaves, leading to the speciation of some hydroids associated with *Posidonia*.

Regarding Posidonia, it is also worth mentioning the study by Gravili et al. (2021), which provides further evidence supporting the findings of Boero et al. (1981; 1985). Gravili et al. (2021) report differences in the density of *Posidonia* leaves and their phenology in response to variations in pH observed in the stations along the vent systems (Gravili, Cozzoli, & Cambi, 2021). Dense colonization of hydroids in *Posidonia oceanica* exposed to ocean acidification has also been recorded in other studies, such as those conducted in Ischia by Donnarumma et al. (2014) and Mecca et al. (2020). Gravili et al. (2021) further confirm that hydroid epiphytes are among the few organisms likely to survive future scenarios of global

ocean acidification, thus serving as optimal tools for evaluating the conditions of *Posidonia* meadows and their associated fauna.

Piraino (1990) conducted a study on the zonation patterns of 16 hydroid species within the "Stagnone di Marsala", a lagoon with slightly hyperhaline conditions. He identified two distinct communities of epiphytic hydroids: one associated with *Cymodocea* leaves and the other with Posidonia. The community linked to *Cymodocea* showed significant seasonal changes, indicating a stochastic colonization process within that habitat. Conversely, the epiphytic community associated with Posidonia exhibited enhanced stability and included species that were well-adapted to the biotic environment.

The growth behavior of hydroids on *Posidonia oceanica* is influenced by both the physical conditions of the environment and the interspecific competition. Some species, such as *A. harpago* and *L. angulata*, are specifically adapted for feeding in areas of low water velocity and are mainly found on the distal ends of older leaves. On the other hand, species like *C. asymmetrica* and *S. perpusilla* are not as well-suited for capturing planktonic prey and tend to occupy the base of the leaves. This downward growth helps to reduce competition with other epiphytic organisms. Additionally, the downward growth orientation of hydrorhizal structures limits the potential growth points, which may constrain both the rate of growth and the overall size of the hydroids. In larger colonies of *S. perpusilla*, continuous resorption of the uppermost hydroid tissues occurs, while the hydrorhizae extend downwards along the leaves. The spatial distribution of *A. harpago* across different leaf locations is influenced by the resorption of older hydrocauli and mortality rates (Hughes, Johnson, & Smith, The growth patterns of some hydroids that are obligate epiphytes of seagrass leaves, 1991).

In their research, Pardi et al. (2006) observed a significant interaction between geographic regions and habitat types for hydroids, noting considerable spatial variability within each habitat. This variability was especially pronounced among marine plants situated only a few meters apart compared to those located several kilometers away.

Brahim et al. (2014) concluded that the variations in assemblages could be linked to human interference and the movement of water, particularly in shallow areas. Their findings indicated that zonation is associated with environmental factors, and epiphytic hydroids can serve as effective bioindicators. Furthermore, the distribution of epiphytic species in relation to hydrodynamic conditions plays a crucial role in determining the structure, geometry, and abundance of animal communities linked to marine phanerogams (Brahim, et al., 2015).

- *Ep. Cystoseira*

Two distinct studies have explored the colonization and distribution of epiphytic hydroids on brown algal species within the genus *Cystoseira*, utilizing varied approaches and leading to contrasting conclusions: Faucci et al. (2000) and Fraschetti et al. (2006). The former concentrated on the seasonal and spatial patterns of epiphytic hydroid distribution, while the latter investigated the distributional dynamics of hydroids across the three segments of the *Cystoseira* thallus.

Faucci et al. (2000) reported no significant variations in diversity or evenness among the communities associated with the three *Cystoseira* species, though they did note changes in species composition. They found no evidence of host specificity among the epiphytic hydroids on *Cystoseira*, except for a possible novel species. Their findings indicated the presence of a seasonal cycle likely influenced by various abiotic factors and highlighted differences in both colony height and population density among the hydroid species. The authors concluded that abiotic elements, such as water movement, exert the most substantial influence on the community structure, with biological factors playing a less critical role.

In contrast, Frachetti et al. (2006) discovered that the distribution patterns of hydroids significantly varied among the three sections of the *Cystoseira* thallus. They identified a general distribution trend, showing a decrease in the occurrence of epiphytes from the basal and middle sections toward the distal end, while also observing significant variations across different spatial scales. Some hydroid species were exclusively located on the basal part of *Cystoseira*. This study suggests that hydroid colonization on *Cystoseira* may manifest differently along each thallus, exhibiting variable structural patterns in assemblages at finer spatial scales compared to individual algal plants.

- *Ep. Cymodocea*

Bracun et al. (2020; 2021), by examining the spatial and temporal patterns of diversity and presence of epibionts on individual leaves of *Cymodocea nodosa*, observed an increase in epibiont coverage that progressed from the basal to the apical sections, regardless of the depth and age of the leaves. The presence of autotrophic and heterotrophic organisms reflects the entire leaf surface and the shoots, particularly regarding various species of hydroids, including *C. linearis*, *K. pinnata*, and *P. pusilla*. *C. linearis* is the most widespread, although it shows no preference for any specific leaf segment and is more commonly found in May and October. In contrast, *P. pusilla* is more prevalent on older leaves across all segments, particularly in deeper waters and later in the season. Anthoathecate hydroids are also found in the basal regions of older leaves because if they were positioned in the upper region, they would be more vulnerable compared to others.

Wesselmann et al. (2022) made intriguing discoveries by examining changes in the metazoan community in seagrass meadows of the eastern Mediterranean over the past century, utilizing eDNA metabarcoding from dated sediment samples and the COI gene region. The authors highlighted an increase in the diversity of the macrofaunal community associated with seagrass meadows, linked to the structural complexity of the plants forming the habitat. As stated by the authors of the study, *Posidonia oceanica* contributes to the formation of structurally more complex meadows compared to smaller seagrasses like *Cymodocea nodosa* and *Halophila stipulacea*.

The metazoan communities displayed a gradual shift in diversity and richness around the 1980s, marked by a decline in diversity over time in bony fish and soft corals, alongside a simultaneous rise in other taxonomic groups such as the phylum *Arthropoda* and *Porifera* in more recent years. The most significant wave of exotic species arrivals occurred in 1998, triggered by a sudden change in the sea surface temperature of the eastern Mediterranean. Furthermore, the phyla *Cnidaria*, *Porifera*, and *Echinodermata* were absent from the meadows of *C. nodosa*, while *Porifera* and some orders of *Cnidaria* were missing from the meadows of *H. stipulacea*, though all were detected in *P. oceanica*.

- *Ep. Halimeda tuna*

The research conducted by Llobet (1991) investigated the distribution and prevalence of hydroids on the leaves of *Halimeda tuna* in the Mediterranean Sea, emphasizing the potential species interactions and the abiotic factors that influence their distribution. The findings indicate that the location on the thallus significantly affects hydroid distribution. Those hydroids located on the proximal segments throughout the year are characterized by relatively large hydrothecae and numerous hydranths. In contrast, the hydroids found on the median segments are more vulnerable to interspecific competition, with some species forming dense monospecific colonies that exclude others. The study supports the notion that horizontal distributions are affected by competition with algae, as certain hydroid species were found to be more prevalent on the undersides of *H. tuna* leaves, where competition is reduced. Nevertheless, many uncertainties still exist regarding the specific roles of biotic and abiotic factors in the distribution of hydroids on *H. tuna* leaves.

In a separate investigation, Llobet et al. (1991) explored the reasons behind the summer decline of several epiphytic hydroids, including *O. crenata*, on *H. tuna*. They identified the host's life cycle and interspecific competition with epiphytic algae as key contributing factors. The results revealed that epiphytic algae tend to increase in abundance towards the end of winter, leading to significant losses of hydranths for *O. crenata*, a small and delicate hydroid that can be damaged,

suffocated, or have its feeding disrupted by epiphytic algae. It was observed that *O. crenata* is more commonly found on the median segments of the alga and relatively rare on the proximal ones, a pattern attributed to competition with other hydroids and more abundant epiphytic algae on the proximal segments. The study concluded that the reduced numbers of epiphytic hydroids in the summer result from competition with algal growth during spring and summer; however, this explanation does not fully account for the absence of large colonies of *O. crenata* towards the end of June and into July.

- *Ep. Mytilus galloprovincialis*

Five studies have been conducted on *Eugymnanthea inquilina*, an endobiont that inhabits the bivalve *Mytilus galloprovincialis*.

Piraino et al. (1994) studied the ecology of *E. inquilina* in the Ionian Sea, specifically along the coast of Taranto. Their research revealed that *E. inquilina* has a seasonal distribution and shows a preference for specific bivalve hosts, making it a useful indicator of the marine ecosystem's health. Rayyan et al. (2002) found that *E. inquilina* was absent in natural bivalve populations but prevalent in farmed mussels, suggesting a link between the hydrozoan's presence and mussel population density. This finding was reinforced by Žižek et al. (2012), who proposed that the host-endobiont relationship might be better understood as parasitism rather than commensalism. However, Mladineo et al. (2012) observed that despite the high infestation rates of both turbellarians and hydroids, the overall impact on the condition and reproductive effort of *M. galloprovincialis* was minimal. They argued that the interaction between Mediterranean mussels and hydrozoans may not be entirely parasitic, contrary to what earlier studies suggested.

- *Ep. Crab*

Di Camillo et al. (2018) focused their research on the species *Geryon longipes*, a crab commonly found in the muddy depths of the Mediterranean Sea, particularly in the southern Adriatic region. This crab serves as a host to a variety of epibionts that inhabit its exoskeleton, which is a non-living, temporary surface, favoring opportunistic species with limited interactions with the host. Di Camillo et al. (2008) identified a significant link between the size of the crabs and the presence of epibionts. Younger crabs from the Portunidae family molt more frequently before they reach maturity, making it harder for epibionts to settle and grow on their exoskeletons. Conversely, mature crabs molt less often, allowing the epibionts to establish themselves more easily. Hydroids often settle in the joints between segments, rapidly filling the available space, and are also commonly found in more protected areas like the coxa, ischium, and base sections. Over time, certain

hydrozoan groups have developed more specific symbiotic relationships with their hosts, leading to increased speciation.

- *Ep. Ephelota*

Tazioli et al. (2013) explored the annual life cycle of *Ephelota gemmipara* in the Adriatic Sea in relation to the hydroid *Eudendrium racemosum*. The active phases of the organism begin in April, triggered by rising water temperatures, which exceed 13°C during spring. As the host *E. racemosum* reaches its peak development, *E. gemmipara* also experiences its maximum proliferation, although sexual reproduction and encystment occur when both the water temperature and the abundance of the hydroid decrease. This pattern indicates that while temperature fluctuations may drive the life cycle of *E. gemmipara*, its development is also closely tied to its relationship with *E. racemosum*. *E. racemosum* plays a more complex role than merely serving as a settlement substrate for *E. gemmipara*; its dense, branched structure allows *E. gemmipara* to rise above the seafloor, reducing competition with other benthic organisms. Tazioli et al. (2013) conclude that *E. gemmipara* and *E. racemosum* have an interdependent relationship shaped by seasonal temperature changes, with *E. racemosum* also acting as a vital food source, which *E. gemmipara* prefers over other organisms covered in perisarc.

2.3.7 Discussion

From the results of the research presented above, a complex and varied picture emerges of the bio-ecological dynamics that govern the life of hydroids in the Mediterranean. Biogeographical studies, as well as those on the microbiome, life cycle, trophism, and symbiotic interactions, underline the fundamental role played by hydroids in safeguarding marine ecosystems. This role aligns with the wide variety of habitats that hydroids occupy, as well as the strong seasonal variability in their life cycles.

Regarding this latter aspect, it has been found that the life cycle of hydroids is strongly influenced by environmental factors such as temperature and nutrient availability. For example, Svoboda's (1973) study on *Corymorpha nutans* highlighted that this species has a limited seasonal life cycle but is capable of regenerating through damaged or senescent hydranths. Coma et al. (1998), analyzing the energy budget of *Campanularia everta*, demonstrated the hydroid's ability to modulate energy expenditure based on food availability. These studies, along with others cited throughout the chapter, show that hydroids can adapt even to adverse conditions thanks to optimal energy resource management. This is undeniably crucial in a marine environment like the Mediterranean, characterized by marked seasonality and diverse ecological habitats.

From a trophic point of view, many studies have found that, throughout their life cycle, hydroids consistently consume suspended organic matter, thereby expanding their feeding strategies. In this regard, the study by Cerrano et al. (2015) demonstrated that the presence of *Lytocarpia myriophyllum* meadows enriches meiofauna biodiversity. Other studies, such as Coma et al. (1995) on *Campanularia everta*, also added that hydroids can capture large amounts of amorphous organic particulate matter. Through these means, hydroids positively influence the quality of the organic matter present in their habitat, improving the overall health of the marine environment.

These capabilities are most likely derived from the symbiotic interactive characteristics of hydroids and, especially, their microbiome.

True symbiotic interactions are also found at the epibiont level, with plants such as *Posidonia oceanica*, capable of hosting communities of epiphytic hydroids. As observed by Boero et al. (1985), these relationships are influenced by environmental factors (water movement, trophic activities) that make epiphytic hydroids excellent indicators of the health of seagrass ecosystems. Such symbioses sometimes even help hydroids survive in conditions of ocean acidification (Gravili et al., 2021). Therefore, it can be assumed that in the event of global climate change, hydroids will be able to survive and thrive again in new environmental conditions. This concept is further confirmed by the ability of hydroids to colonize not only rocks and detrital substrates but also living organisms such as *Mytilus galloprovincialis* (Žižek et al., 2012).

As for the microbiome (an aspect that will be explored further in the subsequent chapters), studies such as that of Di Camillo et al. (2012) have highlighted a wide bacterial diversity associated with hydroid epithelium, with a close relationship between hydroids and the microbes colonizing their epidermal tissue. It follows that the symbiotic aspect, at the microbiota level, is one of the potential ecological implications that characterize hydroids and confer exclusive properties upon them. Indeed, Mediterranean hydroids show a wide range of symbiotic relationships with marine organisms, including diatoms, luminous bacteria, and other marine species, as demonstrated by the studies of Stabili et al. (2011) and Gravili et al. (2012). In other words, there is a complex mutualistic relationship between bacteria and hydroids: at the microbiota level, the former obtain nutrients from the hydroid, while the latter benefit from luminescence and associated microbial processes. This is a true coevolutionary demonstration between marine organisms and bacteria at the microbiota level, showing how hydroids act as support platforms for various microbial communities, in turn creating new ecosystems that benefit Mediterranean marine biodiversity.

2.3.8 Conclusion

In conclusion, the review of Mediterranean hydroid studies conducted above highlights the role these organisms play in safeguarding the environmental health of the sea, as well as in benthic trophic networks, thanks to their broad adaptive capacity and the energy and feeding characteristics of the microbiota. These aspects, as we have seen, help to preserve meiofauna biodiversity and the quality of organic matter (Cerrano, Bianchelli, Di Camillo, Torsani, & Pusceddu, 2015).

The ability to serve as a habitat for other microorganisms, creating mutualistic relationships capable of countering rising sea temperatures, may play an increasingly significant role in a Mediterranean facing climate change. In this respect, studies on the microbiomes associated with hydroids, such as that by Di Camillo et al. (2012), represent an emerging field of research that is expanding the understanding of the complex interactions between hydroids and microorganisms. The microbiome therefore significantly influences both the health and functionality of hydroids and the health of marine environments. The epibiont relationships between hydroids and *Posidonia oceanica*, as highlighted by Boero et al. (1985) and more recently by Gravili et al. (2021), represent an important tool for monitoring the health of marine ecosystems.

Despite the progress made, significant knowledge gaps remain at both the microbiotic and geographic levels. From the numerous studies analyzed, it emerges that certain areas, including Calabria, have been underexplored. Likewise, certain hydroid species, particularly those living in association with marine plants such as *Cymodocea nodosa* and *Halimeda tuna*, deserve further investigation due to their distinctive biological complexity (Bo, et al., 2011). Regarding the microbiome, there are still many shortcomings concerning its functionality, particularly in association with bacteria—an aspect that could be even more forward-looking if connected with the theme of biodiversity.

The conservation of Mediterranean hydroids and the study of their microbiota are therefore not only a priority for the protection of local biodiversity but also for preserving the stability and functionality of marine ecosystems in the context of rapid climate change. Consequently, future studies should focus both on broader geographic distribution and a comprehensive understanding of their microbiota characteristics, providing tools useful not only for scientific and academic purposes but also, and above all, for the management and protection of Mediterranean marine resources.

CHAPTER 3

HYDROID AS MARINE ANIMAL FOREST: THE FIRST GLIMPSE ABOUT THE ASSOCIATED SYMBIOSIS

3.1 Introduction

The Marine Animal Forests (MAFs) are formed by three-dimensional marine benthic organisms that create new habitats for many other species with a key role as ecosystem engineers (Rossi, Bramanti, & Covadonga, 2017). The biodiversity among the MAFs is usually higher respect the surrounding area hosting also species of commercial interest. Many taxa can form MAF and some of them, like corals, was more studied with the effect of a lack of knowledge for the rest. Hydroids are considered among the main elements of zoobenthic communities, and in some case showed the ability to form forests (Di Camillo, et al., 2018) increasing both habitat complexity and biodiversity (Di Camillo, et al., 2018; Bavestrello, et al., 2008).

Many papers have documented the rich flora and fauna associated to hydroids and the majority percentage focused on mollusks (Di Camillo, et al., 2018). Hydroids, in fact, can change the geological habitat features by affecting water movement, light penetration, and providing settling space, shelter or food to other species. The forests release planulae, medusoids, or medusae that contribute to benthopelagic coupling and affect biogeochemical cycles (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017). Despite their crucial ecological role, hydroids are often underestimated in the classification of habitats and benthic communities research, mainly due to the lack of hydroid specialists in the definition of habitats, coupled with insufficient quantitative data (Becerro, 2008).

Microorganisms play essential roles in the health and resilience of cnidarians and the microbiome composition is influenced by different parameters such as phylogeny, locality and microhabitat (McCauley, Jackson, & Loesgen, 2023). A key bacteria core was found to be present in the different cnidaria taxa but to date data regarding the microbiome composition of the subphylum Hydrozoa is almost absent (McCauley, Jackson, & Loesgen, 2023). One of the few studies that focused on this topic analysed the microbiome of the hydroid *Ectopleura crocea* recording an extraordinary bacterial biodiversity, with over 100 genera and 500 bacterial taxa identified (Di Camillo, et al., 2012). Molecular analyses identified the predominance of two OTUs belonging to the families Flavobacteriaceae and Comamonadaceae. Members of Flavobacteriaceae, represented by the genus Polaribacter, exhibit a potential symbiotic relationship with the hydroid, providing protection against pathogens and competitors while contributing to host nutrition

(Di Camillo, et al., 2012). Moreover, were also observed that the presence of these OTUs was influenced by seasonality and water temperature, with Polaribacter abundance peaking in March and decreasing as spring warming progresses, coinciding with the seasonal regression of the hydroid. This connection suggests a critical interaction between bacterial flora and host health, positing that the loss of protective bacteria may leave the hydroid vulnerable to infections (Di Camillo, et al., 2012).

Among the biodiversity hosted in the hydrozoan forest there are also present predators that evolve mechanisms to protect themselves from the defence of the hydroids (Greenwod, Garry, Hunter, & Jennings, 2004) and in some cases are specialized in eating them (Martin & Walther, 2002). This is the case of the nudibranchs. They are marine invertebrates belonging to the order Nudibranchia (Phylum: Mollusca; Class: Gastropoda) that have been observed in a huge variety of habitats, from polar to tropical waters and from abyssal depths to shallow coasts. They are predators of sessile benthic, feeding on corals, hydroids, sponges, and algae, (Harris, 1987). The association between nudibranchs and cnidarian colonies has so far been considered a predator-prey relationship, although the cnidarian provides both shelter and nourishment, as well as defensive capabilities, since nudibranchs protect themselves from predators using the branches of hydroid forests (Willis, et al., 2017). In some case they have evolved a strict relation with the prey as the example of the recently described kleptopredation mechanisms between the nudibranch *Cratena peregrina* (Gmelin, 1791) and the hydroid *Eudendrium racemosum* (Cavolini, 1785) where the nudibranch selects and prey preferentially polyps in the colonies that have just eaten (Willis, et al., 2017).

The prokaryotic composition associated with nudibranchs identified differences between the microbiomes present in sediments and seawater, highlighting that nudibranchs acquire part of their microbiome through horizontal transmission from the surrounding environment and part through vertical transmission a phenomenon also observed in other marine organisms such as sponges, bivalves, and ascidians (Tamara, et al., 2023). The bacterial composition in different compartments of nudibranchs, such as mucus and gut, varies in response to specific environmental conditions, including temperature and water acidity, as well as to a diet rich in bioactive compounds, which exerts selective pressure on microbial communities (Tamara, et al., 2023).

The present study aims to increase the knowledge of the microbiome composition associated to hydroid forest comparing it with the surrounded environments, water and sediment. Moreover, to understand the association between the hydroid colonies and its associated fauna, the microbiome of the different nudibranchs associated to the forest were analysed examining whether

similarities and diversities exist in the acquisition of prokaryotic symbionts among the different species.

3.2 Matherials and Methods

The study area of Punta Pellaro was selected based on previous explorative scuba diving conducted between May and June 2023 in the Ionian Sea along the west side of Reggio Calabria coasts (Calabria region, Italy). Samples were collected the 25th of July 2023 at the selected site (38°1’20.49’’N 15°38’28.52’’E, see Figure 9) at 18 m depth. The seafloor was characterised by a predominance of rock substrate with sand pockets. The flat rock hosted a dense forest of hydroid with a rich associated fauna, as three different species of nudibranchs. Among the forest, six hydroid colonies were selected with the associated nudibranchs and entirely sampled by using sterile bags. In addition, six replicates of water (2 L per each replicate) were collected in the surrounding area using Niskin bottle. Sample of sediments were collected with 50 mL tubes taking the layer 0-3 cm in the closer sand pockets. All samples were stored in refrigerated box (~ 4°C) until the arrival in laboratory.

Figure 9. Punta Pellaro, sampling site in the Ionian Sea.

3.2.1 Sorting and sampling pre-processing

Upon arrived in laboratory, samples were sorted separating hydroids from nudibranchs (Figure 10). Hydroids were washed using filtered sea water and individually stored in six 1.5 mL tubes at -80°C. Nudibranchs, soon after stereoscopic observation, were separated in three different species and individually collected in 1.5 mL tubes and stored at -80°C. Water samples were filtered on 0.22 µm nitrocellulose filters to collected microbial communities and then stored at -80°C. Falcon tubes containing sediments were left in vertical position for 30 minutes at +4°C allowing sedimentation for the subsequent removal of excess water. Sediments were stored at -80°C.

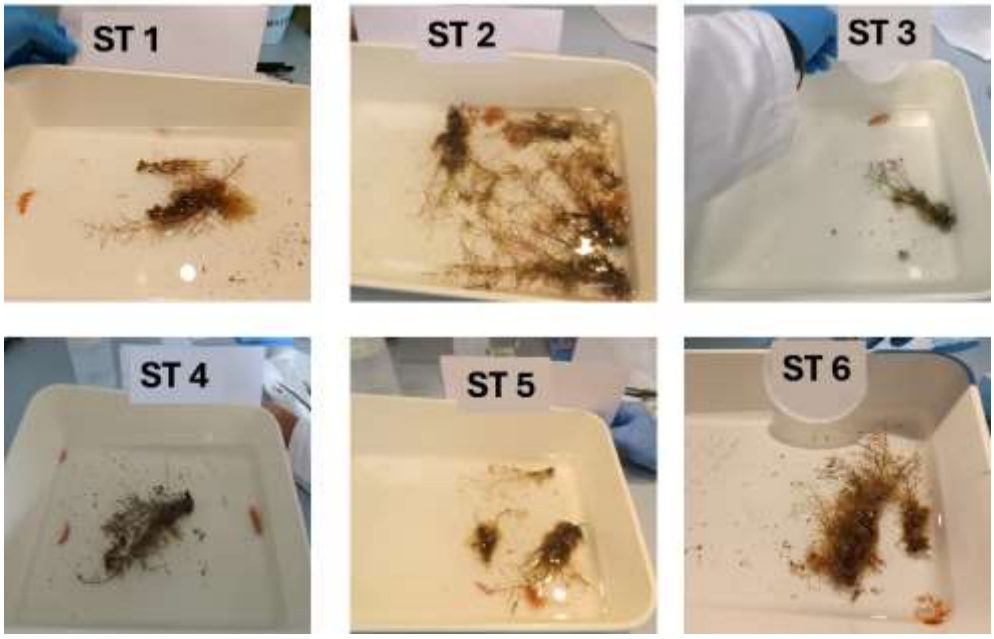


Figure 10. Sample replicates before sorting. Six colonies of hydroids with associated nudibranchs were collected and sorted.

3.2.2 DNA extraction

Hydroid and nudibranch samples were extracted using the DNeasy Blood & Tissue Kit (Cat. No. 69504, QIAGEN). Briefly, homogeneous aliquots (~ 25 mg) of each sample were incubated with 20 µL of Proteinase K and additional buffer (200 µL Buffer AL) at 56°C for 10 min in a thermoblock. The mixture was pipetted into the DNeasy Mini spin column and centrifuged. Wash steps were carried out at this point to remove all cellular components from the column, using ethanolic wash buffers and centrifugation (500 µL of AW1 and 500 µL of AW2). Last step is the elution by pipetting 100 µL of buffer AE directly onto the DNeasy membrane.

Column was incubated at room temperature for 1min, and then centrifuged to elute total DNA.

Protocols for the DNA extraction from filtered water samples and sediments were similar; filtered water samples were extracted using DNeasy PowerWater Kit (Cat. No. 14900-100-NF, QIAGEN), while sediments with DNeasy PowerSoil Pro Kit (Cat. No. 47014, QIAGEN). Filters were cut in smaller pieces and placed into 5 mL PowerWater Bead Pro Tube with lysis buffer (1 mL PW1); sediments were weighted to create aliquots of 250 mg and placed into 2 mL PowerBead Pro Tube with lysis buffer (800 µL CD1). All samples were homogenized using TissueLyser at 50 Hz for 2 intervals of 5 min each.

At the end, beads and solid components (e.g., filter fragments, sediments, cell structures) were discarded by centrifugation and liquid fractions containing DNA were pipetted into MB Spin Column, allowing DNA to bind resin. Wash steps were carried out at this point to remove non-specific binders from the column, using ethanolic wash buffers and centrifugation. Elution was the last step, by pipetting elution buffer directly onto the DNeasy membrane (100 µL for filtered water samples and 50 µL for sediments). Column was incubated at room temperature for 1min, and then centrifuged to elute total DNA.

At the end of all extraction procedures, DNA obtained from the different matrices were quantified using Qubit fluorometer, device able to measure fluorescence intensity of fluorescent dye binds to double-stranded DNA (dsDNA, High Sensitivity, cat. N. Q32851). DNA samples (50 ng) were run on 0.8% agarose gel electrophoresis for comparison of band distribution respect to suitable marker, excluding sample degradation. Samples with high integrity and enough amount of DNA (> 10 ng μL^{-1}) were send to Next Generation Sequencing (NGS) external service (Eurofins Genomics Europe).

3.2.3 PCR amplification for molecular taxonomy

Molecular barcoding was performed for both the hydroids and nudibranchs. PCR was set up using specific primers and following the standard PCR cycle.

Primer	Sequence (5'-3')	Reference	organism	Length (bp)
16SHA	TCGACTGTTTACCAAAAACATAGC	Cunningham and Buss 1993	hydroid	640
16SHB	ACGGAATGAACTCAAATCATGTAAG	Cunningham and Buss 1993	hydroid	640
LCOI	GGTCAACAAATCATAAAGATATTGG	Folmer et al 1994	nudibranch	660
HCOI	TAAACTTCAGGGTGACCAAAAAATCA	Folmer et al 1994	nudibranch	660

Table 2. Primers used for the characterization of hydroids and nudibranchs.

PCR products were run on 1.5% agarose gel electrophoresis to check the quality of the results and the possibility of multiples bands. The samples were purified using the QIAquick PCR Purification Kit and following the standard protocol. The purified products were sequenced using an external service (Eurofins Genomics Europe).

3.2.4 Sanger sequencing and microbiome profiling

Sanger sequencing and microbiome profiling was performed by Eurofins Genomics. Briefly, metabarcoding sequencing was performed on each samples using V3-V4 16S rRNA regions for the purposes of characterising bacterial community composition using paired-end Illumina MiSeq reads. The first step of microbiome profiling is the removal of all reads containing ambiguous bases ("N"). *de-novo* algorithm of UCHIME was applied to identify and remove chimeric reads (Edgar, Haas, Clemente, Quince, & Knight, 2011). The resulting reads was analysed using Minimum Entropy Decomposition (DEM) (Eren, Morrison, Lescault, Reveillaud, & Sogin, 2015). This step produces a computationally efficient means to partition marker gene datasets into Operational Taxonomic Units (OTUs), which are sequence clusters that significantly differ to all the other. The MED procedure is essential to find and remove random noise in the dataset; all the sequences with abundance lower than 0.02% are filtered and removed.

DC-MEGABLAST alignments were carried out to annotate taxonomic information to OTUs; database used was: /mnt/nsa3/projects/active/bioit_development/ebe_transfer/mdxMicrobiomeProfiling/ncbi_nt/nt_02-03_well_classified_only/nt.filtered.fa (Release 03/02/2020). In

addition, further taxonomic assignments were performed by processing OTUs with QIIME software package (version 1.9.1, http://qiime.org/). Abundances of bacterial taxonomic units were normalized through lineage-specific copy numbers of the relevant marker genes to improve estimates (Angly, et al., 2014).

3.3 Results

3.3.1 Taxonomy

Sequenced amplicons were blasted on NCBI database for the determination of species. The molecular marker analysis has confirmed the morphological identification of the hydroid as *Eudendrium racemosum* (Cavolini, 1785) and the nudibranchs as *Flabellina affinis* (Gemlin, 1791), *Cratena peregrina* (Gemlin, 1791)and *Dondice* sp.

3.3.2 Metabarcoding: group of samples analysed and statistics

Samples were clustered into two groups: Water-Sediments-Hydroids (WSH) and Water-Sediments-Hydroids-Nudibranchs (ALL).

WSH group was composed by 10 samples (see Table 4), where microbiome of 4 hydroids was correlated with microbial community of the surrounding (water and sediment matrices). This cluster was designed to show the only microbial community of hydroids, highlighting similarity and dissimilarity with their surroundings. In the Table 3 and 4 are reported some statistics to summarize the results of reading processing and taxonomic assignment. The copy-number correction was performed for bacterial species (Angly, et al., 2014). This correction was made by a ratio between the number of reads assigned to a species and the known or assumed copy-number of marker genes/regions.

Description	N°	%
Total number of input sequences	668345	100.0%
Remaining sequences after pre-processing and quality filtering	668269	100.0%
Remaining sequences after chimera detection and filtering	662195	99.1%
Total number of sequences assigned to OTUs	370022	55.4%
Total number of sequences assigned to taxa	370022	55.4%
Copy-number corrected total count	143335	-
Total number of OTUs	1494	100.0%
Number of OTUs assigned to taxa	1494	100.0%

Table 3. Total number of OTUs correlates with the diversity of the data set. After removing noise, the fraction of OTUs assigned to taxa describes how well the microbiome is represented in the used reference database.

Sample	1	2	3	4	5
Water 1	67 526	98.0%	63.6%	63.6%	13 832
Water 2	70 930	97.8%	66.5%	66.5%	14 806
Water 3	70 374	99.2%	68.0%	68.0%	15 529
Hydroid 1	63 795	99.6%	58.3%	58.3%	13 950
Hydroid 2	64 035	99.5%	60.8%	60.8%	15 865
Hydroid 3	57 589	99.0%	56.0%	56.0%	13 390
Hydroid 4	69 095	99.5%	51.7%	51.7%	15 079
Sediment 1	67 767	99.6%	39.3%	39.3%	12 768
Sediment 2	73 651	99.4%	47.2%	47.2%	16 621
Sediment 3	63 583	99.3%	42.0%	42.0%	11 495

Table 4. Number of OTUs correlates with the diversity of data set for each sample of the WSH group. 1) input sequences; 2) sequences after pre-processing and chimera removal; 3) sequences assigned to OTUs; 4) sequences assigned to taxa; 5) count after lineage-specific copy-number correction.

ALL group was formed by 17 samples (see Table 6), where microbiome of hydroids was not only correlated with environmental matrices but also with their associated nudibranchs (*Flabellina* sp., *Dondice* sp. and *Craten a* sp.). This cluster was created to describe how hydroid holobiont shape its microbial community in relation to associated fauna (nudibranchs) and the surrounding environment (water and sediments). This total correlation aims to highlight how hydroids influence and exchange portion of microbiome with associated nudibranchs. In the Table 5 and 6 are reported some statistics to summarize the results of reading processing and taxonomic assignment. The copy-number correction was performed for bacterial species (Angly, et al., 2014). This correction was made by a ratio between the number of reads assigned to a species and the known or assumed copy-number of marker genes/regions.

Description	**N°**	**%**
Total number of input sequences	1 155 713	100.0%
Remaining sequences after pre-processing and quality filtering	1 155 576	100.0%
Remaining sequences after chimera detection and filtering	1 149 521	99.5%
Total number of sequences assigned to OTUs	824 828	71.4%
Total number of sequences assigned to taxa	824 828	71.4%
Copy-number corrected total count		-
Total number of OTUs	2 015	100.0%
Number of OTUs assigned to taxa	2 015	100.0%

Table 5. Total number of OTUs correlates with the diversity of the data set. After removing noise, the fraction of OTUs assigned to taxa describes how well the microbiome is represented in the used reference database.

Sample	**1**	**2**	**3**	**4**	**5**
Water 1	67 526	98.0%	63.6%	63.6%	13 833
Water 2	70 940	97.9%	66.6%	66.6%	14 891
Water 3	70 359	99.1%	68.8%	68.8%	15 572
Hydroid 1	63 795	99.6%	58.3%	58.3%	13 957
Hydroid 2	64 035	99.5%	60.8%	60.8%	15 865
Hydroid 3	57 589	99.1%	56.0%	56.0%	13 388
Hydroid 4	69 095	99.5%	51.7%	51.7%	15 082
Sediment 1	67 767	99.6%	39.3%	39.3%	12 768
Sediment 2	73 662	99.4%	47.6%	47.6%	16 781
Sediment 3	63 583	99.3%	42.0%	42.0%	11 495
Flabellina 1	71 468	100.0%	95.3%	95.3%	12022
Flabellina 2	57 889	100.0%	95.0%	95.0%	10 833
Flabellina 3	71 176	100.0%	93.1%	93.1%	26 520
Flabellina 4	52 095	100.0%	94.3%	94.3%	14 543
Cratena 1	53 573	100.0%	83.8%	83.8%	27 860
Cratena 2	54 486	100.0%	96.0%	96.0%	31 275
Dondice 1	57 436	100.0%	91.7%	91.7%	39 096
Dondice 2	69 239	100.0%	95.0%	95.0%	53 387

Table 6. Number of OTUs correlates with the diversity of data set for each sample of the WSH group. 1) input sequences; 2) sequences after pre-processing and chimera removal; 3) sequences assigned to OTUs; 4) sequences assigned to taxa; 5) count after lineage-specific copy-number correction.

3.3.3 Microbial communities of Water-Sediments-Hydroids (WSH)

Phylum level

The WSH group showed that at the Phylum level the microbiomes composition was dominated by the Proteobacteria in all samples analysed (Figure 11). In detail, this phylum represents more than the 50% of the microbial community and in the water samples it reached more than 70%. The second phylum in order of abundance

was the Bacteroidetes. In the hydroid samples it reached more than 40% of microbial composition. The same phylum is also present in sediments and water but in lower percentage, about 12% and 9%, respectively. Actinobacteria is a highly representative phylum for sediment matrix, showing an abundance of 21%. This phylum is very low represented in the hydroids and water (3% and 2%, respectively). Water showed the presence of Firmicutes (10%), phylum that is quite almost absent in hydroid (0.3%) and not recorded in the sediments. The phylum Cyanobacteria is present with low abundance only in water and hydroids, 1% in both samples (see Table 7).

Other phyla are present only in single component of WSH group. This is the case of Thaumarchaeota that are recorded only water samples (2%), Acidobacteria in only sediments (2%) and Tenericutes in only hydroid microbial composition (1%). Some other phyla are also recorded in some sub-groups, but in percentage lower than 1%.

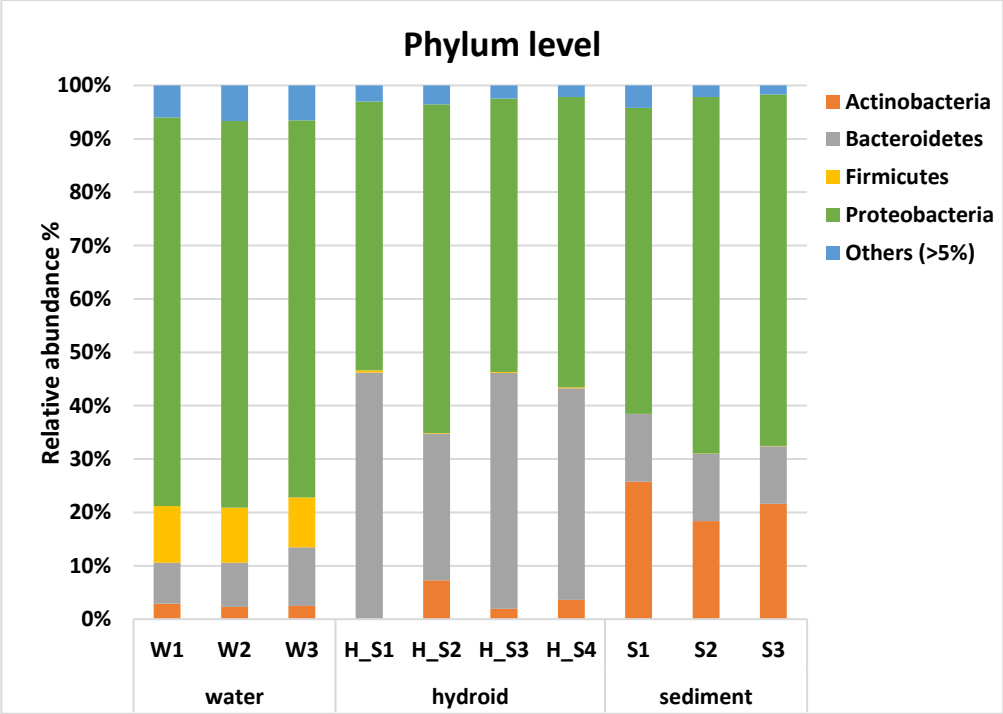


Figure 11. Taxonomy plot. Histograms reports composition of microbial communities at Phylum level of WSH group.

Phylum	W1	W2	W3	H_S1	H_S2	H_S 3	H_S 4	S1	S2	S3
Actinobacteria	2.9	2.3	2.5	0.1	7.3	3.6	1.9	18.4	21.6	25.8
Bacteroidetes	7.6	8.3	11.0	46.1	27.4	39.7	44.2	12.6	10.8	12.7
Firmicutes	10.7	10.3	9.4	0.4	0.1	0.2	0.2	0.0	0.1	0.0
Proteobacteria	72.8	72.4	70.6	50.3	61.6	54.4	51.2	66.8	65.8	57.4
Others (>5%)	6.0	6.7	6.5	3.0	3.5	2.1	2.4	2.2	1.7	4.2

Table 7. Percentages of most representative phyla in all replicates of water (W), hydroid (H) and sediment (S) samples.

Order level

Considering all the matrices only eleven orders showed a relative abundance more than 10%. Hydroids samples showed high percentages of Rhodobacterales (up to 28%), Cytophagales (up to 20%) and Flavobacteriales (up to 17%). In addition, their microbial community was also composed by significant amount of Cellvibrionales (7%) and Rhizobiales (4%).

Sediments host two bacterial orders that were not present in all other matrices, Acidimicrobiales (16%) and Chromatiales (14%). The other orders recorded in sediment were shared with hydroid and water, Rhodobacterales (12%), Rhizobiales (10%), Cellvibrionales (7%), Flavobacteriales (6%) and Cytophagales (4%).

Water samples shared with hydroids and sediments two orders: Flavobacteriales and Rhodobacterales, that was recorded with significant abundance (8% of whole community). Four other orders characterize only this matrix: Pseudomonadales (14%), Gammaproteobacteria (12%), Alphaproteobacteria (12%) and Bacillales (10%).

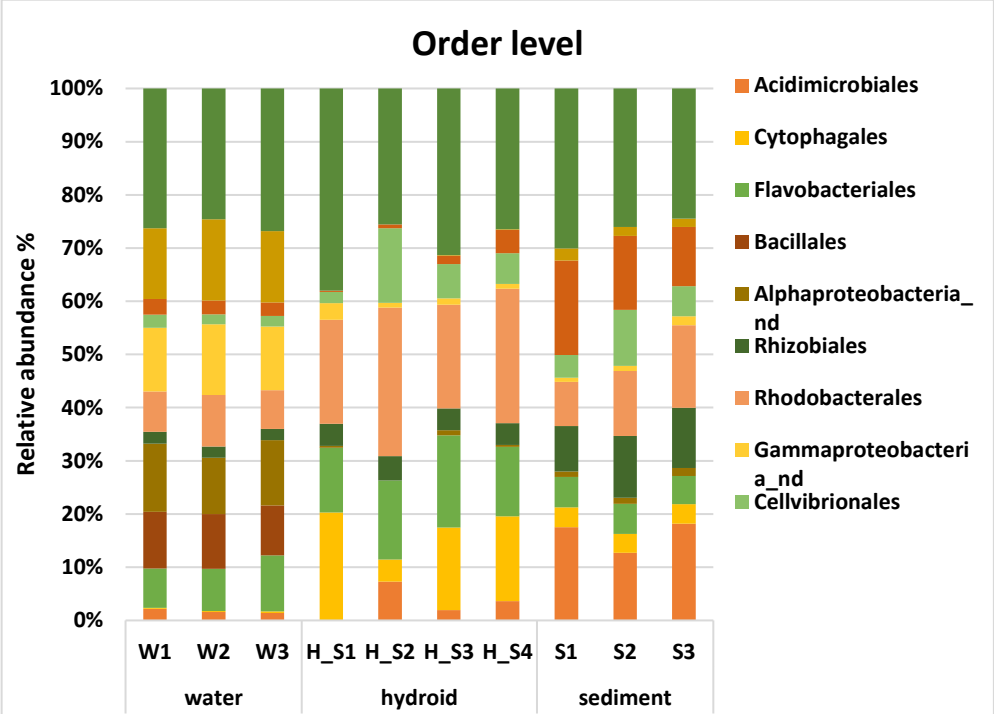


Figure 12. Taxonomy plot. Histograms reports composition of microbial communities at Order level of WSH group.

Order	W1	W2	W3	H_S1	H_S2	H_S3	H_S4	S1	S2	S3
Acidimicrobiales	2.2	1.6	1.4	0.0	7.3	3.6	1.9	12.7	18.2	17.5
Cytophagales	0.2	0.2	0.3	20.3	4.2	16.0	15.6	3.6	3.7	3.7
Flavobacteriales	7.4	7.9	10.5	12.2	14.9	13.0	17.3	5.7	5.3	5.7
Bacillales	10.7	10.3	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alphaproteobacteria_nd	12.8	10.6	12.3	0.3	0.0	0.3	1.0	1.1	1.5	1.1
Rhizobiales	2.3	2.1	2.1	4.1	4.5	4.1	4.1	11.6	11.3	8.5
Rhodobacterales	7.6	9.7	7.3	19.6	27.9	25.3	19.5	12.2	15.5	8.3
Gammaproteobacteria_nd	12.0	13.3	12.0	3.1	0.9	0.9	1.2	1.0	1.7	0.8
Cellvibrionales	2.4	1.9	2.0	2.1	14.0	5.8	6.5	10.5	5.6	4.3
Chromatiales	3.0	2.6	2.6	0.2	0.7	4.4	1.6	13.9	11.2	17.7
Pseudomonadales	13.3	15.3	13.4	0.0	0.0	0.1	0.1	1.7	1.6	2.3
Other (>10%)	26.3	24.6	26.8	38.0	25.6	26.5	31.3	26.0	24.4	30.0

Table 8. Percentages of most representative orders in all replicates of water (W), hydroid (H) and sediment (S) samples.

Principal coordinate analysis (PCoA) based on weighted UniFrac distance matrices clearly separated the samples according to matrices (Figure 13 A) with the hydroid distinctly separated from sediment and water.

The same result was found with the cluster analysis derived from the distance matrices created by the beta diversity analysis using UPGMA clustering. (Figure 13 B). The tree grouped together water and sediments, demonstrating how these two environmental matrices contain many overlaps in terms of microbial composition.

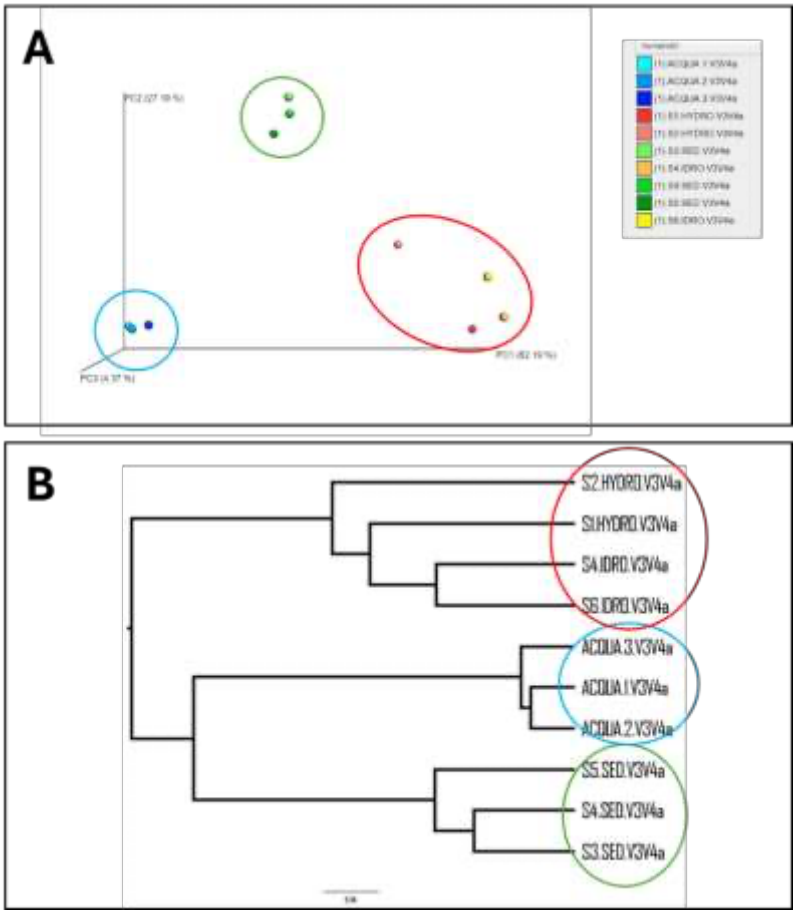


Figure 13. (A) three dimensional PCoA plot and (B) UPGMA weighted tree of WSH group.

3.3.4 Microbial communities of Water-Sediments-Hydroids-Nudibranchs (ALL)

Phylum level

When we analysed the ALL group, Proteobacteria phylum was the only present in all sample (Figure 14). This phylum was reported in all matrices with high percentages, with the only exception of *Dondice* that showed 4% of Proteobacteria. Water and sediments contain larger portion of this phylum (72% and 63% respectively), while half of bacterial communities of hydroids, *Cratena* and *Flabellina* were formed by Proteobacteria (54%, 49% and 50%, respectively). As already shown for WSH group, Actinobacteria and Bacteroidetes phyla constitute significant part of microbial compositions of water, sediments and hydroids. In particular, Actinobacteria is largely present in sediments (22%), with same lower percentages in water and hydroids (3%). Bacteroidetes represent the 39% of total microbial community of hydroids, while it is present at 9% in water and sediment matrices.

Tenericutes showed interesting trend, since they are part of nudibranchs and hydroids. This phylum represents half of microbiome of *Flabellina* and *Cratena* (49% and 51% respectively), almost all *Dondice* microbiome (96%) and it is present at 1% on hydroids. The last phylum present on more than one sample is Cyanobacteria. They are part of microbial communities of water and hydroids at the same percentage (1%).

Finally, four phyla were found to be unique of specific samples. Acidobacteria were only present in sediment samples at low concentration (1%), while microbial composition of water contains 10% of Firmicutes, 3% of Thaumarchaeota and 1% of Balneolaeota.

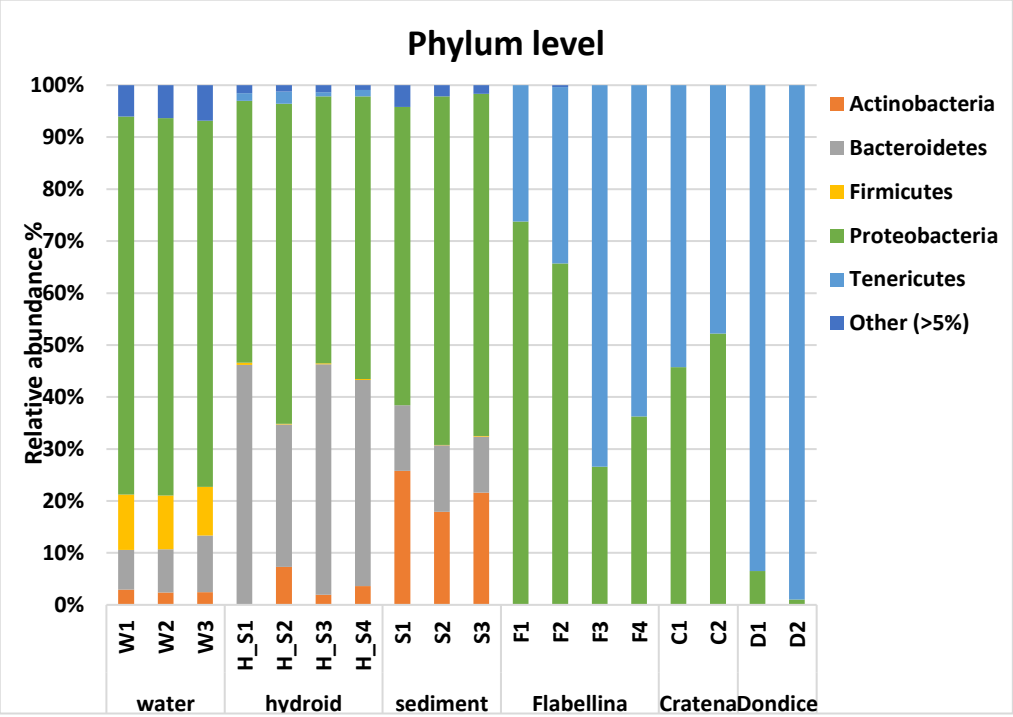


Figure 14. Taxonomy plot. Histograms reports composition of microbial communities at Phylum level of ALL group.

Phylum	water			hydroid				sediment			*Flabellina*				*Cratena*		*Dondice*	
	W1	W2	W3	H_S1	H_S2	H_S3	H_S4	S1	S2	S3	F1	F2	F3	F4	C1	C2	D1	D2
Actinobacteria	2.9	2.4	2.5	0.1	7.3	1.9	3.6	25.8	17.9	21.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bacteroidetes	7.6	8.3	10.9	46.1	27.4	44.3	39.6	12.7	12.8	10.8	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Firmicutes	10.7	10.4	9.4	0.4	0.1	0.2	0.2	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Proteobacteria	72.8	72.6	70.5	50.4	61.6	51.4	54.4	57.4	67.1	65.8	73.8	65.7	26.5	36.2	45.8	52.2	6.5	1.1
Tenericutes	0.0	0.0	0.0	1.5	2.3	0.8	1.2	0.0	0.0	0.0	26.2	33.9	73.4	63.8	54.2	47.8	93.5	98.9
Other (>5%)	6.0	6.3	6.8	1.5	1.3	1.3	0.9	4.2	2.1	1.7	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0

Table 9. Percentages of most representative Phyla in all replicates of water (W), hydroid (H), sediment (S), Flabellina, Cratena and Dondice samples.

Order level

Analysing composition at order level, nudibranchs showed high similarity, since Mycoplasmatales significantly contributed to microbial communities of *Flabellina*, *Cratena* and *Dondice* (Figure 15 and Table 10). This order was recorded at 49 and

51% in *Flabellina* and *Cratena*, respectively, and at 92% in *Dondice*. Hydroid samples also showed Mycoplasmatales, but in 1.5%.

Cellvibrionales is the other common order recorded in nudibranchs. This order was recorded at 30% in *Cratena* and 2% in *Flabellina* and *Dondice* samples; it was also present in all the other matrices, as water hydroids and sediments (among 2 and 7%).

Microbial community of *Flabellina* contained Oceanospirillales at 48%, an order present in water samples at 4% and in lower amount in hydroids and *Dondice* (around 1%).

Gammaproteobacteria characterized the microbial community of *Cratena* with 19% of relative abundance, while in the other 2 nudibranchs it was present in percentages lower than 0.5%. This order was also recorded also in significant amount in water samples (12%) and percentages between 1.3 and 1.5 in sediments and hydroids.

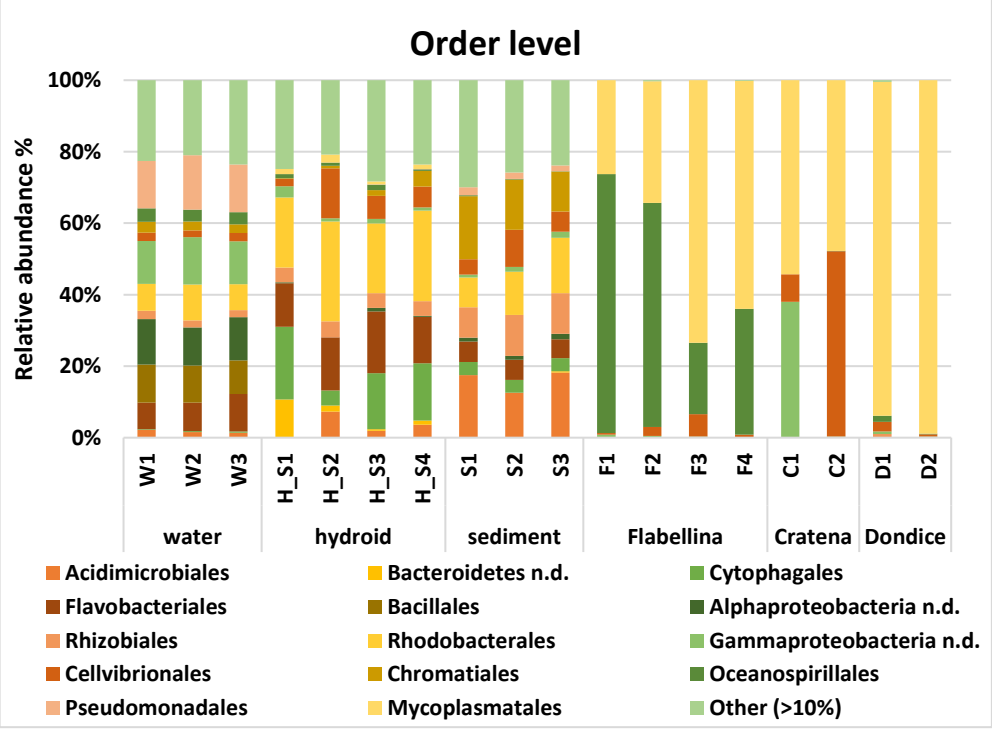


Figure 15. Taxonomy plot. Histograms reports composition of microbial communities at Order level of ALL group

Order	water			hydroid				sediment			*Flabellina*				*Cratena*		*Dondice*	
	W1	W2	W3	H_S1	H_S2	H_S3	H_S4	S1	S2	S3	F1	F2	F3	F4	C1	C2	D1	D2
Acidimicrobiales	2.2	1.6	1.4	0.0	7.3	1.9	3.6	17.5	12.6	18.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Bacteroidetes n.d.	0.0	0.0	0.0	10.7	1.7	0.5	1.2	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cytophagales	0.2	0.2	0.3	20.3	4.2	15.6	16.0	3.7	3.6	3.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Flavobacteriales	7.4	8.0	10.5	12.2	14.9	17.3	13.0	5.7	5.6	5.3	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0
Bacillales	10.7	10.4	9.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Alphaproteobacteria n.d.	12.8	10.6	12.1	0.3	0.0	1.0	0.3	1.1	1.1	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Rhizobiales	2.3	2.0	2.0	4.1	4.5	4.1	4.1	8.5	11.5	11.3	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.0
Rhodobacterales	7.6	10.0	7.3	19.6	27.9	19.5	25.3	8.3	12.1	15.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Gammaproteobacteria n.d.	12.0	13.2	12.0	3.1	0.9	1.2	0.9	0.8	1.3	1.7	0.8	0.5	0.2	0.0	38.0	0.3	0.7	0.3
Cellvibrionales	2.4	1.9	2.3	2.1	14.0	6.5	5.8	4.3	10.4	5.6	0.5	2.5	6.3	0.8	7.7	51.9	2.7	0.6
Chromatiales	3.0	2.5	2.4	0.2	0.7	1.6	4.4	17.7	14.1	11.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Oceanospirillales	3.8	3.3	3.4	1.1	0.9	1.5	0.5	0.2	0.2	0.1	72.4	62.6	19.9	35.3	0.0	0.1	1.7	0.2
Pseudomonadales	13.3	15.2	13.4	0.0	0.0	0.1	0.1	2.3	1.8	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Mycoplasmatales	0.0	0.0	0.0	1.5	2.3	0.8	1.2	0.0	0.0	0.0	26.2	34.0	73.4	63.8	54.2	47.8	93.5	98.9
Other (>10)	22.7	21.0	23.6	24.8	20.8	28.3	23.6	29.9	25.8	23.8	0.0	0.3	0.0	0.2	0.0	0.0	0.5	0.0

Table 10. Percentages of most representative Orders in all replicates of water (W), hydroid (H), sediment (S), Flabellina, Cratena and Dondice samples.

Principal coordinate analysis (PCoA) analysis based on weighted UniFrac distance matrices separated the samples according to matrices (Figure 16 A).

The same result was found with the cluster analysis derived from the distance matrices created by the beta diversity analysis using UPGMA clustering. (Figure 16 B). The tree showed two main groups one with hydroid, water and sediments, and the other with all the nudibranchs. The microbiome composition of *Flabellina* is closer to *Cratena* respect to *Dondice* species that showed a more peculiar composition (Figure 16 B).

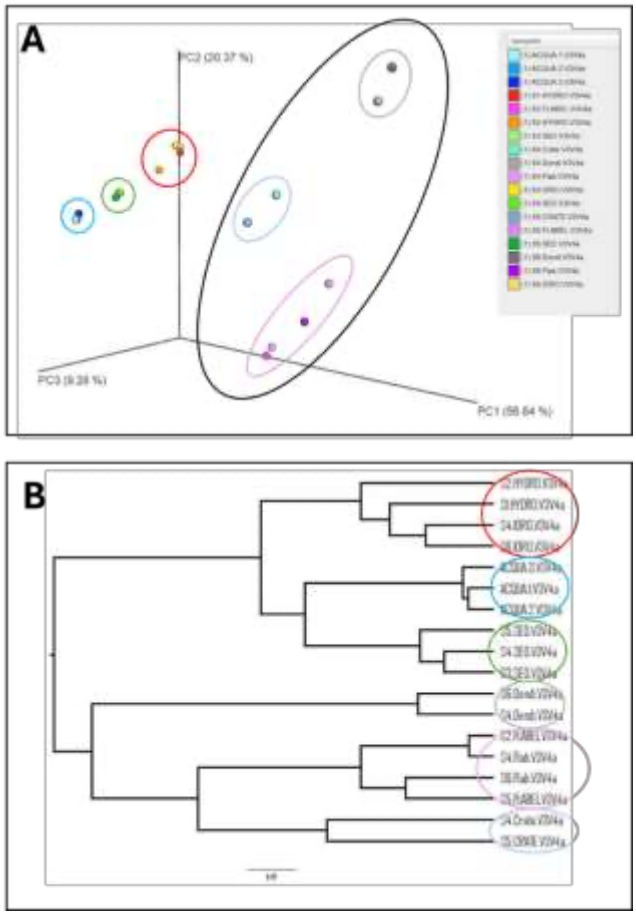


Figure 16. (A) three dimensional PCoA plot and (B) UPGMA weighted tree of ALL group.

3.4 Discussion

Many papers have highlighted the importance of the microbiome in cnidarians as functional for nutrient cycling (Carbon, Nitrogen, Phosphorus and Sulfur), homeostasis, protection, response to environmental fluctuations, and ecosystem resilience (McCauley, Jackson, & Loesgen, 2023). However, not all taxa have

received the same attention in the investigation of this aspect, as is the case for the Hydrozoa. Hydroids can establish several kinds of interactions with many organisms, highlighting that their forests represent a mosaic of microhabitats that can be exploited by highly diversified organisms (Di Camillo, et al., 2018). The present work, however, represents the first complete investigation of the hydrozoan microbiome, linking it not only with the surrounding environmental matrix but also with the predators (i.e., nudibranchs) that live associated with them.

The first result of the present work highlights that the microbiome of *Eudendrium racemosum* is mainly composed of the phyla Proteobacteria and Bacteroidetes. This result is in line with what was described before for other cnidarians and for the hydroid *Ectopleura crocea*, even if the dominant orders were different (McCauley, Jackson, & Loesgen, 2023; Di Camillo, et al., 2012). In *E. crocea*, the dominant orders were Burkholderiales and Flavobacteriales with the genera *Delftia* and *Polaribacter* (Di Camillo, et al., 2012), while in *E. racemosum* the orders Cytophagales, Flavobacteriales, Rhodobacterales, and Cellvibrionales were dominant with the genera *Microscilla*, *Pibocella*, *Hyphomonas*, and *Dasania*.

The microbiome composition can change in relation to many factors such as the period of sampling, depth, host phylogeny, and life-stage (McCauley, Jackson, & Loesgen, 2023), as also observed in the analysis of the microbiome of *E. crocea* (Di Camillo, et al., 2012). This highlights that these preliminary results of hydroid microbiome are still in their infancy and many more analyses are needed to understand their role, as highlighted in many other organisms. This is also important because it is known that many coral species can produce antifouling molecules, and several bacteria species are known to be directly involved in the biosynthesis of these secondary metabolites (Proksch, Edrada, & Ebel, 2002).

Comparing the hydroid microbiome with the surrounding environmental matrices' composition, this study highlighted that the microbiome of the hydroid had few points in common. Proteobacteria represented the main phylum for the water and sediment microbiome as well, but the dominant orders and genera were different, with no overlap with the hydroid microbiome. This phylum, in fact, represents the most abundant one in many matrices and in cnidarians (McCauley, Jackson, & Loesgen, 2023).

Recently, the presence of chitinolytic bacteria belonging to the genus Vibrio has been reported in association with the perisarc of different species of hydroids (Stabili, Gravili, Piraino, Boero, & Alifano, 2006; Stabili, Gravili, Tredici, Boero, & Alifano, 2011). This genus is also present in the *E. racemosum* microbiome, but in a low percentage. Its absence in the surrounding environments led to the hypothesis that it might be typical of the hydroid microbiome.

As already highlighted, studies on Mediterranean marine biodiversity are very poor if we consider some specific group of animals. It is the case of Mediterranean nudibranchs, on which few investigations have been conducted so far to clarify their ecological, chemical, genetic and physiological features (Lombardo & Marletta, 2023).

Hydroids represent a key habitat for many epifaunal organisms, such as nudibranchs. Thus, microbiomes of hydroids and three common hydroid-associated nudibranchs were analysed together with the aim to describe shaping of bacterial taxa within this holobiont and if similarities and diversities exist in the acquisition of prokaryotic symbionts among these species and surrounding environment.

No data are reported in literature about microbial community associated with the three species of Mediterranean nudibranchs here analysed: *Flabellina affinis*, *Cratena peregrina* and *Dondice* sp. Other nudibranchs species and their associated bacteria have been investigated for their production of bioactive compounds. This is due to the absence of shell, thus nudibranchs developed chemical defence strategies against predators and pathogens (Dean & Prinsep, 2017). This chemical barrier is constituted by an external layer of mucus composed by lipid and proteins, which represent a formidable substrate for the attraction of symbiotic bacteria (Lopes, Aveiro, Cruz, Cartaxana, & Domingues, 2024).

One of the most informative studies on nudibranchs microbiome has been published in 2023 by Stuij and colleagues (Stuij, et al., 2023). In this study, seven nudibranchs were analysed: *Doriprismatica atromarginata* (family Chromodorididae), *Jorunna funebris* (family Discodorididae), *Phyllidiella nigra*, *Phyllidiella pustulosa*, *Phyllidia carlsonhoffi*, *Phyllidia elegans*, and *Phyllidia picta* (all family Phyllidiidae). Researchers focused on gut and mucus microbiome and found that Proteobacteria, Tenericutes, Chloroflexi, Thaumarchaeota and Cyanobacteria were the mostly recorded phyla in these samples. In addition, mucus and gut presented a microbiome composition with many dissimilarities respect with surrounding bacteria (i.e., compared with phyla composing microbial communities of seawater and sediments). Same study also highlighted that the order Mycoplasmatales (Tenericutes) was mostly abundant in *Doriprismatica atromarginata* and *Jorunna funebris*.

Comparing results with our work, Tenericutes was recorded in nudibranchs and hydroids microbiomes. This phylum constituted half of *F. affinis* and *C. peregrina* microbiomes and more than 95% of *Dondice* sp. microbiome; it is also present at lowest percentage on hydroids (1%). Same microbiome similarity was also observed at order level, where the microbial community of the three nudibranchs was significantly composed by Mycoplasmatales. This order represents about 50% of *F. affinis* and *C. peregrina* microbiomes and more than 90% of *Dondice* sp.

microbiome. Mycoplasmatales was also present in hydroid microbial community, but at lower value (1.5%). Seawater and sediment samples did not contain this bacterial order, supporting the hypothesis that Mycoplasmatales was specific of the holobiont microbial community, which is not influenced by environmental bacteria.

Predominance of Mycoplasmatales order in marine organisms has been observed in other invertebrates (Van Heuven, et al., 2018; Van De Water, Allemand, & Ferrier-Pagès, 2018) and are described with parasitic association in vertebrates (Van De Water, Allemand, & Ferrier-Pagès, 2018). They also have already been described in high abundance in other species of nudibranchs (Abdelrahman, Patin, & Hanora, 2021; Cleary, Swierts, & Coelho, 2918). Possible explanation of high abundance of Mycoplasmatales in nudibranchs rather than hydroids can be found in the high content of amino acids and fatty acids in host composition. Especially mucus contains these important macromolecules, thus nudibranchs can be considered suitable substrate for specific group of bacteria, such as Mycoplasmatales (King, Judd, Kuske, & Smith, 2012; Sheng, Soon, & Chang, 2022). Bacteria use these macromolecules for metabolic and growth mechanisms (Zhukova, 2014). Together with parasitic association, some studies also described the symbiont relationship among Mycoplasmas and nudibranchs with a beneficial interaction, since they can be involved in digestion processes in nudibranchs gut (Fraune & Zimmer, 2008). Due to the documented presence of Mycoplasmatales in nudibranchs living diversified marine ecosystems, further investigation will help to clarify type of relationship with benthic organisms and elucidate some metabolic pathways of ecological and biotechnological interest.

Among the bacterial class *Gammaproteobacteria*, *Cellvibrionales* and *Oceanospirillales* are two of the major orders; they cover fundamental roles in different marine ecosystems and are considered the keystone taxa of microbiomes (Liao 2020). Bacteria of the order *Cellvibrionales* have been recorded in hydroids and *C. peregrina* microbiomes, with presence also in sediments. *Oceanospirillales* order was reviled in *F. affinis* microbial community, but also in its surrounding (i.e., in water samples).

In particular, order *Cellvibrionales* has been often found in marine ecosystems with low nutrient levels (oligotrophic environments) (Spring, Scheuner, Göker, & Klenk, 2015). Also order *Oceanospirillales* has been described as inhabitant of superficial layer of deep-sea marine sediments (Bacosa, et al., 2018). No more information can be found in literature about these two bacteria orders associated with nudibranchs. These bacteria were also found in other molluscs. It is the case of large bivalve *Acesta excavate* (Limidae) collected from coral reefs on the northeast Atlantic margin (Norway). Bacteria belonging to this order has interesting aerobic degradation mechanisms that can find application in bioremediation

processes. They can degrade complex organic compounds, since they produce hydrolytic enzymes and biosurfactant molecues (Garrity & Bell, 2005). In fact, hydrocarbonoclastic bacteria of the order *Oceanospirillales* have been found in high concentrations in oil contaminated marine samples (Neethu, Saravanakumar, Purvaia, & al., 2019).

Our results demonstrate the co-occurrence of nudibranch-hydroid specific bacteria taxa and prokaryotic influence by the surrounding. We can conclude that the complex nudibranch-hydroid acquires portion of their microbiome from water and sediments microorganisms, following also a horizontal transmission. But they also exhibited specific bacterial taxa only present in nudibranch and hydroid microbiomes and not present in the surrounding, thus showing a vertical transmission with prokaryotic influence between hydroids and the associated animals. The vvertical transmission of associated microorganisms is a processes already described in many marine organisms, for instance, sponges (Webster, et al., 2010), bivalves (Krueger, Gustafson, & Cavanaugh, 1996), ascidians, bryozoans and oligochaetes (Bright & Bulgheresi, 2010; Hosokawa, Kiluchi, Nikoh, Shimada, & Fukatsu, 2006). This ecological mechanism reflects a strong symbiotic relationship between the benthic organisms and the associated fauna.

CONCLUSION

As noted throughout this research, Mediterranean hydroids, due to their adaptability and the complexity of their characteristic microbiome, play an important ecological role in all marine ecosystems. One of the factors in which they have a significant impact is the maintenance of biodiversity, particularly in environments with specific geographical features, such as the Strait of Messina. In this ecological environment, their ability to form three-dimensional colonies, such as the forests of *Eudendrium racemosum*, makes this species essential for the corresponding benthic structure and trophic network of the marine ecosystem, contributing to its stability and biodiversity. These hydroid colonies, in fact, not only provide refuge for a variety of organisms with which they live in symbiotic relationships, but also facilitate the transfer of energy between the benthic and pelagic compartments, acting as vital ecological intermediaries (Di Camillo C. G., Bavestrello, Cerrano, & Gravili, 2017; Castriota, Falautano, Battaglia, & Maraventano, 2017).

Studies on the microbiome associated with hydroids, such as that by Di Camillo et al. (2012), are shedding new light on the complex interactions between hydroids and microorganisms. These investigations reveal that the microbiota not only influences the health and functionality of hydroids but also plays a decisive role in the conservation of marine ecosystems. The epibiontic relationships between hydroids and *Posidonia oceanica* (Boero, Chessa, Chimenz, & Fresi, 1985; Gravili, Cozzoli, & Cambi, 2021) serve as key indicators for monitoring the health of marine environments. As highlighted in the analysis conducted in Chapter 2, however, despite these advances, significant knowledge gaps persist regarding both microbiotic and geographic aspects. Regions such as Calabria remain underexplored, as do hydroid species associated with marine plants like *Cymodocea nodosa* and *Halimeda tuna* (Bo, et al., 2011).

Moreover, understanding of microbiome functionality is still limited, despite its importance in biodiversity preservation. Hydroids' interactions with their environment are enriched by the presence of symbiotic microorganisms, which play a role in shaping ecological dynamics and the survival strategies of hydroid colonies. For instance, studies on the microbiome of species such as *Hydractinia echinata* have shown that marine bacteria not only protect hydroids from potential pathogens but also influence their growth and morphogenesis. Notably, analyses of these microbiomes reveal that marine bacteria produce a range of bioactive metabolites, including antimicrobial, antifungal, and morphogenetic compounds, which modulate host biological responses (Guo, et al., 2017; McCauley, Jackson, & Loesgen, 2023).

The study of *Eudendrium racemosum* within the Strait of Messina, presented in the final chapter of this thesis, has highlighted these ecological and microbiological interactions. In this dynamic environment, characterized by strong currents and high environmental variability, *E. racemosum* has demonstrated remarkable adaptability to trophic conditions by feeding on suspended organic particles and bivalve larvae. Additionally, the presence of symbiotic bacteria in this ecosystem has shown that microbiological interactions are essential for the survival and success of hydroids, influencing both their ecological role and physiological processes (Castriota, Falautano, Battaglia, & Maraventano, 2017).

As discussed, research on Mediterranean marine biodiversity is notably sparse for certain groups of animals. This includes Mediterranean nudibranchs, for which few studies have clarified their ecological, chemical, genetic, and physiological characteristics. Hydroids represent a key habitat for many epiphytic organisms, such as nudibranchs. Consequently, the microbiomes of hydroids and three common nudibranchs associated with hydroids were analyzed to explore bacterial taxa formation within this holobiont and to identify similarities and differences in the acquisition of prokaryotic symbionts among these species and their surrounding environment.

Our research highlights that no prior studies have documented the microbial community associated with the three Mediterranean nudibranch species analyzed here: *Flabellina affinis*, *Cratena peregrina*, and *Dondice* sp. While other nudibranch species and their associated bacteria have been investigated for bioactive compound production, our findings demonstrate the co-occurrence of specific bacterial taxa in both nudibranchs and hydroids, as well as prokaryotic influences from the surrounding environment. This suggests that the nudibranch-hydroid complex acquires part of its microbiome through horizontal transmission from water and sediment microorganisms. However, our study also identified specific bacterial taxa unique to the microbiomes of nudibranchs and hydroids, absent in the surrounding environment, indicating vertical transmission of prokaryotes between hydroids and associated organisms. Vertical transmission of associated microorganisms is a process documented in many marine organisms, including sponges, bivalves, ascidians, bryozoans, and oligochaetes, reflecting strong symbiotic relationships between benthic organisms and their associated fauna (Dean & Prinsep, 2017; Lopes, Aveiro, Cruz, Cartaxana, & Domingues, 2024).

Beyond these ecological observations, the microbiome of hydroids has attracted growing interest in pharmacology due to its potential for bioactive compound production. These compounds have various therapeutic applications, positioning hydroids as natural reservoirs with potential for medical and therapeutic uses.

Evidence supporting the pharmacological potential of hydroids includes the identification of morphogenetic and antimicrobial molecules produced by symbiotic bacteria. Exploring the interaction mechanisms between hydroids and their symbionts, as well as analyzing the metabolites produced, could pave the way for the discovery of novel natural drugs and therapeutic biomolecules (Guo, et al., 2017).

For instance, bacteria of the *Streptomyces genus* are prolific producers of secondary metabolites with antimicrobial and antitumor activities (Abdelrahman, et al., 2022). When associated with *Chromodoris quadricolor, Streptomyces produces* compounds that protect the host from bacterial infections and predators. Metabolite analysis of Streptomyces has revealed previously undescribed bioactive compounds, underscoring their potential for innovative drug development (Abdelrahman, et al., 2022). Similarly, marine bacteria such as Actinobacteria are rich sources of natural compounds that could be used to combat infectious diseases or develop anticancer therapies (Guo, et al., 2017). As shown for the WSH group, the phyla Actinobacteria and Bacteroidetes represent significant components of the microbial compositions of water, sediments, and hydroids. Specifically, Actinobacteria are abundant in sediments (22%) but less prevalent in water and hydroids (3%), findings that future studies could confirm.

Parallel studies on Hydractinia echinata and other hydroid species reinforce the potential of these microorganisms as producers of pharmacologically relevant molecules. The exploration of hydroids and their symbionts could lead to groundbreaking discoveries in medicine (Guo, et al., 2017). Thus, the ecological discoveries reported in this research pave the way for pharmacological advancements, particularly in hydroid microbiology. Further investigation of their functionality within marine ecosystems is essential, not only for biological or ecological reasons, as demonstrated in this thesis, but also for their pharmacological potential. Many of these capabilities remain unexplored, as a large portion of biosynthetic genes in marine bacteria are silent under standard culture conditions, requiring advanced techniques for expression and laboratory study.

In conclusion, the studies presented here demonstrate that hydroids and their associated microorganisms serve as ecological keystones within marine trophic networks and represent a promising resource for biotechnology and pharmacology. Future research on hydroid microbiomes and their symbiotic relationships, utilizing advanced technologies such as genomic sequencing and metabolomic analysis, will not only enhance understanding of these organisms' roles in protecting and conserving marine ecosystems but also foster the development of novel therapeutic solutions (McCauley, Jackson, & Loesgen, 2023).

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Allegations

Allegato 1: Supplemental Material (SM)

	Authors	Title	Year	Document Type	1_step_esclusion	2 step esclusione	3 step esclusione
1	Wolsky A.	Mode of cleavage of the eggs of hydroides norvegica in the mediterranean	1955	Article	p		
2	Werner B.	Die Verbreitung und das jahreszeitliche Auftreten der Anthomeduse Rathkea octopunctata M. Sars, sowie die Temperaturabhängigkeit ihrer Entwicklung und Fortpflanzung	1958	Article	nM		
3	Werner B.	The nematocysts of the Cnidaria, with special reference to the Hydroida - I. Classification and importance for systematics and evolution; [Die Nesselkapseln der Cnidaria, mit besonderer Berücksichtigung der Hydroida - I. Klassifikation und Bedeutung für die Systematik und Evolution]	1965	Article	hy	t	
4	Por F.D.; Ferber I.	The hebrew university – smithsonian institution collections from the suez canal (1967 – 1972)	1972	Article	nM		
5	Svoboda A.	Underwater observations on the life cycle of Corymorpha nutans (Hydrozoa)	1973	Article	hy	e	r
6	GINSBURG R.N.; S	Growth and submarine fossilization of algal cup reefs, Bermuda	1973	Article	nM		
7	Ben-Eliahu M.N.	Polychaete cryptofauna from rims of similar intertidal vermetid reefs on the mediterranean coast of israel and in the gulf of elat: Serpulidae(polychaeta sedentaria)	1976	Article	p		
8	Amoureux L.; Rulli	Systematique et ecologie d'annelides polychetes de la presqu'il du sinai	1978	Article	p		
9	Larson R.J.	The Medusa of Velella velella (Linnaeus, 1758) (Hydrozoa, Chondrophorae)	1980	Article	hy	m	
10	Boero F.	Systematics and Ecology of the Hydroid Population of two Posidonia oceanica Meadows	1981	Article	hy	e	ep
11	Flügel E.	Evolution of Triassic reefs: Current concepts and problems	1982	Article	out		
12	Edwards C.; Harve	Observations on the hydroids coryne pintneri and thecocodium brieni new to the British list	1983	Article	nM		
13	Aleem A.A.	The Suez Canal as a habitat and pathway for marine algae and seagrasses	1984	Article	nM		
14	Boero F.; Chessa L	The Zonation of Epiphytic Hydroids on the Leaves of Some Posidonia oceanica (L.) DELILE Beds in the Central Mediterranean	1985	Article	hy	e	ep
15	Fattorusso E.; Lan	Sterols of four Mediterranean hydroids	1985	Article	hy	ch	
16	BOERO F.; FRESI E	Zonation and Evolution of a Rocky Bottom Hydroid Community	1986	Article	hy	e	e
17	Gili J.M.; Ros J.D.;	Types of bottoms and benthic Cnidaria from the trawling grounds (littoral and bathyal) off Catalonia (NE Spain)	1987	Article	hy	e	d
18	Aiello A.; Fattorus	Isolation and structure elucidation of two new polyhydroxylated sterols from the mediterranean hydroid eudendrium glomeratum	1987	Article	hy	ch	
19	Barange M.; Gili J.	Feeding cycles and prey capture in Eudendrium racemosum (Cavolini, 1785)	1988	Article	hy	e	tr
20	Stergiou K.I.	Feeding habits of the lessepsian migrant Siganus luridus in the eastern Mediterranean, its new environment	1988	Article	out		
21	Mills C.E.; Goy J.	In situ observations of the behavior of mesopelagic Solmissus narcomedusae (Cnidaria, Hydrozoa)	1988	Article	hy	m	
22	Ardizzone G.D.; Gi	Temporal development of epibenthic communities on artificial reefs in the central Mediterranean Sea	1989	Article	hy	f	
23	Gravina M.F.; Ardi	Polychaetes of an artificial reef in the central mediterranean sea	1989	Article	p		
24	Carré D.; Carré C.	Complex reproductive cycle in Eucheilota paradoxica (Hydrozoa: leptomedusae): Medusae, polyps and frustules produced from medusa stage	1990	Article	hy	m	
25	Valdes J.L.; Roman	Zooplankton composition and distribution off the coast of Galicia, Spain	1990	Article	out		
26	Piraino S.; Morri C.	Zonation and Ecology of Epiphytic Hydroids in a Mediterranean Coastal Lagoon: The 'Stagnone' of Marsala (North-West Sicily)	1990	Article	hy	e	ep
27	Llobet I.; Gili J.-M.	Horizontal, vertical and seasonal distributions of epiphytic hydrozoa on the alga Halimeda tuna in the Northwestern Mediterranean Sea	1991	Article	hy	e	ep
28	Llobet I.; Coma R.	The population dynamics of Orthopyxis crenata (Hartlaub, 1901) (Hydroza, Cnidaria), an epiphyte of Halimeda tuna in the northwestern Mediterranean	1991	Article	hy	e	ep
29	Östman C.; Piraino	Nematocysts of the Mediterranean hydroid Halocordyle disticha	1991	Article	hy	t	
30	Hughes R.G.; John	The growth patterns of some hydroids that are obligate epiphytes of seagrass leaves	1991	Article	hy	e	ep
31	Goy J.	Hydromedusae of the Mediterranean Sea	1991	Article	hy	m	
32	Phyllis; Knight-Jon	Sabelliform polychaetes, mostly from turkey's aegean coast	1991	Article	p		
33	Bellan D.	Speciation and biogeography in the Mediterranean Sea; [Speciation et biogeographie en mer Mediterranee]	1992	Article	nM		
34	Ben-Eliahu M.N.;	Serpulids (annelida: Polychaeta) along the mediterranean coast of israel—New population build-ups of lessepsian migrants	1992	Article	p		
35	BOERO F.; BOUILL	Zoogeography and life cycle patterns of Mediterranean hydromedusae (Cnidaria)	1993	Article	hy	m	
36	Ilan M.; Ben-Eliah	Three deep water sponges from the eastern mediterranean and their associated fauna	1994	Article	out		
37	Alvarez-Claudio C.	Some records of the superfamily Plumularioidea L. Agassiz, 1862 (Cnidaria, Hydrozoa) from the Bay of Biscay	1995	Article	nM		
38	Coma R.; Gili J.M.	Trophic ecology of a benthic marine hydroid, Campanularia everta	1995	Article	hy	e	tr
39	Ardizzone G.D.; Be	Colonization and disappearance of Mytilus galloprovincialis Lam. on an artificial habitat in the Mediterranean Sea	1996	Article	out		
40	Gravili C.; Boero F.	Zanclea species (Hydroidomedusae, Anthomedusae) from the Mediterranean	1996	Article	hy	t	
41	Coma R.	Quantification of sexual reproduction in the marine benthic hydroid Campanularia everta	1996	Article	hy	e	ep
42	Mills C.E.; Pugh P.	Medusae, siphonophores and ctenophores of the Alborán Sea, south western Mediterranean	1996	Article	hy	m	
43	Goy J.	The Medusae (Cnidaria, Hydrozoa) and their trophic environment: an example in the north-western Mediterranean	1997	Article	sc		
44	Boero F.; Gravili C.	The rediscovery of codonorchis octaedrus (Hydroidomedusae, anthomedusae, pandeidae), with an update of the mediterranean hydroidomedusan biodiversity	1997	Article	hy	t	
45	Buecher E.; Jacque	Long-term fluctuations of Liriope tetraphylla in Villefranche bay between 1966 and 1993 compared to Pelagia noctiluca pullulations	1997	Article	hy	m	
46	Cerrano C.; Amore	The polyp and the medusa of zanclea costata gegenbaur (Cnidaria, Hydrozoa)	1997	Article	hy	t	
47	Bavestrello G.; Cer	Damage by fishing activities to the Gorgonian coral Paramuricea clavata in the Ligurian Sea	1997	Article	out		
48	Peña Cantero A.L.;	On the species of filellum hincks, 1868 (Cnidaria: Hydrozoa) with the description of a new species	1998	Article	hy	t	
49	Andersen V.; Franc	Vertical distributions of macroplankton and micronekton in the Ligurian and Tyrrhenian Seas (northwestern Mediterranean)	1998	Article	out		
50	Genzano G.N.	Hydroid epizoites on hydroids Tubularia crocea and Sertularella mediterranea from the intertidal of Mar del Plata (Argentina)	1998	Article	nM		
51	Gili J.-M.; Bouillon	A new species of Krampella (Hydrozoa, Hydroidomedusae, Tiarannidae) from the deep waters of Antikythira Strait (Cretan Sea, North East Mediterranean)	1998	Article	hy	m	
52	Cerrano C.; Bavest	Biological cycle of Podocoryna exigua (Cnidaria: Hydrozoa) from a sandy bottom of the Ligurian Sea	1998	Article	hy	e	e
53	Coma R.; Ribes M.	An energetic approach to the study of life-history traits of two modular colonial benthic invertebrates	1998	Article	hy	e	e
54	Genzano G.N.; Roc	Association between hydroid species and their substrates from the intertidal zone of Mar del Plata (Argentine)	1998	Article	nM		
55	Relini G.; Tixi F.; R	The macrofouling on offshore platforms at Ravenna	1998	Article	hy	f	
56	Gili J.-M.; Bouillon	Submarine canyons as habitats of prolific plankton populations: Three new deep-sea Hydroidomedusae in the western Mediterranean	1999	Article	hy	m	
57	Buechner E.; Gilbo	Temporal persistence in the vertical structure of the assemblage of planktonic medusae in the NW Mediterranean Sea	1999	Article	hy	m	
58	Morri C.; Bianchi C	Hydroids (Cnidaria: Hydrozoa) from the Aegean Sea, mostly epiphytic on algae	1999	Article	hy	e	d
59	Pagès F.; Pugh P.R.	The discovery of an Antarctic epipelagic medusan in the Mediterranean	1999	Article	hy	m	
60	Kocak F.; Ergen Z.	Fouling organisms and their developments in a polluted and an unpolluted marina in the aegean sea (turkey)	1999	Article	out		
61	Genzano G.N.; Zan	Natural history of Bimeria vestita wright, 1859 (Hydrozoa, Bougainvilliidae) in the rocky intertidal of Mar del Plata (Argentina)	1999	Article	nM		
62	Benović A.; Lučić D	Does change in an Adriatic hydromedusan fauna indicate an early phase of marine ecosystem destruction?	2000	Article	hy	m	
63	Bavestrello G.; Bia	Bio-mineralogy as a structuring factor for marine epibenthic communities	2000	Article	hy	e	ex
64	Marques A.C.; Peñ	Mediterranean species of Eudendrium Ehrenberg, 1834 (Hydrozoa, Anthomedusae, Eudendriidae) with the description of a new species	2000	Article	hy	t	
65	McKinney F.K.; Jak	Spatial niche partitioning in the Cellaria meadow epibiont association, northern Adriatic Sea	2000	Article	hy	f	
66	Terlizzi A.; Conte E	Biological succession on silicone fouling-release surfaces: Long-term exposure tests in the Harbour of Ischia, Italy	2000	Article	out		
67	Benović A.; Lučić D	Ecological characteristics of the mljet island seawater lakes (South Adriatic Sea) with special reference to their resident populations of medusae	2000	Article	hy	m	
68	Bavestrello G.; Puc	Life history of Perarella schneideri (Hydrozoa, Cytaeididae) in the Ligurian Sea	2000	Article	hy	e	tr
69	Bouillon J.; Pagès F	Deep-water Hydromedusae from the Lacaze-Duthiers submarine canyon (Banyuls, northwestern Mediterranean) and description of two new genera, Guillea and Parateclaia	2000	Article	hy	m	
70	Guidetti P.; Moder	Composition, abundance and stratification of macrobenthos in the marine area impacted by tar aggregates derived from the Haven oil spill (Ligurian Sea, Italy)	2000	Article	out		
71	Fauzzi A.; Boero F.	Structure of an epiphytic hydroid community on Cystoseira at two sites of different wave exposure	2000	Article	hy	e	ep
72	Souissi S.; Yahia-K	Spatial characterization of nutrient dynamics in the Bay of Tunis (south-western Mediterranean) using multivariate analyses: Consequences for phyto- and zooplankton distribution	2000	Article	out	nutrient	
73	Rees J.T.	A pandeid hydrozoan, Amphinema sp., new and probably introduced to Central California: Life history, morphology, distribution, and systematics	2000	Article	nM		
74	Rodríguez-Ruiz S.;	Seasonal changes in feeding habits of Diplodus annularis (L., 1758) off southeast Iberian Peninsula; [Cambios estacionales en la dieta de Diplodus annularis (L., 1758) en el sudeste ibérico]	2001	Article	out		
75	Mariottini G.L.; Ca	Variations of ATP content in V79 cells treated with crude toxins of--Aequorea aequorea (Cnidaria: Hydrozoa) and Rhizostoma pulmo (Cnidaria: Scyphozoa). A preliminary study.	2001	Article	hy	m	
76	Rayyan A.; Christid	First record of the bivalve-inhabiting hydroid Eugymnanthea inquilina in the eastern Mediterranean Sea (Gulf of Thessaloniki, north Aegean Sea, Greece)	2002	Article	hy	e	ep
77	Genzano G.N.; Zan	Hydroid populations from sublittoral outcrops off Mar del Plata, Argentina: Abundance, seasonality and reproductive periodicity	2002	Article	nM		
78	Stergiou K.I.; Karp	Feeding habits and trophic levels of Mediterranean fish	2002	Article	out		
79	Kress N.; Tom M.;	The use of coal fly ash in concrete for marine artificial reefs in the southeastern Mediterranean: Compressive strength, sessile biota, and chemical composition	2002	Conference paper	hy	e	ex
80	Robson E.A.	The story of alcyonium: From halcyon birds to zoophytes	2002	Article	out		
81	Carrassón M.; Cart	Trophic relationships in a Mediterranean deep-sea fish community: Partition of food resources, dietary overlap and connections within the benthic boundary layer	2002	Article	out		
82	Yahia M.N.D.; Goy	Distribution and ecology of Medusae and Scyphomedusae (Cnidaria) in Tunis Gulf (SW Mediterranean); [Distribution et écologie des Méduses (Cnidaria) du golfe de Tunis (Méditerranée sud occidentale)]	2003	Article	hy	m	
83	Mapstone G.M.	Redescriptions of two physonect siphonophores, apolemia uvaria (lesueur, 1815) and tottonia contorta margulis, 1976, with comments on a third species ramosia vitiazi stepanjants, 1967 (Cnidaria: Hydrozoa: Apolemiidae)	2003	Article	hy	s	
84	Puce S.; Bavestrell	On the occurrence of coryne eximia allman (cnidaria, corynidae) in the mediterranean sea	2003	Article	hy	e	r
85	Bedini R.; Canali M	Epiphytic communities on Posidonia Oceanica (L.) delile leaves along the north tyrrhenian coasts (N.W. Mediterranean sea, Italy)	2003	Article	hy	e	ep
86	Zakaria H.Y.	Pelagic coelenterates in the waters of the western part of the Egyptian Mediterranean Coast during summer and winter	2004	Article	hy	m	
87	Bouillon J.; Medel	Fauna of the Mediterranean Hydrozoa	2004	Review	hy	t	
88	Warren J.D.; Dam	Zooplankton in the Ligurian Sea: Part II. Exploration of their physical and biological forcing functions during summer 2000	2004	Review	out		
89	Fernández De Puel	Hydrographical characteristics and zooplankton distribution in the Mallorca channel (Western Mediterranean): Spring 2001	2004	Conference paper	out		
90	Rayyan A.; Photis	(Metazoan parasite species in cultured mussel Mytilus galloprovincialis in the Thermaikos Gulf (North Aegean Sea, Greece)	2004	Article	out		
91	Batistić M.; Kršinić	Gelatinous invertebrate zooplankton of the South Adriatic: Species composition and vertical distribution	2004	Article	hy	m	
92	Puce S.; Tazioli S.	Nematocyst arrangement on the tentacles of the polyps of eudendrium (cnidaria, hydrozoa)	2005	Article	hy	t	
93	Schuchert P.	Taxonomic revision and systematic notes on some Halecium species (Cnidaria, Hydrozoa)	2005	Article	hy	t	
94	Govindarajan A.F.;	Species identification of bivalve-inhabiting marine hydrozoans of the genus Eugymnanthea	2005	Article	hy	e	ep
95	Benović A.; Lučić D	Bathymetric distribution of medusae in the open waters of the middle and south Adriatic Sea during spring 2002	2005	Article	hy	m	
96	Di Camillo C.; Puce	Relationships between benthic diatoms and hydrozoans (Cnidaria)	2005	Article	hy	e	fa
97	Di Camillo C.; Puce	Coralline algae epibiontic on thecate hydrozoans (Cnidaria)	2006	Article	hy	e	fa
98	Cinar M.E.; Bilecer	New records of alien species on the Levantine coast of Turkey	2006	Article	hy	a	
99	Pardi G.; Piazzi L.;	Spatial variability of Posidonia oceanica (L.) Delile epiphytes around the mainland and the islands of Sicily (Mediterranean Sea)	2006	Article	hy	e	ep
100	Cinar M.E.; Katağa	Temporal changes of soft-bottom zoobenthic communities in and around Aliaıcak Harbor (Izmir Bay, Aegean Sea), with special attention to the autecology of exotic species	2006	Article	out		
101	Cinar M.E.	Serpulid species (Polychaeta: Serpulidae) from the Levantine coast of Turkey (eastern Mediterranean), with special emphasis on alien species	2006	Article	p		

102	De Vito D.; Piraino	Evidence of reverse development in Leptomedusae (Cnidaria, Hydrozoa): The case of Laodicea undulata (Forbes and Goodsir 1851)	2006	Article	hy	e	r
103	Fraschetti S.; Terlizz	The distribution of hydroids (Cnidaria, Hydrozoa) from micro- to macro-scale: Spatial patterns on habitat-forming algae	2006	Article	hy	e	ep
104	Zega G.; Pennati R	Serotonin involvement in the metamorphosis of the hydroid Eudendrium racemosum	2007	Article	hy	e	ex
105	Boero F.; Bucci C.;	Obelia (Cnidaria, Hydrozoa, Campanulariidae): A microphagous, filter-feeding medusa	2007	Article	hy	e	r
106	Hosia A.; Pagès F.	Unexpected new species of deep-water Hydroidomedusae from Korsfjorden, Norway	2007	Article	nM		
107	Fernández de Puel	Zooplankton time-series in the Balearic Sea (Western Mediterranean): Variability during the decade 1994-2003	2007	Article	out		
108	Gravili C.; Bouillon	The life cycle of Gastroblasta raffaelei (Cnidaria, Hydrozoa, Leptomedusae, Campanulariidae) and a review of the genus Gastroblasta	2007	Review	rw		
109	Malej A.; Turk V.;	Direct and indirect trophic interactions of Aurelia sp. (Scyphozoa) in a stratified marine environment (Mljet Lakes, Adriatic Sea)	2007	Article	sc		
110	Romagnoli T.; Bavv	Microalgal communities epibiontic on the marine hydroid Eudendrium racemosum in the Ligurian Sea during an annual cycle	2007	Article	hy	e	fa
111	Denitto F.; Migliet	Life cycle of Bougainvillia nana (Cnidaria: Hydrozoa: Bougainvilliidae) from Italy, including a discussion of Bougainvillia muscus in the Mediterranean Sea	2007	Article	hy	e	r
112	Pettengill J.B.; We	Biofouling likely serves as a major mode of dispersal for the polychaete tubeworm Hydroides elegans as inferred from microsatellite loci	2007	Article	p		
113	Miglietta M.P.; Pir	Species in the genus Turritopsis (Cnidaria, Hydrozoa): A molecular evaluation	2007	Article	hy	t	
114	Batistić M.; Jaspric	Annual cycle of the gelatinous invertebrate zooplankton of the eastern South Adriatic coast (NE Mediterranean)	2007	Article	hy	m	
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117	Molinero J.C.; Casi	The influence of the Atlantic and regional climate variability on the long-term changes in gelatinous carnivore populations in the northwestern Mediterranean	2008	Article	hy	m	
118	Gili J.-M.; Duró A.;	Herbivory in small carnivores: Benthic hydroids as an example	2008	Article	hy	e	ex
119	Di Camillo C.; Bo M	Foraminifers epibiontic on Eudendrium (Cnidaria: Hydrozoa) from the Mediterranean Sea	2008	Article	hy	e	fa
120	Çinar M.E.; Katağa	Faunal assemblages of the mussel Mytilus galloprovincialis in and around Alsancak Harbour (Izmir Bay, eastern Mediterranean) with special emphasis on alien species	2008	Article	out		
121	Di Camillo C.; Bo M	The epibiontic assemblage of Geryon longipes (Crustacea: Decapoda: Geryonidae) from the Southern Adriatic Sea	2008	Article	hy	e	ep
122	Stemmann L.; You	Global zoogeography of fragile macrozooplankton in the upper 100-1000 m inferred from the underwater video profiler	2008	Conference paper	out		
123	De Vito D.; Boero F	Redescription of the zooxanthellate Eudendrium moulouyensis (Eudendriidae: Hydrozoa) from the Mediterranean Sea	2008	Article	hy	t	
125	Gravili C.; D'Ambro	Clytia hummelincki (Hydroidomedusae: Leptomedusae) in the Mediterranean Sea	2008	Article	hy	a	d
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132	Lučić D.; Benović A	Diel vertical migration of medusae in the open Southern Adriatic Sea over a short time period (July 2003)	2009	Article	hy	m	
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135	Schuchert P.	The European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Filifera part 5	2009	Article	hy	t	
136	Bevilacqua S.; Fras	The use of taxonomic distinctness indices in assessing patterns of biodiversity in modular organisms	2009	Article	hy	e	ep
137	Cunha A.F.; Jacobs	Seasonal variation of epiphytic hydroids (Cnidaria: Hydrozoa) associated to a subtropical Sargassum cymosum (Phaeophyta: Fucales) bed	2010	Article	nM		
138	Kubota S.; Nomar	Distribution pattern of GFP (green fluorescent protein) in a bivalve-inhabiting hydrozoan, Eutima japonica (Leptomedusae: Eirenidae)	2010	Article	nM		
139	Sabatés A.; Pagès F	Planktonic cnidarian distribution and feeding of Pelagia noctiluca in the NW Mediterranean Sea	2010	Article	sc		
140	Gravili C.; Belmont	Nonindigenous species along the Apulian coast, Italy	2010	Article	hy	a	
141	Stopar K.; Ramšak	Lack of genetic structure in the jellyfish Pelagia noctiluca (Cnidaria: Scyphozoa: Semaeostomeae) across European seas	2010	Article	sc		
142	Tinta T.; Malej A.;	Degradation of the Adriatic medusa Aurelia sp. by ambient bacteria	2010	Article	sc		
143	Prado P.; Alcoverro	Influence of nutrients in the feeding ecology of seagrass (Posidonia oceanica L.) consumers: A stable isotopes approach	2010	Article	out		
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148	Hajji F.; Ouannes-(	Feeding habits of the grass goby, Zosterisessor ophiocephalus (Gobiidae), from the Gulf of Gabes (Tunisia)	2010	Article	out		
149	Zeppilli D.; Mea M	Mud volcanoes in the Mediterranean Sea are hot spots of exclusive meiobenthic species	2011	Article	hy	e	d
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151	Moura C.J.; Cunha	The use of the DNA barcode gene 16S mRNA for the clarification of taxonomic problems within the family Sertulariidae (Cnidaria, Hydrozoa)	2011	Article	hy	t	
152	Gherardi M.; Lepo	A study on spermatogenesis of three Mediterranean serpulid species	2011	Article	p		
153	Fanelli E.; Cartes J.	Food web structure of deep-sea macrozooplankton and micronekton off the Catalan slope: Insight from stable isotopes	2011	Article	out		
154	Belmonte G.; Scirc	Zooplankton composition in Lake Varano (Adriatic Sea coast, Italy)	2011	Article	out		
155	Moura C.J.; Cunha	Polyphyly and cryptic diversity in the hydrozoan families Lafoeidae and Hebellidae (Cnidaria:Hydrozoa)	2011	Article	hy	t	
156	Bo M.; Di Camillo	A tubularid hydroid associated with anthozoan corals in the Mediterranean Sea	2011	Article	hy	e	fa
157	El-Serehy H.A.; Al-	Reproductive strategy of the jellyfish Aurelia Aurita (Cnidaria scyphomedusae) in the Suez canal and its migration between the red sea and Mediterranean	2011	Article	sc		
158	Lučić D.; Benović A	A short-term investigation of diel vertical migrations of the calycophoran siphonophora in the open south adriatic sea (July 2003); [Kratkoročno istraživanje dnevnih vertikalnih migracija kalikofora (siphonophora) u otvorenim vodama južnog jadrana (srpanj 2003.)]	2011	Article	hy	s	
159	Wangensteen O.S.	A wolf in sheep's clothing: Carnivory in dominant sea urchins in the Mediterranean	2011	Article	out		
160	Fuentes V.; Straeh	Life cycle of the jellyfish Rhizostoma pulmo (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean)	2011	Article	sc		
161	Gombač M.; Fondi	Prevalent diseases and pathogens of Slovene cultured mediterranean mussels (Mytilus galloprovincialis); [Najpogostejše bolezni in patogeni organizmi gojenih Slovenskih mediteranskih klapavic (Mytilus galloprovincialis)]	2011	Article	out		
162	Ben-Eliahu M.N.; I	Serpulidae (Annelida: Polychaeta) from the Suez Canal- from a lessepsian migration perspective (a monograph)	2011	Article	p		
163	Duchêne J.-C.	Hydroid and serpulid recruitment patterns using a new laser microtopography technique	2012	Article	hy	e	d
164	Malej A.; Kogovšek	Blooms and population dynamics of moon jellyfish in the northern Adriatic	2012	Conference paper	sc		
165	Ramšak A.; Stopar	Comparative phylogeography of meroplanktonic species, Aurelia spp. and Rhizostoma pulmo (Cnidaria: Scyphozoa) in European Seas	2012	Article	sc		
166	Moura C.J.; Cunha	Evolution of Nemertesia hydroids (Cnidaria: Hydrozoa, Plumulariidae) from the shallow and deep waters of the NE Atlantic and western Mediterranean	2012	Article	hy	t	
167	Gravili C.; Boero F.	Association between luminous bacteria and Hydrozoa in the northern Ionian Sea	2012	Article	hy	e	mi
168	Kogovšek T.; Molir	Interannual size changes of adult Aurelia sp.5 medusae stage in the Marine Protected Area of Mljet Island South Adriatic; [Godišnje promjene veličine adultnih primjeraka meduze Aurelia sp.5 u zaštićenom području otoka Mljeta, južni Jadran]	2012	Article	sc		
169	Purcell J.E.; Atienz	Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea	2012	Article	sc		
170	Mamish S.; Durgha	First record of Aequorea globosa Eschscholtz, 1829 (Cnidaria: Hydrozoa) in the coast of Syria	2012	Article	hy	m	
171	Di Camillo C.G.; Bo	Population dynamics of Eudendrium racemosum (Cnidaria, Hydrozoa) from the North Adriatic Sea	2012	Article	hy	e	tr
172	Touzri C.; Hamdi H	Diversity and distribution of gelatinous zooplankton in the Southwestern Mediterranean Sea	2012	Review	hy	m	
173	Astorga D.; Ruiz J.;	Ecological aspects of early life stages of Cotylorhiza tuberculata (Scyphozoa: Rhizostomae) affecting its pelagic population success	2012	Article	sc		
174	Žitek S.; Gombač M	Occurrence and effects of the bivalve-inhabiting hydroid eugymnanthea inquilina in cultured mediterranean mussels (mytilusgalloprovincialis) in slovenia	2012	Article	hy	e	ep
175	Betti F.; Bo M.; di	Life history of Cornularia cornucopiae (Anthozoa: Octocorallia) on the Conero Promontory (North Adriatic Sea)	2012	Article	out		
176	Licandro P.; Souiss	Long-term variability and environmental preferences of calycophoran siphonophores in the Bay of Villefranche (north-western Mediterranean)	2012	Article	hy	s	
177	Moura C.J.; Cunha	A molecular phylogenetic appraisal of the systematics of the Aglaopheniidae (Cnidaria: Hydrozoa, Leptothecata) from the north-east Atlantic and west Mediterranean	2012	Article	hy	t	
178	Pestorić B.; Krpo-Ć	Pelagic cnidarians in the Boka Kotorska Bay, Montenegro (South Adriatic); [Planktonski zarnjaci boka-kotorskog zaljeva, crna gora (Juzni Jadran)]	2012	Article	hy	m	
179	Gravili C.; Di Camil	Hydrozoan species richness in the Mediterranean Sea: Past and present	2013	Article	hy	e	d
180	Cartes J.E.; Fanelli	Deep-sea macroplankton distribution (at 400 to 2300m) in the northwestern Mediterranean in relation to environmental factors	2013	Article	out		
181	Piraino S.; de Vito	Destructive standard squares or low-impact visually driven collection? A comparison of methods for quantitative samplings of benthic hydrozoans	2013	Article	out		
182	Boudouresque C.F	Paracentrotus lividus	2013	Book chapter	out		
183	Di Camillo C.G.; Gi	Seasonal patterns in the abundance of Ectopleura crocea (Cnidaria: Hydrozoa) on a shipwreck in the Northern Adriatic	2013	Article	hy	e	d
184	Berline L.; Zakardji	Modeling jellyfish Pelagia noctiluca transport and stranding in the Ligurian Sea	2013	Article	sc		
185	González-Duarte M	Hydroid assemblages across the Atlantic-Mediterranean boundary: Is the Strait of Gibraltar a marine ecotone?	2013	Article	hy	e	d
186	González-Duarte M	Sertularia marginata (Cnidaria: Hydrozoa) in the Mediterranean: An alien species in expansion?	2013	Article	hy	a	
187	Soto Ángel J.J.; Pei	Shallow-water benthic hydroids from the Maltese Islands (Central Mediterranean)	2013	Article	hy	e	d
188	Acevedo M.J.; Fue	Maintenance, feeding and growth of Carybdea marsupialis (Cnidaria: Cubozoa) in the laboratory	2013	Article	sc		
189	Tezcan Ö.D.; Sarp	An unusual marine envenomation following a rope contact: A report on nine cases of dermatitis caused by Pennaria disticha	2013	Article	nM		
190	Rosa S.; Pansera M	Interannual variability, growth, reproduction and feeding of Pelagia noctiluca (Cnidaria: Scyphozoa) in the Straits of Messina (Central Mediterranean Sea): Linkages with temperature and diet	2013	Article	sc		
191	Di Camillo C.G.; Bo	Distribution, ecology and morphology of Lytocarpia myriophyllum (Cnidaria: Hydrozoa), a Mediterranean Sea habitat former to protect	2013	Article	hy	e	d
192	D'Ambra I.; Graha	Predation patterns and prey quality of medusae in a semi-enclosed marine lake: Implications for food web energy transfer in coastal marine ecosystems	2013	Article	sc		
193	Gul S.; Gravili C.	Aequorea pensilis (Cnidaria: Hydrozoa) bloom and first record from Pakistan coast (North Arabian Sea)	2013	Article	nM		
194	Çinar M.E.	Alien polychaete species worldwide: Current status and their impacts	2013	Article	p		
195	Iazza B.; González-	First report of the marine hydroids Eudendrium glomeratum, E. merulum and Garveia grisea (Cnidaria: Hydrozoa) from the Moroccan Atlantic coast	2013	Article	nM		
196	Calder D.R.	Some shallow-water hydroids (Cnidaria: Hydrozoa) from the central east coast of Florida, USA	2013	Article	nM		
197	Tilves U.; Purcell J.	Predation by the scyphozoan Pelagia noctiluca on Mnemiopsis leidyi ctenophores in the NW Mediterranean Sea	2013	Article	sc		
198	Gul S.; Gravili C.	On the occurrence of Porpita porpita (Cnidaria: Hydrozoa) at Pakistan coast (North Arabian Sea)	2014	Article	nM		
199	Romagnoli T.; Tott	SEM analysis of the epibenthic diatoms on eudendrium racemosum (Hydrozoa) from the Mediterranean Sea	2014	Article	hy	e	fa
200	Purcell J.E.; Milisen	Digestion and predation rates of zooplankton by the pleustonic hydrozoan Velella velella and widespread blooms in 2013 and 2014	2014	Article	hy	s	
201	Marques R.; Albou	Pelagic population dynamics of Aurelia sp. in French Mediterranean lagoons	2014	Article	sc		
202	Çinar M.E.; Yokeş	Checklist of Cnidaria and Ctenophora from the coasts of Turkey	2014	Review	rw		
203	Brahim M.B.; Mab	Bathymetric variation of epiphytic assemblages on Posidonia oceanica (L.) Delile leaves in relation to anthropogenic disturbance in the southeastern Mediterranean	2014	Article	hy	e	ep

102	De Vito D.; Piraino	Evidence of reverse development in Leptomedusae (Cnidaria, Hydrozoa): The case of Laodicea undulata (Forbes and Goodsir 1851)	2006	Article	hy	e	r	
103	Fraschetti S.; Terlizz	The distribution of hydroids (Cnidaria, Hydrozoa) from micro- to macro-scale: Spatial patterns on habitat-forming algae	2006	Article	hy	e	ep	
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158	Lučić D.; Benović A	A short-term investigation of diel vertical migrations of the calycophoran siphonophora in the open south adriatic sea (July 2003); [Kratkoročno istraživanje dnevnih vertikalnih migracija kalikofora (siphonophora) u otvorenim vodama južnog jadrana (srpanj 2003.)]	2011	Article	hy	s		
159	Wangensteen O.S.	A wolf in sheep's clothing: Carnivory in dominant sea urchins in the Mediterranean	2011	Article	out			
160	Fuentes V.; Straeh	Life cycle of the jellyfish Rhizostoma pulmo (Scyphozoa: Rhizostomeae) and its distribution, seasonality and inter-annual variability along the Catalan coast and the Mar Menor (Spain, NW Mediterranean)	2011	Article	sc			
161	Gombač M.; Fondı	Prevalent diseases and pathogens of Slovene cultured mediterranean mussels (Mytilus galloprovincialis); [Najpogostejše bolezni in patogeni organizmi gojenih Slovenskih mediteranskih klapavic (Mytilus galloprovincialis)]	2011	Article	out			
162	Ben-Eliahu M.N.; I	Serpulidae (Annelida: Polychaeta) from the Suez Canal- from a lessepsian migration perspective (a monograph)	2011	Article	p			
163	Duchêne J.-C.	Hydroid and serpulid recruitment patterns using a new laser microtopography technique	2012	Article	hy	e	d	
164	Malej A.; Kogovšel	Blooms and population dynamics of moon jellyfish in the northern Adriatic	2012	Conference paper	sc			
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167	Gravili C.; Boero F.	Association between luminous bacteria and Hydrozoa in the northern Ionian Sea	2012	Article	hy	e	mi	
168	Kogovšek T.; Malir	Interannual size changes of adult Aurelia sp.5 medusae stage in the Marine Protected Area of Mljet Island South Adriatic; [Godišnje promjene veličine adultnih primjeraka meduze Aurelia sp.5 u zaštićenom području otoka Mljeta, južni Jadran]	2012	Article	sc			
169	Purcell J.E.; Atienz	Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea	2012	Article	sc			
170	Mamish S.; Durgh	First record of Aequorea globosa Eschscholtz, 1829 (Cnidaria: Hydrozoa) in the coast of Syria	2012	Article	hy	m		
171	Di Camillo C.G.; Be	Population dynamics of Eudendrium racemosum (Cnidaria, Hydrozoa) from the North Adriatic Sea	2012	Article	hy	e	tr	
172	Touzri C.; Hamdi H	Diversity and distribution of gelatinous zooplankton in the Southwestern Mediterranean Sea	2012	Review	hy	m		
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