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**IDROZOI CILENI E NON SOLO:  
LA FAUNA A IDROZOI DEI FIORDI**

**CHILEAN HYDROZOANS AND BEYOND:  
THE HYDROZOAN FAUNA OF THE FJORDS**

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## SUMMARY

I fiordi sono insenature costiere sommerse dalle acque marine presenti alle alte latitudini, spesso coperti da ghiacciai. Rappresentano vulnerabili ambienti di transizione caratterizzati da parametri chimico-fisici peculiari, che permettono lo sviluppo di una fauna unica nel suo genere. Tra gli organismi caratterizzanti le complesse comunità dei fiordi, gli idroidi ricoprono un ruolo chiave, spesso considerati importanti specie strutturanti (*habitat formers*) con un rilevante impatto sui processi che coinvolgono il benthos e la colonna d'acqua (*benthic-pelagic coupling*). In questo contesto si inserisce il seguente elaborato di tesi, che ha avuto come scopo principale il riconoscimento sistematico delle specie di idroidi presenti nei campioni raccolti nella Patagonia cilena, al fine di caratterizzarne la diversità tassonomica e strutturale.

I campionamenti, avvenuti in immersione subacquea, sono stati condotti in 7 stazioni lungo il fiordo di Puyuhuapi (Regione di Aysen, Chile) a Marzo del 2019 a sei diverse profondità: 5, 10, 15, 20, 25 e 30 metri.

In generale, 26 specie di idroidi sono state identificate, di cui 19 appartenenti all'ordine Leptothecata e 7 all'ordine Anthoathecata. La maggior parte delle specie fanno parte delle famiglie di Sertularellidae (5) e Campanulariidae (3) tra i Leptothecata, e alla famiglia dei Bougainvillidae (3) tra gli Anthoathecata.

Confrontando le specie da noi identificate con quelle descritte in lavori precedenti condotti nello stesso fiordo, 16 specie risultano essere nuovi record per l'area di studio considerata, mentre la specie *Rhysia* sp. non era mai stata precedentemente osservata in Patagonia. Mentre non è stato possibile discernere un trend per quanto riguarda il numero di specie raccolte dalla "bocca" del fiordo verso le stazioni più interne, un gradiente batimetrico è invece risultato chiaro, con un numero minore di specie raccolte alle profondità più superficiali (5 e 10 m), probabilmente in relazione alla presenza dello strato d'acqua salmastro superficiale.

Il dataset creato sulla base di questi campioni è stato poi implementato attraverso la raccolta di dati ottenuti mettendo insieme le informazioni disponibili in letteratura, spesso frammentarie e/o basate principalmente su osservazioni locali, sugli idrozoi presenti nei fiordi a livello mondiale, con lo scopo di racchiudere all'interno di un unico dataset la fauna a idrozoi caratterizzante la fauna dei fiordi. In particolare, Norvegia e Cile rappresentano le aree geografiche con il maggior numero di pubblicazioni e il maggior numero di specie registrate, per cui sono state considerate per ulteriori analisi statistiche. Le analisi effettuate mostrano che le due regioni, nonostante presentino specie in comune, hanno una composizione in specie significativamente diversa, probabilmente legata alla loro distanza geografica

e alle diverse caratteristiche (chimiche, fisiche e biologiche) delle aree considerate. Inoltre, come risulta dalle curve di rarefazione della diversità delle specie delle due regioni, lo sforzo di campionamento applicato fino ad ora nella Patagonia cilena sembra non essere ancora sufficiente per rappresentare adeguatamente la sua reale biodiversità, con la necessità di ulteriori studi dove diversi tipi di tecniche e target (es. campionamenti di plankton e benthos, indagini acustiche e video, analisi tassonomiche e molecolari, studi filogenetici basati sul DNA barcoding) dovrebbero essere integrati per avere una visione d'insieme più completa, basata su un approccio ecosistemico.

In conclusione, questo studio ha permesso non solo di colmare lacune nella conoscenza della composizione in specie e della distribuzione degli idroidi nell'area di studio considerata, ma anche di riassumere le conoscenze esistenti sulla loro distribuzione mondiale, creando una baseline tassonomica utile nel definire possibili cambiamenti nella composizione in specie legati a impatti antropici diretti e indiretti (es. pesca, cambiamento climatico, diving, acidificazione oceanica).



## Chapter 1

### *1. INTRODUCTION*

#### *1.1. HYDROZOA*

All organisms belonging to the monophyletic phylum of Cnidaria are grouped by the presence of cnidocysts, the most important taxonomic character. The phylum is divided into five classes: Anthozoa Ehrenberg, 1834 (with the polyp stage only), Scyphozoa Goette, 1887 (with polyps giving rise to medusae via strobilation), Cubozoa Werner, 1973 (giving rise to medusae through polyp metamorphosis), Staurozoa Marques and Collins, 2004 and Hydrozoa Owen, 1843 (giving rise to medusae through budding).

According to the World Register of Marine Species (WoRMS, 2021), 3859 currently accepted species belong to the monophyletic class Hydrozoa of the phylum Cnidaria. Because of the multitude types of life cycle and the various morphological features, it has always been difficult for taxonomists identifying sets of unambiguous putative synapomorphies for Hydrozoa (Daly et al., 2007; Marques and Collins, 2004). The nomenclature itself has been complicated by the assignment of different generic and specific names to the two morphologic stages of a same species, (Gili and Hughes, 1995), inducing a great proliferation of synonymies (May and Nee 1995).

Two monophyletic subclasses have been identified within the class Hydrozoa: Hydroidolina Collins, 2000 (3695 species) and Trachylina Haeckel, 1879 (164 species), a division well supported also from the molecular point of view (Collins, 2002). Collins (2002) and Collins et al. (2006) underlined that the production of the medusa via the entocodon<sup>1</sup> and the lateral budding are most likely to be synapomorphies of all hydrozoan species and not key features at the base of the division between the two clades, as previously hypothesized.

The subclass Trachylina is organized into 4 orders (Actinulida, Limnomedusae, Narcomedusae, Trachymedusae) and it is characterized by statocysts of ecto-endo-dermal origin in the medusa stage (Daly et al., 2007).

The subclass Hydroidolina can be divided into three orders: Anthoathecata (1366 species), comprehensive of athecate hydroids<sup>2</sup> and anthomedusae, Leptothecata (2139 species), including thecate hydroids and leptomedusae, and Siphonophorae (190 species), divided into three suborders, Calycothecata, Cystonectae and Physonectae. Statocysts, if present, are usually of ectodermal origin; another feature distinguishing the group is the possible formation of polymorphic colonies, a state that is present only in one genus (*Monobrachium*)

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<sup>1</sup> i.e., masses of proliferating cells located between the ectoderm and the endoderm along the lateral portions of polyps.

<sup>2</sup> Hydroids are organisms composed by a base, a stem and one or more terminal polyps (zooids) (Hickman, 2016).

of Trachylina. While Siphonophorae are easily discernible thanks to their holopelagic, highly polymorphic colonial organization, Anthoathecata and Leptothecata can be recognised on the basis of the absence or presence, respectively, of a skeletal covering in the polyp stage; furthermore, Anthomedusae do not have statocysts and the gametogenic tissue is confined to the manubrium, whereas in Leptomedusae gametogenic tissue is restricted to the radial canals (Daly et al., 2007).

#### *1.1.1. BIOLOGY*

Hydrozoa are diblastic organisms: the only two germ layers present are the ectoderm (from which derives the epidermis) and the endoderm (from which derives the gastrodermis, surrounding the celenteron), separated by an acellular matrix containing water, fibres and proteins, called mesoglea.

As cnidarians, they generally show two different alternated life stages, the polyp and the medusa, which mainly differ for the organization of the oral-aboral axis: the polyp has a mouth, directed upward, usually surrounded by tentacles, while in the medusa these structures face downward.

Some species have evolved a life cycle completely lacking the polyp stage (e.g., Trachylinae) or the medusa stage (e.g., *Hydra* spp.) (Collins, 2002). Another typical characteristic is the presence of cnidocysts, stinging organelles contained within cnidocytes. Different types of cnidocysts accomplish different

functions (Purcell and Mills, 1988): nematocysts, spirocysts and ptychocysts are respectively responsible for penetrating, rolling and agglutinating purposes. The whole set of cnidocysts present in a species, their dimensions and their distribution define the cnidome, an important taxonomic diagnostic character. The discharge of the capsule lead to the eversion of the inner tubule and is usually triggered by a mechanical or chemical stimulation of the cnidocil, an external receptor structure of the cnidocyte. Tentacles are usually deeply armed with cnidocysts, whose mode of distribution represents a classification feature (Östman, 2000; Pica and Puce, 2017).

Hydromedusae commonly show a tetramerous radial symmetry. They are mainly composed by: (i) the bell, also known as “umbrella” and able to reach various sizes, whose main part is represented by the mesoglea which acts as a sort of hydrostatic skeleton; (ii) the velum, a muscular horizontal marginal diaphragm which delimits the space enclosed by the umbrella (the subumbrellar cavity), having a great role in medusa swimming; (iii) the tentacles, arise from the free rim of the umbrella and observable in different numbers and shapes, often associated to sensory cells and sense organs; (iv) the bulbs, enlargements of the marginal tentacle bases (they may be absent), sometimes carrying ocelli,

light-sensitive sense organs; (v) other marginal structures, such as statocysts<sup>3</sup>; (vi) the manubrium, a tubular or quadrangular projection of various length and form created from the centre of the subumbrella hangs, which contains the gastric cavity and joins the radial gastrovascular canals and the subumbrellar cavity through the mouth; (vii) the gastrovascular system, formed by the gastric cavity, the radial canals, the circular canal and the tentacular canals (if present), involved in the digestion and distribution of food, the circulation of oxygen, waste, cnidoblasts or even gametes; (viii) the gonads, whose position and shape are of great relevance for the medusan classification (Bouillon et al., 2004; Bouillon et al., 2006).

Hydroids are generally benthic colonial organisms, with a basal structure (an adhesive gelatinous or glandular disk or an anchoring system of rootlets), which allow the attachment to the substrate and a pedicel or hydrocaulus bearing one or more hydranths (Bouillon et al., 2006). The hydranth, which could be of different shapes and sizes (ranging from 1 mm up to 1 cm, e.g., *Tubularia* spp.), is composed by: (i) a distal hypostome or mouth, usually surrounded by tentacles, which enables the polyp's feeding, being involved also in the first stages of prey ingestion (after this step, the polyp may become unresponsive to

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<sup>3</sup> Statocysts are sense organs specialized in controlling gravity and low frequency vibrations; they appear in numerous groups of invertebrates, from radiates to arthropods (Hickman, 2016).

further contacts with potential preys, e.g., *Thyroscyphus marginatus* (Allman, 1877)); (ii) the gastric column, not divided by septa, where the digestion takes place; (iii) the sphincter, a muscular ring at the base of the hydranth which divides the gastric column from the pedicel to allow the local digestion of prey items, isolating the column from the rest of the gastrovascular system (Bouillon et al., 2004; Bouillon et al., 2006). The undigested material is egested via the mouth from the gastrovascular cavity.

Colonial polyps are linked through an hydrorhiza or a stolon and can grow following a horizontal or vertical pattern. The former involves two extreme growth strategies, distinguishing guerrilla from phalanx species (Humphrey and Pyke 1998; Hughes 1989). In the latter, an erect colony where an upright hydrocaulus bears more than one hydranth (branched arrangement of the main hydrocauline stem) can be recognised. In the case of large arborescent colonies, the hydranths may be located peripherally to maximize food catching potential (Gili and Hughes, 1995).

Hyperplastic stolons, heavily armed with nematocysts, can be produced from the growing hydrorhiza with the aim of killing tissues of the nearby hydroid colonies, as a competition result (Buss et al. 1984, Buss and Grosberg 1990); nevertheless, sometimes the fusion between closely related colonies may occur (Shenk 1991, Shenk and Buss 1991). Besides this, growth patterns can

generally represent adjustments of the animal to the specific substratum on which it lives (e.g., obligate epiphytes) (Gili and Hughes, 1995).

The coenosarc, the epithelial epidermal layer of the living tissue, is covered by the perisarc (Mendoza-Becerril et al., 2017), a protective sheath generally composed by chitin or proteins (sometimes with calcareous elements to form the coenosteum, e.g., Stylasteridae and Milleporidae) that acts as an exoskeleton (Bouillon et al., 2006). Flexibility of the otherwise rigid perisarc is conferred by annulations: they permit hydrocaulus to bend and face water movement (essential for food provision in benthic suspension feeders), reducing the forces transmitted to the hydrorhiza and decreasing also the flow velocities experienced by the hydranths (Gili and Hughes, 1995). Pelagic hydroids usually lack perisarc, even if some species can still show structural elements of perisarc origin (Bouillon et al., 2006).

Hydrocaulus in erect forms can be mono- or poly-siphonic, depending on the number of coenosarc tubes present, usually divided into internodes or segments, and the form of the colony could depend on the growth pattern, mainly monopodial (with a terminal hydranth or a terminal growing point) or sympodial, according to the presence of a single main stem or a “false axis”, actually formed by successive branches (Bouillon et al., 2006).

Hydrothecae, gonothecae and nematothecae are also made of perisarc. The hydrotheca can be present (Leptothecata) or not (Anthoatecata, even though they can present a pseudohydrotheca), with different shapes, enveloping the polyp and having a chitinous diaphragm (perforated at the base) or a definite floor (with a hole called hydropore, as in the families Syntheciidae, Sertulariidae, and Plumulariidae). The hydrotheca can be sessile or pedicellate, with or without a lid or an operculum closed over the contracted hydranth, whose shape can represent a diagnostic feature to recognise species (Bouillon et al., 2006). Hydrothecae can show renovations and they may have alternate or opposite arrangement on stem and branches; they usually allow the polyp to withdraw within it, even if in Haleciids and Plumulariids polyps are too large to do it. Sometimes (e.g., in Plumulariidae and Aglaopheniidae) nematothecae of different kinds, containing the nematophores (clusters of nematocysts), can be observed across hydroids, with defensive, cleaning or anti-fouling functions (Gili and Hughes, 1995). The gonothecae are chitinous structures surrounding the blastostyles or the gonophores, they are typically closed on top (often operculate), until the gametes or the developing embryos are ready to be released; they could mirror the sexual dimorphism, if present. The gonothecae may be single or aggregated into compound bodies, such as the "coppinia" of



many Lafoeidae species; a very high degree of complexity is reached in the case of the “corbula” structure of the Aglaopheniidae (Cornelius, 1995).

Many hydroid colonies are polymorphic, showing polyps which differ structurally according to their function: gastrozooids (feeding behaviour), gonozooids (reproduction, they could reflect a sexual dimorphism), dactylozooids (defence of the colony) and acanthozooids (protective individuals not provided with cnidocysts, but constituting chitinous spines) (Bouillon et al., 2006).

Organisms belonging to Siphonophorae should be considered as a separated item, due to their peculiarity: they can be colonial, pelagic, swimming or floating, forming highly polymorphic modular colonies of polypoid and medusoid zooids attached to a stem or stolon supported by a floating and swimming system. The complete and fully developed animal is referred to as the polygastric stage (Bouillon et al., 2006; Mapstone 2014).

Usually Hydroidomedusae, except for the Siphonophorae where the planula gives rise to specialized larvae (i.e., calyconula and siphonula) developing directly into the siphonophoran adult polygastric stage, follow the classic life cycle with fertilised eggs, planula, hydroid, medusa, eggs and sperms, fertilised eggs and so on. However, several modifications of this scheme can be observed across the class. Species can be either gonochoric or hermaphrodites, but

simultaneous hermaphrodites occur rarely. Even if it is admitted that sex determination is genetic (Littlefield, 1994), in several cases (e.g., *Hydra*, *Clytia*) it appears to be ruled by environmental conditions, mainly by temperature (Carré and Carré, 2000). Gametes are generally of ectodermal origin. Male spawning normally occurs in the water and no copulation is known for this clade. The existence of sperm attractants (chemotaxis), produced by the eggs, was first demonstrated in the Hydrozoa (Miller, 1972; Miller 1966a,b). Fertilisation is usually external, with free spawning of both males and females (synchronisation of the release of gametes is necessary to enhance fertilization rates); however, in a few species, internal fertilisation may occur with the direct release of planula larvae. In certain hydroids, the planula does not immediately leave the gonophore, but continues its development in it, either partially, producing an intermediate stage, the actinula (e.g., *Tubularia*, *Myriothele*), or completely, with a normal polyp leaving the gonophore (certain gonophores of *Cordylophora*). Planula encystment is probably very common in the development of hydroids with fixed gonophores since many species reproduce sexually at the end of the favourable season and then disappear; in these circumstances, the sexual reproduction involves the disappearance of all active stages.

The formation of clumps, achieved in some species thanks to the gregarious behaviour of planulae during the settlement, can improve fertilization rates, but, on the other hand, it may also enhance intraspecific competition for space and food. From the temporal perspective, a prolonged reproductive period may be necessary to maximise the reproductive output and spread the risk of failure of larvae; the timing can be deeply influenced by geographic and environmental conditions (Williams, 1976; Bavestrello and Cerrano 1992).

It is also important to consider that the reproductive effort is highly costly (in some species it is also confined to a restricted region of the colony): once the process begins, if necessary, the tissues of other parts of the colony will be resorbed to provide material for reproductive development (e.g., *Laomedea flexuosa* Alder, 1857) (Roosen-Runge 1970; Gili and Hughes, 1995).

The asexual reproduction, which allows the growth of the colony, can occur in different ways: (i) longitudinal or transversal fission; (ii) podocysts or propagules (under adverse ecological conditions, some hydroid colonies isolate fragments of hydrocauli, hydrocladia or stolon, enveloped by perisarc, ensuring the propagation and direct dissemination of the species); (iii) budding of planula-like bodies, or frustules, of different types; (iv) resting stages or cysts (encysted embryos and planulae, more common in solitary forms); (v) polyp budding (polypoid structures formed by some medusae, linked to the colony

formation or the population increase in solitary forms); (vi) medusa budding (giving rise to free sexual phase, the medusa, or to sessile, reduced gonophores and producing different types of medusoids, capable of swimming but not feeding) (Bouillon et al., 2006).

Autotomy seems a widely used technique across hydroids, of great importance in their reproduction (Mackie 1974, Cornelius 1981) and perhaps happening in response to changes of environmental factors (e.g., temperature or oxygen concentration).

Stolonization, which in some species has been observed to be dependent on energy reserves (e.g., *Obelia dichotoma* (Linnaeus, 1758)), is of major significance especially for epiphytic species.

Clearly, different reproductive strategies will lead to a genotype dispersal to varied extents (Gili and Hughes, 1995) and this will determine the level of genetic divergence between hydrozoan populations. However, as reported by Cornelius (1981) and Gili and Hughes (1995), hydroids were perhaps unique among metazoans because many species have near-cosmopolitan distributions. These distributions and the absence of local or regional speciation could be maintained by gene flow by rafting throughout their long evolutionary history. Nevertheless, recently molecular approaches have brought to the surface the existence of many cryptic species, whose identification is possible only through

the use of modern tools, as DNA barcoding (Miglietta et al., 2018; Moura et al., 2008). Hence, the integration of phylogenetic and morphological investigations is crucial to clarify systematic relationships (e.g., Miglietta et al., 2009, 2019).

### *1.1.2. ECOLOGY*

Hydrozoa are mainly present in the marine environment in colonial forms, quite common and often abundant in shallow water communities, on hard substrata (Boero, 1984; Gili and Hughes, 1995). Since their life cycle is characterised by an asexual polypoid stage and a sexual medusan stage, thus these organisms have representatives both in the planktonic and in the benthic compartment. As a result of their high plasticity, hydrozoan species can adapt to very different environmental conditions being quite ubiquitous, with a distribution ranging from tropical superficial waters to the deep sea (up to 3000 m depth) (Bouillon et al., 2004; Di Camillo et al., 2017; Gili and Hughes, 1995; Voronkov et al., 2010; Cairns, 2011). However, due to their aerobic respiration (with O<sub>2</sub> assimilation taking place by diffusion through epidermis of exposed tissues), hydroids inhabit environments in which the oxygen concentration exceeds 5 ml/L, a parameter depending on changes in variables such as temperature (linked to light exposure), salinity, metabolic activities and rates, seasonal cycles, etc. (Gili and Hughes, 1995).

Hydrozoa are typically carnivores, being among the most important planktonic and benthic predators (i.e., consuming fish larvae, crustaceans, and other planktonic and benthic organisms) (Gravili, 2016, Purcell and Mills 1988), even if some species may feed on bacteria, protozoans, phytoplankton or dissolved organic matter (Daly et al., 2007; Bouillon et al., 2006) (Gili et al. 1998).

Preys are usually captured through the killing or stunning effect of nematocysts discharge, an energetic-expensive operation that is limited if unnecessary (e.g., an eating hydranth is able to inhibit the feeding behaviour of the next one) (Clark and Cook, 1986); type and size of nematocysts influence the dimension of the chosen prey, while capture rates (varying even within a colony in specific environmental conditions) may be related to items abundance (Gili and Hughes, 1995).

In turn, hydroids can be eaten by turbellarians, aplacophorans, gastropods, polychaetes and pycnogonids (able to consume also developing larvae) (Salvini-Plawen, 1972); some of specialist predators appear to be immune to nematocysts venom or even able to store and re-utilise these organelles with a defensive purpose (kleptocnidae, often occurring in nudibranchs) (Gili and Hughes, 1995).

Different environmental conditions are responsible of phenotypic variations in hydroid morphology regarding the allocation of reserve substances, the branching pattern, the regulation of growth rates of different zones, etc. For instance, feeding rates determine the size of hydranths and the position of the new formed polyps (also linked to the pedicel length) within a given colony (Campbell ,1968; Hale, 1973; Boero, 1984; Gili and Hughes, 1995). Instead, the shape and size of the whole colony is mainly related to the effect of water movement (speed and direction of currents): in highly exposed areas, for example, colonies become smaller and develop a stronger or more flexible hydrocaulus, adaptations being tied to a high feeding efficiency (Gili and Hughes, 1995).

The same species can produce arborescent or reduced colonies based on the physico-chemical/biological circumstances it is experiencing, because of temperature alterations (e.g., *Obelia geniculata* (Linnaeus, 1758)). The salinity causes change in the external morphology as well, modifying cells size and tissues density (Gili and Hughes, 1995).

Hydroid distribution tends to be deeply variable in time and patchy in space, because of their dispersal behaviour and environmental heterogeneity. The latter is triggered by several factors: (i) water movement (usually inversely related to depth and deeply influencing colony size and shape, especially

referring to currents direction), crucial for supplying food and gases, removing wastes and sediments, allowing dispersion of gametes, planulae and medusae; (ii) light, whose task is carried out during the planulae settlement (guided by phototropism) and which can exert controversial effects on colony aging and growth; (iii) exposure to air, although relatively few species occur intertidally, protecting themselves from desiccation remaining wet or damp throughout the low tide period forming clumps or settling on algae; (iv) salinity, even if most hydroids are subtidal and usually do not experience reduced salinities (along decreasing salinity gradients the typical marine species disappear and are substituted by euryhaline species or by those adapted to low salinities); (v) substrata, both biotic and abiotic; (vi) sedimentation, usually linked to the inclination of the substratum and the continental runoff, which smothers colonies and deters larval settlement; (vii) temperature, whose role in determining the composition of hydroid population in time (e.g., seasonality) is noteworthy. However, pollution can also represent an important variable in species distribution and composition, making tolerant species able to survive and flourish in impacted sites (Gili and Hughes, 1995; Gili et al. 1987, 1989a; Thorson 1964; Brock and Strehler 1963; Calder, 1976).

Most of the knowledge about hydrozoan succession comes from experiments about colonization of artificial substrata: these organisms seem to be more



abundant in the initial stages and in the later stages of the community development, especially as epibionts (Bouillon et al., 2004; Gili and Hughes, 1995; Boero, 1984).

Furthermore, even the direct competition for space with algae (also in relation with seasonality at shallower depths) is critical in determining hydroids distribution: for example, in winter large colonies of *Eudendrium glomeratum* Picard and *E. ramosum* (L.) occupy the spaces used by algae in summer, in most of cases forming facies (Boero, 1984).

Hydroids can establish different kinds of symbiotic relationship, being both epibionts and hosts, providing different parts of the colony which can be occupied, such as the perisarc (especially for the larval recruitment of numerous invertebrates), the bare epidermis, or even inside tissues (coenosarc), by prokaryotic or eukaryotic organisms with various feeding behaviours. The basal part of the colony is usually more colonised than the apical portion, probably related to the presence of cleaning/defensive zooids and the higher growth rate of branches in the latter one (Di Camillo et al., 2017).

Concerning hydrozoan epibionts, being substratum specialist (e.g., epiphytes can colonise not only different species of seagrasses/seaweeds, but even diverse portions with fixed discernible distribution patterns) or making associations with other animals (e.g., hydroids and hermit crabs) are good solutions to fight

the interspecific competition in epifaunal communities (Boero, 1984; Puce et al., 2008, Fraschetti et al., 2002; Pinna et al., 2021; Roveta et al., 2022). Specific larval preferences seem to be driven by chemoreception (Gili and Hughes, 1995).

Millard (1973) introduced for the first time the concept of auto-epizoism, describing “the modified habit of hydroids which settle on conspecifics. These relationships show a complete range from epiphytism and epizoism to inquilinism, commensalism, mutualism and parasitism”. Hydroids may be parasitized or grazed by protozoans, fungi and pycnogonid larvae. Examples of endosymbiosis with microalgae are available in the literature: for instance, it has been recorded in several species of *Aglaophenia* and in sertulariids *Tridentata distans* (as *Amphisbetia distans* (Lamouroux, 1816)) and *Sertularella polyzonias* (Linnaeus, 1758) where gastrodermal cells contain the symbiotic dinoflagellates *Gymnodinium* or *Symbiodinium* (Pyrrhophyceae), making these animals sensitive to light variations and, thus, having consequences on their bathymetric distribution (Gili and Hughes, 1995).

Regarding the large-spatial scale, a bathymetric trend can be pinpointed, where generally the species richness is higher in shallow water communities, decreasing with depth and, parallelly, with light and water movement). Going down to the water column, hydroids tend to show an acrophilyc behaviour,

climbing on other organisms to be elevated above the bottom where the circulation is higher (Boero, 1984).

Thus, hydrodynamism is the most important factor in determining the distribution of hydroids, consequently delineating the substratum type and the modality of reproduction (fixed gonophores or medusae) (Boero, 1984; Gili et al. 1987, 1989a, Morri et al. 1991).

An update on the current hydrozoan zoogeography has been provided by Gravili, 2016, who reported that: (i) the greatest percentage of species common among the oceans was within the Arctic and Antarctic regions characterized by their uninterrupted ranges of coastal areas and most of hydrozoan endemisms belongs to the Antarctic fauna, probably related to the unique extreme environmental conditions; (ii) some species experience the “equatorial submergence”, being present both in polar area and at bathyal depths with a continuous distribution in waters not exceeding 4 °C; (iii) about 10% of the tropical Atlantic hydrozoan fauna is common to Pacific, Atlantic and Indian oceans; (iv) the similar species composition between the two sides of Panama isthmus proves that the settlement of the populations took place before the closure of the isthmus itself; (v) in temperate areas, species develop seasonal tendencies if superficial water temperature change more than 10°C across the year (the Meditterrenaen Sea is the most well-studied basin, whose endemisms

account for about 20% of the whole hydrozoan fauna); (vi) the majority of organisms belonging to Siphonophorae are cosmopolitan, with species richness greater in oceanic than coastal waters, peaking in subtropical waters.

Therefore, problems in studying the ecology of benthic hydroids are generally related to: (i) their small size, (ii) the fact that they are often overlooked, (iii) difficulties in identification (especially if lacking the reproductive structures), (iv) the high phenotypic plasticity within the species, (v) difficulties in collection, and (vi) their complicated life cycles (Gili and Hughes, 1995).

### *1.1.3. ECOLOGICAL ROLE*

Many hydroid species are forest-formers, affecting water movement and light penetration, representing a secondary hard substrate colonizable by other organisms, shelter, or food to several associated species, thus enhancing local biodiversity and improving the ecosystem functioning and services. The modular organization and the potential unlimited growth due to the asexual reproduction allow, especially for species able to form multi-serial colonies, to increase the fractal complexity of the bottom and to create a mosaic of various microhabitats. Unfortunately, the importance of these habitat-formers is underappreciated, usually giving more attention to algae-dominated assemblages: the capacity of many hydrozoan species of undergoing periods of dormancy can have led to an underestimation of their abundance and ecological

role. However, it should be considered that hydroids growth is not limited by light as it happens for algae; hence, these organisms can create forests also at higher depths (Di Camillo et al., 2017).

Two main kinds of hydroid forests can be discerned. (i) Deciduous hydroid forests occur of shallow waters at cold and temperate latitudes, mainly formed by species able to undergo dormancy if periodic adverse environmental conditions occur. Seasonal habitats, whose duration changes according to both abiotic and biotic drivers (mainly temperature), are typical, even if some species have shown endogenous circannual rhythms of growth moulding their abundances. Reserve substances as polysaccharides and lipid granules have been observed in vacuoles of gastrodermal cells and can be subsequently translocated and stored in small sections of persistent hydrorhiza. (ii) Perennial hydroid forests, usually present in their erect form, are instead enduring, forming very big colonies that can indicate habitat health conditions (Gili and Hughes, 1995; Di Camillo et al., 2017).

Naturally, the formation of hydroids forests is possible only when the food availability in the surrounding environment is enough to sustain the development of these suspension feeders, whose role in the exploitation of large quantities of seston have huge feedback in the control of secondary production in coastal waters. Dense aggregations can prevent the settlement of competitors

by feeding on their approaching larvae, following an inhibition model as one of the modes of community development (e.g., *Obelia dichotoma*) (Gili and Hughes, 1995; Bouillon et al., 2004; Di Camillo et al., 2017).

Even if various feeding strategies can be observed across Hydrozoa, their key role in energy transfer across the planktonic and the benthic realms is surely essential in the modification of biogeochemical cycles and in the benthic-pelagic coupling perspective, considering their feeding behaviour and the release of medusae or planulae (Bouillon et al., 2004; Di Camillo et al., 2017; Gili and Hughes, 1995). However, their contribution to these processes is still poorly investigated. In fact, hydrozoans accounts just for a small fraction of the total community biomass, having a minor role if compared with active suspension feeders, such as bivalves. Nonetheless, the recorded high capture rates and densities represent evidences of the task they perform in energy transfer between the two compartments (Bouillon et al., 2004).

Unfortunately, many threats are stressing the communities they create, and, notably, their habitat complexity. Direct anthropic impacts involved are bottom trawling, pollution, urban expansion, tourism, aquaculture (with the harvest of precious and often endangered species of commercial interest), mining and introduction of alien species. In addition, indirect human pressures must be considered as well, with the role of climate change in ocean acidification and

global warming; for instance, species we usually find in southern areas are moving northward, menacing the local autochthonous fauna. On the other hand, some species are less vulnerable than others, showing fast adaptability, like those ones well-suited to develop on artificial substrates and belonging to fouling communities, able to undergo encystment and creating problems to human activities (e.g., aquaculture systems) (Sandifer and Smith 1979; Boero 1984).

Hydroids have been identified as suitable bioindicators for environmental monitoring because of: (i) the ubiquity, (ii) the sessile habit of colonies, (iii) the differential sensitivity to stress, (iv) a rather rapid response to disturbances, (v) morphological modifications in individual colonies of some benthic hydrozoans, and (vi) local fluctuations in abundance and distribution as proxies of changes (Topcu et al., 2016).

Monitoring based on bioindicators is a relatively young approach, begun in the early 1970s. Obviously, the impact of the human being on the surrounding environment dates back to long time before, thus it is not feasible to know how communities have changed overtime up to 1970s. However, from those years, the number of publications concerning the topic has increased steadily and quickly, in view of the need to assess environmental changes in a manner that can be repeated regularly and will provide early warning of future risk,

detecting not only possible hazards but even trends (Burger, 2006; Betti et al., 2021). The use of benthic organisms as indicators have been suggested both in the literature and by European legislations like the Water Framework Directive (WFD,2010) and the Marine Strategy Framework Directive (MSFD, 2008), especially to detect long-term environmental perturbations deriving from many kinds of pollution. In the Annex V of the WFD for the assessment of the ecological status of a coastal area it is necessary to consider: (1) the level of species diversity (taxonomic composition) and abundance of invertebrate taxa, and (2) the presence/absence of sensitive taxa and taxa indicative of pollution. Recently, European policies have also been implemented to increase the net of partnerships and stakeholders aiming to reach an ecosystem-based approach for control and handling of European marine resources, as reported in “the Rome Declaration presented at the EurOCEAN 2014 Conference (October 2014, Rome), an official event of the Italian EU Presidency” (Gravili, 2016).

In fact, hydrozoan species belonging to typical fouling communities (composed by few, large dominant species, usually belonging to more primitive families, with an overall lower diversity) can be very useful to identify the presence of direct anthropogenic impacts, like maritime traffic or urbanisation, or indirect ones, such as introduction and establishment of non-indigenous species (Yilmaz et al., 2020). Other authors (Roveta et al., 2021) have also emphasized



the importance of cnidarians (together with other sessile taxa), including Hydrozoa, in the detection of contaminants such as heavy metals.

Some recent papers have already attempted the use of specific taxa to trace their biogeography as a result of climate change (e.g., *Halecium* spp., Gravili and Boero 2017). The effects of global warming are clear analysing the changes overtime of Mediterranean biodiversity: a growing increase of thermophilic species can be noticed within the basin, entering from either the Gibraltar Strait or the Suez Channel (“Lessepsian migrants”), due to the rising temperatures which require them to reduce the distributional range, moving northward and endangering once again the survival and the heterogeneity of local autochthonous organisms (Gravili, 2016; Bianchi 2007; Bianchi and Morri 2004; Philippart et al. 2011).

Additionally, biological indicators are useful tools to ensure the effectiveness of conservative management measures which have been enforced within established marine protected areas; in this case, the creation of taxonomic baselines is gainful to discriminate long-term changes and also to highlight problems currently threatening the study areas, perhaps worthy of protection in the future (Mihoub et al., 2017).

The ecological role of Hydrozoa is still underrated and far from being fully understood, with the lack of appropriate conservation strategies aiming to protect the assemblages they create. In fact, directives currently in force are quite vague from the point of view of marine communities' management and biodiversity safeguard. Future research should regard both quantitative studies, with a special need of comparable data between/within assemblages and a standardised unit of abundance to be employed (Gili and Hughes, 1995) and the correlation between hydroids distribution and populations dynamics with biotic and abiotic factors. Moreover, long-term monitoring programs aimed to detect variations in composition, abundance and reproductive period of hydroids assemblages should deserve more attention because nowadays the mere census of species is no longer enough (Di Camillo et al., 2017), helping to confirm the stability and consistency of the changes in the hydroid assemblages over time, excluding the influence of other factors such as the natural fluctuation of the marine benthic populations (González-Duarte et al. 2014).

## *1.2. FJORDS*

### *1.2.1. PHYSICAL-CHEMICAL FEATURES*

The word “fjord” derives from the Norwegian homonymous term that means “landing place”. These incisions were explored and described for the first time

by Darwin during his voyage on the Beagle ship (1831-1836). Most fjords have been formed during the Pleistocene glaciations (Quaternary Period), and are deep narrow coastal notches of glacial origin, reminding a terrestrial environment: the melting of glaciers and the rise of the sea level have brought the coasts previously eroded by the glaciers to the current diving level (Pearson et al., 1980; Holtedahl, 1967; Syvitski et al., 1987; Syvitski and Shaw, 1995). These enclosed marine areas are submerged U-shaped valleys, whose connection with the open sea is often restricted by sills, usually formed through the accumulation of the sediments transported by the glacier itself (moraine), a very important factor affecting the circulation patterns (Pearson et al., 1980). They can be found exclusively at high latitudes: across the northern hemisphere they are present in Norway (including Svalbard islands), Western Scotland, North-Western Ireland, Greenland, Alaska, Canada (both on Western and Eastern Side, comprising the Canadian Arctic Archipelago as well), Iceland and Faroe Islands, while in the southern hemisphere their distribution is confined to Antarctica, South Georgia, Kerguelen Islands, Patagonia and New Zealand, over the 41°S (Syvitski et al., 1987).

The species distribution within a fjord is determined by ecological gradients (Syvitski and Shaw, 1995), both latitudinal (N-S, correlated mainly to temperatures) and longitudinal (W-E, associated with the salinity).

Fundamental features of these peculiar ecosystems are (i) the proximity to the mainland and (ii) the restriction of water exchange due to the morphology of the basin itself, especially its enclosure (Pearson et al., 1980). The first aspect (i) has a great relevance in relation to input of nutrients and sediments (Syvitski et al., 1987), making this environment characterised by a huge productivity and events, such as landslides, which have a deep impact on the surrounding communities; a too large release of sediment loads could also affect suspension-feeders survival itself. Vertical and horizontal gradients in organisms' distribution and species composition are related to sedimentation rates and granulometry of the sediment respectively (Pearson et al., 1980). The second trait (ii) is usually involved in a permanent stratification of the water column, with important consequences in particular for benthic organisms; it deeply affects temperature and salinity gradients and the free exchange of planktonic larvae within the basin (Pearson et al., 1980).

The positive water circulation within these systems is typified by a two-layer flow, “an outward flowing surface layer [of brackish water] and an inward moving compensating current, replacing salt entrained into the surface zone” (Syvitski and Shaw, 1995). This involves the creation of a well-layered estuarine stratification, where the fjord water column is divided into two main parts with different densities and the consequent creation of a permanent

pycnocline: (i) a superficial layer made of brackish water, nutrient-enriched and with low salinity/temperature (wide more or less 5-10 m, with a salinity about <10), derived from the release of huge amounts of freshwater from rain, rivers and melting processes of the coastal glaciers; (ii) the lower stratum with typical marine characteristics (Betti et al., 2017; Palma and Silva, 2004; Syvitski and Shaw, 1995). Sometimes, the presence of a deep stagnant zone, with the possible occurrence of hypoxic or anoxic crisis, could be observed (Pérez-Santos et al., 2018).

The different layers are maintained due to the reduced water circulation within the enclosed basin, together with the frozen sheet that could be ascribed to the harsh climate of those high latitudes ( $T$  is generally  $< 10\text{ }^{\circ}\text{C}$ ) and a well-defined thermocline. Furthermore, the wave motion (influenced by winds and tidal amplitude) is usually minor than on exposed shores and all these factors concur to minimize the vertical mixing. That is why a clear biological zonation can be noticed.

One of the first authors to provide a general summary on macrobenthos of fjords around the world has been Pearson, in a chapter belonging to the section “Benthic ecology” of the book “Fjord oceanography” published in 1980 (Pearson et al., 1980). In this work, the author has reported that the first attempt of a quantitative survey about benthic fjordic macrofauna was carried out by

Peterson and Boysen Jensen in 1911 with initial observations based on the Limfjord complex, Denmark (actually, this region owns lagoon-like features) and completed through extensive surveys in the Kattegat and Belt areas and in the Christianafjord (Oslofjord, Norway).

Pearson highlighted the low number of studies referred to fjords in the southern hemisphere (just 3 surveys carried out here compared to the 74 realised in the north available at that moment): a source of this imbalance was found in the deficiency of benthic studies in this part of the world. In particular, ecological investigations of Chilean/Patagonian fjord complexes were still lacking and only two papers by Harley (1964) and McKnight and Estcourt (1978) were focused on the macrobenthic communities' distribution in relation to major physical variables in Milford, Caswell and Nancy Sounds (New Zealand) (Freeland et al., 1980).

Furthermore, Pearson also tried to analyse which environmental factors affect the distribution and abundance of fjordic macrobenthos.

In brief, many studies have been conducted overtime on fjordic environment and associated communities, according to the fact that these inlets constitute a natural laboratory for improving scientific knowledge and being of great significance for anthropogenic activities as well (Farmer and Pearson, 1983; Pearson et al., 1980; Syvitski et al., 1987; Syvitski and Shaw, 1995).

### 1.2.2. BENTHIC FJORDIC COMMUNITIES

Thanks to the heterogeneous environment and the great habitat variability, the community structure within the fjords definitely differs from that one of the open ocean (Galea 2007; Galea et al. 2007a,b) or of true estuarine systems (Pearson et al., 1980). Both benthic biodiversity and abundance are huge in reference to the large food input coming from the coastal washout, acting as “either carbon or nutrient sinks” (Pearson et al., 1980). This trait is also responsible for possible observable cases of gigantism in organisms like crabs, pycnogonids, anemones or chitons (e.g., *Chiton magnificus* Deshayes, 1827 in Chilean fjords).

A very complex food web characterises this ecosystem, where suspension-feeders are the most symbolic trophic level in relation to the high organic loads and with cnidarians and sea stars at the apex of the food chain. Moreover, ecosystem engineers play a crucial role in the increased fractal complexity of the habitat (e.g., colonies of Red Tree Coral *Primnoa pacifica* Kinoshita, 1907 in the Southeastern Alaskan Fjords, Waller et al., 2011), creating various niches that other organisms can occupy and boosting biodiversity, favoured by the biological isolation too (e.g., genetic separation of different populations of the starfish *Coscinasterias muricata* Verrill, 1867 in the New Zealand fjords, Perrin et al., 2004) (Häussermann et al., 2016). Emblematic examples are the

anthozoan reefs typifying these places, often represented by deep-water corals, like those ones created in the Chilean fjords by *Desmophyllum dianthus* (Esper, 1794) (Försterra and Häussermann, 2003; Forsterra et al., 2017) or in the Norwegian fjords by *Desmophyllum pertusum* (Linnaeus, 1758) (possibly representing “early hotspot for ocean warming and acidification”, Juva et al., 2021).

The brackish layer is eutrophic and deeply turbid, closing off most of the solar radiation. In the intertidal zone, where tides are often large, euryhaline species can be found, especially barnacles and mussels; among the vagile fauna, organisms like shrimps or sea stars can be observed (Betti et al., 2017). In relation to the light exposure, algae, especially belonging to the genus *Ulva*, grow well here. In the upper part of the subtidal zone (between the end of the previous layer and 15 m depth), salinity and temperature are constant and usually filter feeders dominate communities, including sponges, soft corals, polychaetes and ascidians (Ahn et al., 2016; Betti et al., 2017, 2021; Pearson et al., 1980; Häussermann et al., 2016). Vagile animals are numerous and characterised by diverse food strategies, representing different trophic levels. In the lower part of the subtidal zone between 15 and 40 m depth, communities that you did not expect can be found here, in relation with the light decrease, such as cold-water corals which are generally confined to the deep-sea



(Försterra and Häussermann, 2003; Juva et al., 2021), a phenomenon called “deepwater emergence” (Häussermann et al., 2016). In fact, there are lots of large filter-feeders and micro-carnivores (large sponges, madrepores, black corals, stylasterid hydroids and brachiopods, e.g., Hartill et al., 2020).

Not only hard-bottom communities can be detected (e.g., Holte et al., 2004): little bights or steps among the almost vertical walls of the fjords allow typical soft-bottom organisms to colonize this kind of substratum (e.g., the nemertean *Lineus longissimus* (Gunnerus, 1770)). The high organic loads determine the presence of a rich associated fauna, also of commercial interest (for instance, the prawn *Nephrops norvegicus* (Linnaeus, 1758)).

On the other hand, just a few organisms can live in the deeper hypoxic stratum, such as irregular echinoids and polychaetes, organised in assemblages like those ones discernible in the deep-sea. However, abundant isopods and amphipods are located within the sediment, having the important role of scavengers and being involved in remineralisation processes (e.g., Legezyńska, 2001). The small number of individuals here detected is mainly caused by the low water exchange and the high organic load, both premises for the proliferation of bacteria that, by way of microbial degradation, consume oxygen causing further hypoxia or anoxia (Zaikova et al., 2010). Conditions creating once again a harsh environment for organisms’ survival.

### *1.2.3. CHILEAN FJORDS*

The southern coast of Chile is highly structured presenting a large number of islands, channels and fjords from the latitudes of Cape Horn (ca. 56°S) to the Reloncaví Estuary (Puerto Montt, ca. 41°30'S); this area belongs to the Magellanic province of the Temperate South America realm (Spalding et al., 2007) and, enlarges the coast (linear length of about 1,500 km) to a length of almost 90,000 km and an area of about 240,000 km<sup>2</sup> (Galea et al., 2007a,b; Häussermann et al., 2016; Palma and Silva, 2004). The deepest channel in the world can be found here, that is Canal Messier, reaching 1,200 m depth.

The Chilean fjords region can be considered as a transition zone from multiple points of view (hydrography, geomorphology, biology, climate, etc.) between the Antarctic Area dominated by the Southern Ocean and the Pacific temperate region (Northern Chile included). Its huge extension is given by the meeting between two parallel mountain ranges, the coastal mountains on the western side and the Andes on the eastern edge, allowing fjords penetration toward the inland (Galea et al., 2007a,b). The oceanic climate involves extremely high rainfall, homogeneously distributed throughout the year, with an annual mean ranging between 1,500 and 4,500 mm. The other big freshwater input comes from the melting of coastal glaciers.

The salty water within Patagonian fjords derives mainly from the intrusion of oceanic Sub-Antarctic Water (SAAW), having salinities between 33 and 34 PSU and from which the northward Humboldt Current and the southward Cape Horn Current derive; it can reach 100 m depth thanks to the West Wind Drift upwelling effect against the Chilean coasts. Nevertheless, the water mass is normally not able to penetrate deeper due to the constraint given by the shallow sills formed by the continental shelf adjacent to the coastal margin (usually max 150 m deep) (Palma and Silva, 2004). As seen before, this leads to the creation of a well-layered estuarine stratification, with a positive estuarine circulation (Palma and Silva, 2004), and the presence of a buoyant brackish surface layer up to depths of 10 m, whose thickness, salinity and temperature vary considerably across seasons if compared with the underlying deep salty stratum (Betti et al., 2017, 2020, 2021).

The organic and inorganic enrichment of waters within these inlets boosts the primary production, determining in turn huge amount of food for zooplanktonic organisms at the base of the food web.

The peculiar circumstances of this whole estuarine system permit the creation of unique and rich communities, a biodiversity hotspot with up to 1,650 species (Häussermann and Försterra, 2009; Häussermann et al., 2016). Even if numerous studies have been carried out from the taxonomic perspective, still

few authors have focused their attention on the ecological requirements of the different species and the drivers defining their distribution (Betti et al., 2021). For instance, Betti et al., 2017, 2020 have set such kind of study in the Puyuhuapi-Jacaf fjord system and along Seño Magdalena.

An accurate inventory of the fjord's invertebrate fauna has been carried out (e.g., Cairns et al. 2005; Galea 2006; Galea, 2007).

Fernandez et al. (2000) have recounted in their paper about a possible positive bathymetric trend in species richness of epi- and infaunal organisms within the fjord area of southern Chile, possibly due to the effect of a strong tidal current and mixohaline waters in shallow bottoms. Despite that, authors have also underlined the requirement of further studies as proof of the described gradient and its causes.

Looking at the South-eastern Pacific littoral biogeography, the existence of a Transitional-Temperate Region between 35°S and 48°S has been hypothesized by Lancellotti and Vásquez (1999), finding here a gradual species replacement, with a mix of macroinvertebrates belonging to the Chilean coastal benthic fauna with either subantarctic (at familiar and ordinal levels) or subtropical (at specific and generic levels) features and denying the presence of a clear distributional break at 42°S (between the warm-temperate and the cold-temperate region, due to the topography) as previously supposed on the basis

of a still limited regional knowledge of that fauna (Brattström and Johansen, 1983).

Great issues for the Chilean fjords' region are represented by the climate change (global warming, ocean acidification, sea level rise, etc.) and the direct human impact: (i) developing aquaculture hatcheries (mainly salmon farming), (ii) harvesting of endangered species or biocenosis destruction due to recreational activities (e.g., *Errina antarctica*, Häussermann and Försterra, 2007), (iii) growing urbanisation and tourism, (iv) oil research, (v) industrial and sewage discharge, (vi) agricultural activities and forestry, and (vii) overfishing (especially bottom trawling), are threatening these delicate ecosystems with consequences whose study is still ongoing (Häussermann et al., 2016). However, the awareness about these matters has been already raised since 1995, with the beginning of the Cimar Fjord Program carried out in interior waters of southern Chile between Puerto Montt and Cape Horn (Palma and Silva, 2004): its purpose was to improve the knowledge about “the characteristics and processes related to the local oceanography, sedimentology, and pelagic and benthic community structure” in order to have baseline data from which possible future alterations due to anthropogenic activities would be estimated. Furthermore, in the last decades lots of expeditions have been carried out with the same aim, for the most part supported by the Huinay

Scientific Field Station (X Region, Chile) and many experts and taxonomists from all over the world have been involved to achieve the goal (Galea, 2007). Moreover, due to the fact that the Chilean fjord region is recognized as a unique, highly fragile and vulnerable ecosystem (Iriarte et al. 2010; Pantoja et al. 2011) and a biodiversity hotspot (Fernandez et al., 2000; Häussermann and Försterra 2009; Häussermann et al., 2016), the establishment of new marine protected areas and reserves represents a fundamental prerequisite to “prevent fast degradation, decline or even the disappearance of these spectacular and unique benthic communities” (Häussermann and Försterra, 2007).

### *1.3. AIM OF THE STUDY*

In the present study the Hydrozoa assemblage living in this ecosystem has been investigated and a taxonomic report about hydroids collected along the Puyuhuapi Channel (Aysen region, Chile) has been provided. The ecological role of these metazoans and the importance of having baseline zoologic lists and “sentinel” species for monitoring have been discussed above, but a correlation between the hydrozoan fauna of different fjords around the world seems to be currently not available in the literature. Therefore, I tried to stress this point, not restricting this research to the mere analysis of Patagonian fjords’ hydroids and hydromedusae but trying to carry out a general comparison to

point out possible redundant trends or relationships between species diversity/composition and typical fjords' environment.

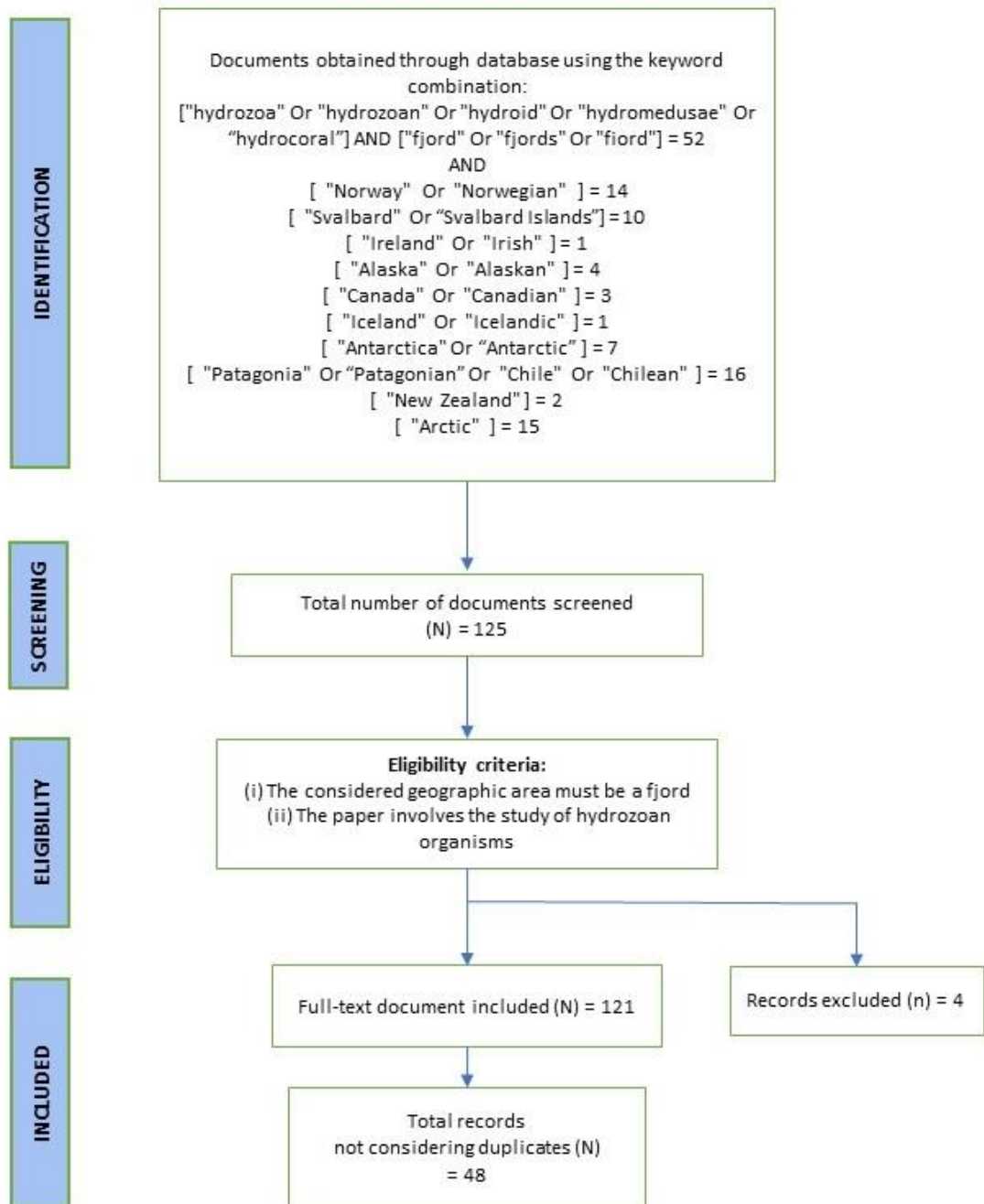
## Chapter 2

### 2. MATERIALS AND METHODS

#### 2.1. LITERATURE COLLECTION

The literature compilation is the result of an extensive bibliographic research on Elsevier's Scopus database (<https://www.scopus.com/>), entering different keywords, ["hydrozoa" Or "hydrozoan" Or "hydroid" Or "hydromedusae" Or "hydrocoral"] AND ["fjord" Or "fjords" Or "fiord"] AND "name of the geographic area" (Fig. 1), in the option "Article title, Abstract, Keywords," in all years until the cut-off date of 31 December 2021. The literature considered in this work includes journal articles and grey literature, as congress proceedings. All documents found with the aforementioned queries have been screened by reading titles and abstracts, excluding those not matching our criteria. Two main eligibility criteria have been set: (i) the considered geographic area must be a fjord; (ii) the paper involves the study of hydrozoan organisms (Fig. 1). Duplicates (e.g., same documents found using different keywords) were counted as one. A flow chart of the searching strategy and the eligibility process is given as Fig. 1.





*Figure 1. Flow chart illustrating the steps for obtaining documents about the study of hydrozoan fauna from fjords around the world from Scopus search engine.*

## 2.2. STUDY AREA

The present study has been conducted along the Puyuhuapi Channel and the Seño Magdalena area in the Aysen region of Southern Chile.

The channel is oriented in a SW-NE direction and the water circulation follows the same path (counter-clockwise). It is approximately 90 km long, with a maximum width of 7 km and it sails along the coast of the Isla Magdalena, circumscribed by other two fjords, the Jacaf Channel in the north-eastern part and the big Moraleda Channel along the north-western side (which is joined to the Pacific Ocean through the Corcovado Gulf) (Betti et al., 2017, 2020, 2021; Pérez-Santos et al., 2018; Montero et al., 2021;). The whole island is under the protection of the Isla Magdalena National Park, established in 1982 to preserve the landscape colonized also by charismatic animals such as the Magellan penguins and the rich avifauna that, together with all the peculiar marine organisms which can be found here, make this land worthy of conservation (especially against the still not well-evaluated human impact) (Betti et al., 2017).

From Seño Magdalena, which is a very narrow and deep incision (the deepest, with ~350 m depth and 14 km of length) located in front of the town of Puerto Cisnes, important freshwater inputs reach the Puyuhuapi fjord because of the presence of Cisnes river (with an average flow rate of about  $233 \text{ m}^3 \text{ s}^{-1}$ ). The

salty water within the Puyuhuapi Fjord derives mainly from the entrance of ocean water masses through its southern mouth, as a consequence of the limited water exchange on the north-eastern side due to the presence of the shallow Jacaf Channel sill (6 km long and just 50 m deep) (Betti et al., 2017; Montero et al., 2021). During the late winter, the water column in the Puyuhuapi Channel becomes partially mixed and the vertical stratification is reduced as a consequence of the diminished freshwater input.

According to Pérez-Santos et al. (2018), temperature profiles in Puyuhuapi Channel do not differ too much between winter and summer, showing a similar structure; the largest gradients have been found between the surface and 70 m depth ranging from 8.5 to 17°C. Concerning the salinity, in the first 10-m layer it varies between 11 and 29 g kg<sup>-1</sup>, while values remain more or less the same below this depth (29 to ~ 34.2 g kg<sup>-1</sup>). Always referring to this bathymetric boundary, high nitrate concentrations were measured, greater in the winter than in fall and summer and related to freshwater inputs.

Puyuhuapi Fjord and Jacaf Channel are both subjected to hypoxic conditions with oxygen concentration < 2 ml L<sup>-1</sup>; these oxygen depleted zones are mainly located at the fjord heads and down to 100m depth, all the year around. Puyuhuapi fjord seems to be “the only north-western Patagonian fjord known to experience such extreme hypoxic conditions” (Pérez-Santos et al., 2018).

Obviously, hypoxia has a significant role on the whole ecosystem, especially in defining aggregation and distribution of zooplankton with consequences on the rest of the trophic chain (in particular on suspension feeders, such as hydroids).

Vertical mixing seems not only to play a crucial role in oxygen depletion, but it affects abundances of zooplankton too, chiefly in fjord sills: at the level of Jacaf sill, a clear increment of both macrozooplankton and fish aggregations could be detected and related to the increased turbulence of this area, which allows enhanced exchanges within the water column and a consequent higher primary productivity (e.g., case study of the squat lobster *Munida gregaria* (Fabricius, 1793), Betti et al., 2020)(Pérez-Santos et al., 2018). The whole situation deeply affects the biogeochemical carbon cycle, modifying its flux, amount, and quality between shallower and deeper layers.

Moreover, it is important to take into account that the larval stages of many species belong to the plankton communities (Pearson et al., 1980): it means that also the settlement and the colonisation of the fjord by its typical fauna and flora depend on physical-chemical drivers (e.g., vertical mixing, hypoxia, salinity, temperature, etc.), which define the different assemblages that can be noticed (Betti et al., 2021).

Regarding hard-bottom megabenthos, Betti et al., 2021 have described ten well-outlined different communities; authors affirm a decreasing diversity pattern along the Puyuhuapi-Jacaf fjord system (from the entrance of the former to the end of the latter); instead, an increasing species richness can be detected from superficial layers down to 20 m depth, before stabilising (Betti et al., 2021).

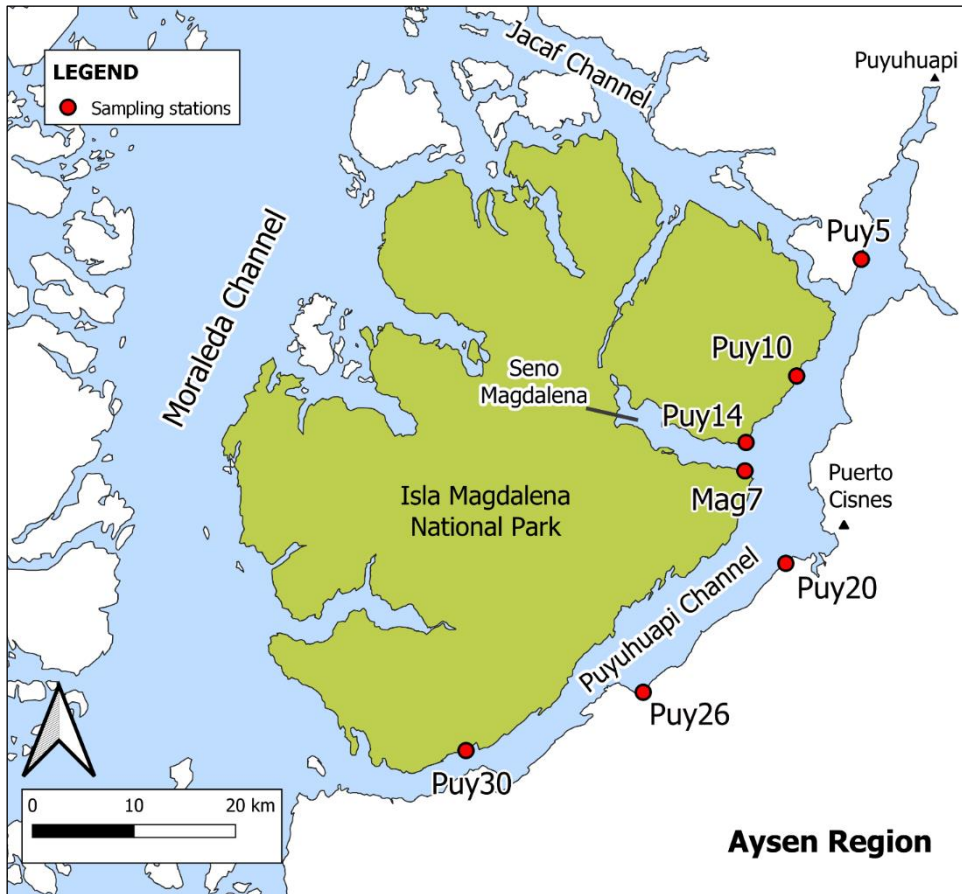
Seño Magdalena, as regards its relatively small dimensions, has been elected as a model study area: for instance, Betti et al., 2017 have carried out here an in-depth analysis (through photographic underwater transects) about the bathymetric, longitudinal, and hydrological zonation patterns of biodiversity (both in terms of richness and abundance) found along the mainly steep, vertical walls of the inlet, based on a community approach. While the longitudinal trend is mainly explained by the turbidity gradient of the estuarine plume, resulting in a general decrease of marine benthic life abundance in the innermost part of the fjord where the organic enrichment and sedimentation are greater (stenohaline species like echinoderms tend to disappear, while sponges and cyanobacteria dominate in these conditions), salinity and silting are the main drivers for what concern the bathymetric gradient.

### 2.3. SAMPLES COLLECTION AND ANALYSIS

Sampling activities have been carried out through SCUBA diving in March 2019 (Table 1; Figure 2).

*Table 1. List of the sites surveyed in March 2019 in Puyuhuapi Channel and Seño Magdalena.*

<b>Area</b>	<b>Site code</b>	<b>Latitude (S)</b>	<b>Longitude (W)</b>
Seño Magdalena	MAG_7	44° 40' 05"	072° 47' 55"
	PUY_5	44° 28' 46"	072° 39' 11"
	PUY_10	44° 35' 01"	072° 44' 02"
Puyuhuapi Channel	PUY_14	44° 38' 34"	072° 47' 50"
	PUY_20	44° 45' 01"	072° 44' 51"
	PUY_26	44° 51' 53"	072° 55' 33"
	PUY_30	44° 54' 59"	073° 08' 51"



*Figure 2. Map of the Puyuhuapi Channel, with the location of the sampling sites.*

At each station, samples were collected from rocky substrates at six depths (5, 10, 15, 20, 25 and 30 m) following the visual oriented sampling method, considered as one of the most effective for the detection of the highest numbers of hydrozoan species within a selected area (Piraino et al., 2013). Hydroid samples have been fixed in 4% buffered formalin. Once in laboratory, species were washed with water and subsequently preserved in 70% alcohol. Specimens were identified at the possible lowest taxonomic level, and the status

of taxa was validated using the updated taxonomic lists of the website World Register of Marine Species (WoRMS, 2021).

#### *2.4. DATA ANALYSIS*

Statistical analyses were conducted using the free software R 4.0.4 and PRIMER 7.0.20 (Clarke and Gorley 2015) with the add-on PERMANOVA+ (Anderson et al. 2008).

Due to the low number of information available in the literature on hydrozoan species of fjords around the world, only the species listed for Norwegian and Chilean fjords were considered for the statistical analysis. Occurrences of hydrozoan species obtained from the literature and our data were included to carry out statistical analyses aiming at testing differences in the hydrozoan communities between Norway and Chile, thus including a single factor: fjords (fixed, 2 levels: Chile, Norway).

Using a similarity matrix of presence-absence data (based on Jaccard similarity), data were analysed with Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001), with 9999 permutations. In case of a significant *p-value*, the analysis of Similarity Percentages (SIMPER) (Clarke 1993) was used to determine species contributions to the dissimilarity in hydroid assemblages within and between the two fjord regions.



The same joint dataset was used to estimate the sampling effort applied at each fjord region. A rarefaction curve per region was built using the *iNEXT* R package (Chao et al. 2014), based on sampling-unit-incidence data (presence/absence), and the Hill number was measured in relation to the species richness ( $q = 0$ ) of each region. To standardize our data, we outrun a similarity matrix per fjord region, acquiring site and hydrozoan species collected in every study toward the definition of the sampling unit and the species diversity respectively. If a document did not specify in which sampling site species were found, all hydrozoan species were considered as found in a single site. In the analysis, if a species was indicated as sp. or spp. in different studies, they were grouped together to minimize bias.

## Chapter 3

### 3. RESULTS

#### 3.1. TAXONOMIC ANALYSIS OF CHILEAN SAMPLES

In the present study, a total of 26 hydroid species (7 Anthoathecata and 19 Leptothecata) were collected at the Puyuhuapi Fjord, belonging to 14 families (Table 2). In some cases (Bougainvillidae spp., Hydractiniidae sp., *Rhysia* sp., Tubulariidae sp., *Sertularella* spp., *Symplectoscyphus* sp., *Halecium* sp., *Clytia* spp.), identification at species level was impossible due to the small amount of available material, poor material, or the lack of structures essential for identification (e.g., gonophores or gonothecae) (Table 2). A table containing further information (site, site code latitude, longitude, depth, and the list of all the identified species) is reported in the supplementary material as Table S1.

The most represented families are Campanulariidae (5 species) and Sertularellidae (3) for Leptothecata, Bougainvillidae (3) for Anthoathecata. *Obelia dichotoma* is the most widespread species, being present at all sampling sites and investigated depths, even though other species (i.e., *Plumularia setacea*, *Clytia linearis* and *Clytia* spp.) have been recorded at all the sampling sites.

Many species occur just below a specific depth: *Plumularia setacea*, *Clytia linearis* and *Clytia* spp. below 10 m, *Hybocodon chilensis*, *Lafoea dumosa*,

*Sertularella* spp., *Sertularella tenella*, *Modeeria rotunda*, *Halecium fjordlandicum*, *Halopteris schucherti* and *Clytia reloncavia* below 15 m, while *Filellum serratum*, *Sertularella curvitheca* and *Halecium* sp. below 20 m depth (Table S1). Some species have been recorded within the intermediate bathymetric layers, especially avoiding the 5 and the 30 m depth: *Bougainvillia pyramidata* (10 and 20 m), Hydractiniidae sp. (15 and 20 m), *Hebella striata* (10 and 25 m), *Symplectoscyphus filiformis* (10 and 20 m), *Phialella* cf. *quadrata* (10 and 15 m) (Table S1). In addition, exclusive species were recorded in both sites and sampling depths, such as *Bougainvillia muscoides* and Tubulariidae sp. were exclusive of the 15 m, *Rhysia* sp. and *Symplectoscyphus* sp. of 25 m, while *Obelia longissima*, *Symplectoscyphus* sp., *Halecium* sp., *Rhysia* sp. and *Obelia longissima* were present only at Puy30, *Bougainvillia muscoides* at Puy10, Hydractiniidae sp. at Puy5, and Tubulariidae sp. at Mag7 (Table 2, S1).

Few species seem to follow a gradient along the fjord axis, being noticed at the sampling stations near the head, Puy5 (*Bougainvillia pyramidata*), or the mouth of the inlet, Puy30 (*Sertularella* sp., *Sertularella tenella*, *Sertularella curvitheca*, *Halopteris schucherti*).

Across the specimens recognised at the lowest taxonomic level, 5 species seem to be endemic to the Chilean region: *Sertularella curvitheca*, *Symplectoscyphus*

*filiformis*, *Halecium fjordlandicum*, *Halopteris schucherti*, *Clytia reloncavia* (Table 2).

Most of the specimens were collected during their reproductive period at least in one site, except for Bougainvilliidae sp., Hydractiniidae sp., *Rhysia* sp., Tubulariidae sp., *Symplectoscyphus* sp., *Clytia* spp., *Clytia reloncavia* and all the species belonging to the genus *Sertularella*.

Usually, several specimens were found unattached to any substrate. Among the non-living substrates, polychaete tubes were the most common, accompanied by shells of bivalve molluscs, exoskeleton of crustaceans, algae and sometimes egg cases (perhaps of some gastropods). Octocorals and bryozoans represented good opportunities for settlement too.

Many of the recognised species were epibionts on other hydroids, such as *Modeeria rotunda*, *Hebella striata*, *Filellum serratum*, *Phialella* cf. *quadrata*, species belonging to genus *Sertularella* and to family Bougainvilliidae.

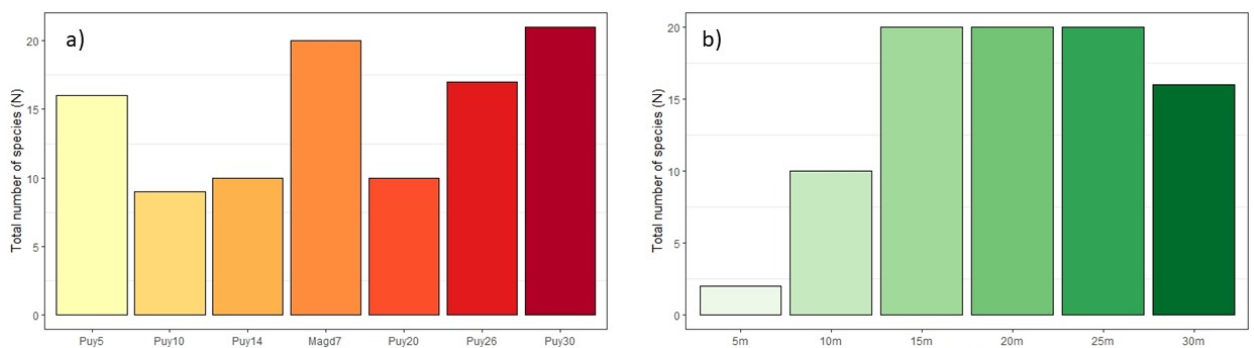
**Table 2.** List of identified hydroids collected at the different sampling sites along Puyuhuapi Channel (E=endemic species; NR=new record).

Hydrozoa	Status	Puy5	Puy10	Puy14	Mag7	Puy20	Puy26	Puy30
Anthoathecata								
Bougainvilliidae								
<i>Bougainvillia muscoides</i>			X					
<i>Bougainvillia pyramidata</i>		X	X		X			
<i>Bougainvillidae</i> sp.		X		X	X	X	X	X
Hydractiniidae								

<i>Hydractiniidae sp.</i>		X						
Rhysiidae								
<i>Rhysia sp.</i>	NR							X
Tubulariidae								
<i>Hybocodon chilensis</i>		X	X		X	X	X	X
<i>Tubulariidae sp.</i>					X			
Leptothecata								
Campanulariidae								
<i>Clytia linearis</i>		X	X	X	X	X	X	X
<i>Clytia reloncavia</i>	E	X		X	X		X	X
<i>Clytia spp.</i>		X	X	X	X	X	X	X
<i>Obelia dichotoma</i>		X	X	X	X	X	X	X
<i>Obelia longissima</i>								X
Haleciidae								
<i>Halecium fjordlandicum</i>	E	X			X	X	X	X
<i>Halecium sp.</i>								X
Halopterididae								
<i>Halopteris schucherti</i>	E				X	X	X	X
Hebellidae								
<i>Hebella striata</i>		X		X	X		X	X
Lafoeidae								
<i>Filellum serratum</i>		X			X		X	X
<i>Lafoea dumosa</i>		X	X	X	X		X	X
Phialellidae								
<i>Phialella cf. quadrata</i>		X		X	X		X	
Plumulariidae								
<i>Plumularia setacea</i>		X	X	X	X	X	X	X
Sertularellidae								
<i>Sertularella curvitheca</i>	E				X		X	X
<i>Sertularella sp.</i>					X		X	X
<i>Sertularella tenella</i>					X	X	X	X

Symplectoscyphidae							
<i>Symplectoscyphus filiformis</i>	E	X		X	X		X
<i>Symplectoscyphus sp.</i>							X
Tiarannidae							
<i>Modeeria rotunda</i>		X	X		X	X	X
Tot. number of species		16	9	10	20	10	17
		20	10	17	21		

Concerning the latitudinal-longitudinal gradient, a lower number of species have been detected for most of the inner stations, but a peak in the number of species can be noticed at Magd7 (20) and Puy 30 (21) (figure 3a). From a bathymetric point of view, a general increasing trend with depth can be observed, with a low number of species at 5 and 10 m depth (with 2 and 10 species, respectively), while the highest number of species (20) was found at 15, 20 and 25 m depth, and then a slight decrease occurs at 30 m (16) (figure 3b).



**Figure 3.** Total number of species recorded at each sampling station (a) and at each depth (b) along the Puyuhuapi Channel.

### 3.2. TAXONOMIC REPORT

#### ORDER ANTHOATHECATA Cornelius 1992

##### Suborder Filifera Kühn, 1913

##### Family Bougainvillidae Lütken, 1850

##### Genus *Bougainvillia* Lesson, 1830

*Bougainvillia muscoides* (M. Sars, 1846)

*Bougainvillia pyramidata* (Forbes and Goodsir,  
1853)

##### Family Hydractiniidae L. Agassiz, 1862

Hydractiniidae sp.

##### Family Rhysiidae Brinckmann, 1965

##### Genus *Rhysia* Brinckmann, 1965

*Rhysia* sp.

##### Suborder Aplanulata Collins, Winkelman, Hadrys and Schierwater, 2005

##### Family Tubulariidae Goldfuss, 1818

##### Genus *Hybocodon* L. Agassiz, 1860

*Hybocodon chilensis* Hartlaub, 1905

ORDER LEPTOTHECATA Cornelius, 1992

Family Lafoeidae Hincks, 1868

Genus *Filellum* Hincks, 1868

*Filellum serratum* (Clarke, 1879)

Genus *Lafoea* Lamouroux, 1821

*Lafoea dumosa* (Fleming, 1820)

Family Hebellidae Fraser, 1912

Genus *Hebella* Allman, 1888

*Hebella striata* Allman, 1888

Family Plumulariidae McCrady, 1859 (Superfamily Plumularioidea  
McCrady, 1859)

Genus *Plumularia* Lamarck, 1816

*Plumularia setacea* (Linnaeus, 1758)

Family Sertularelliidae Maronna et al., 2016 (Superfamily  
Sertularioidea Lamouroux, 1812)

Genus *Sertularella* Gray, 1848

*Sertularella curvitheca* Galea and Schories, 2012

*Sertularella tenella* (Alder, 1857)



Family Symplectoscyphidae Maronna et al., 2016

Genus *Symplectoscyphus* Marktanner-Turneretscher, 1890

*Symplectoscyphus filiformis* (Allman, 1888)

*Symplectoscyphus* sp.

Family Tiarannidae Russell, 1940

Genus *Modeeria* Forbes, 1848

*Modeeria rotunda* (Quoy and Gaimard, 1827)

Family Haleciidae Hincks, 1868

Genus *Halecium* Oken, 1815

*Halecium fjordlandicum* Galea, 2007

*Halecium* sp.

Family Halopterididae Millard, 1962 (Superfamily Plumularioidea  
McCrary, 1859)

Genus *Halopteris* Allman, 1877

*Halopteris schucherti* Galea, 2006

Family Campanulariidae Johnston, 1836

Genus *Obelia* Péron and Lesueur, 1810

*Obelia dichotoma* (Linnaeus, 1758)

*Obelia longissima* (Pallas, 1766)

Genus *Clytia* Lamouroux, 1812

*Clytia linearis* (Thorneley, 1900)

*Clytia reloncavia* Galea and Schories, 2012

*Clytia* sp.

Family Phialellidae Russell, 1953

Genus *Phialella* Browne, 1902

*Phialella* cf. *quadrata* (Forbes, 1848)

## **ORDER ANTHOATHECATA Cornelius 1992**

The order of Anthoathecata currently comprises three suborders, Aplanulata, Capitata and Filifera. Its monophyly seems to be not supported by phylogenetic analysis, therefore Anthoathecata represents a paraphyletic group (Collins et al., 2006; Daly et al., 2007).

### **Suborder Filifera Kühn, 1913**

The suborder comprises 26 families (WoRMS, 2021). Its monophyly is not supported by molecular evidence (Collins et al., 2006; Collins, 2002), even if organisms share putative synapomorphies such as filiferan tentacles on the feeding polyps and desmoneme and eurytele nematocysts (Daly et al., 2007).

## **Family Bougainvilliidae Lütken, 1850**

Bougainvilliidae currently comprises 17 accepted genera (WoRMS, 2021) of hydroids characterised by a firm perisarc terminating either at base of hydranths or forming a pseudohydrotheca; the filiform tentacles can be arranged in one or more whorls, more or less close-set beneath the conical or rounded hypostome. Gonophores could be present as free medusae or fixed sporosacs (Bouillon et al., 2006).

In many samples, hydroids belonging to Anthoathecata, especially Bougainvilliidae, are represented by a very poor and bad preserved material, impossible to recognise with confidence at lower taxonomic levels. Furthermore, many of them, even if morphologically resembling *Bougainvillia muscoides* or *B. pyramidata*, lack gonophores making the identification further difficult.

Galea (2007) has underlined that small colonies, as those ones found in our samples, may have an epizootic habit, colonizing other hydroids.

**Material examined.** Puy5-10 (colony of ~2 cm, growing on a polychaete tube, with hydranths surrounded by a pseudohydrotheca), Puy5-15 (stolonial colony on *Obelia dichotoma*), Puy5-25, Puy5-30 (fertile polysiphonic colony of ~2 cm, ruined), Puy14-15, Puy20-25, Puy26-5 (growing on *Obelia dichotoma*, hydranths lacking pseudohydrotheca), Puy26-15 (fragment of a

fertile colony, resembling *B. pyramidata*), Puy26-20, Puy26-25 (up to 5.3 mm, hydranths surrounded by a pseudohydrotheca), Puy30-15, Puy30-20, Puy30-25 (up to 8 mm), Puy30-30, Mag7-20 (on *Symplectoscyphus filiformis*), Mag7-25 (colony growing on *L. dumosa*), Mag7-30.

### **Genus *Bougainvillia* Lesson, 1830**

Hydroid colonies are usually erect, branched, or unbranched, more rarely stolonal; the hydranth, fusiform to clavate, has a dome-shaped hypostome surrounded by one distal whorl of tentacles, never enveloped by the pseudohydrotheca. Gonophores arise singly or in clusters from hydrocaulus, hydrocladia or hydrorhiza, successively developing into free medusae (Bouillon et al., 2006).

### ***Bougainvillia muscoides* (Sars, 1846)**

(Figure S1)

**Material examined.** Puy10-15 (fertile colony growing on *Lafoea dumosa*).

**Description.** Small stolonal, polysiphonic colony on *Lafoea dumosa*, where polyps arise irregularly along the hydrorhiza. No erect stems have been observed.

Presence of a pseudohydrotheca (perisarc widening distally creating a sort of slight, wrinkle cup in which the posterior third of the hydranth can retract), not covering tentacle bases.

Hydranth (Figure S1: A,B) characterised by a whorl of oral tentacles close-set beneath the rounded hypostome; the part outside the perisarc can reach ~ 500  $\mu\text{m}$  in length.

Many gonophores observable (Figure S1: C,D,E): “balloon-shaped”, arising singly, and developing into free medusae. Gonophores with a radial symmetry and borne on short stalks; the biggest buds measure up to ~ 300  $\mu\text{m}$  in width and ~ 400  $\mu\text{m}$  in length.

Throughout the hyaline perisarc of the bud, the manubrium and the bulbs of the four radial canals of the future medusa can be distinguished.

**Remarks.** The present specimen recalls the pictures provided by Galea (2007) and Schuchert (2007), while, possibly due to the scarcity of the material, erect colonies as described by Rees (1938) have not been observed.

The presence of gonophores has been of crucial importance in the identification of the species.

As already highlighted by Schuchert (2007), there is molecular evidence (given by the phylogenetical analysis of a 590 bp sequence related to the 16S gene)

regarding the fact that specimens from Trondheimsfjord in Norway and from the Chilean fjords are conspecific.

**World distribution.** Boreal waters of the Atlantic and Pacific Oceans (European Waters, Canada), Arabian Gulf and off Mozambique (Galea, 2007), New Zealand.

In particular, Rees (1938) reported that he collected *Bougainvillia muscoides* “at Bognøstrømmen in the Mangerfjord living on *Ascidia mentula* dredged from depths between 10 and 80 m. It was in this fjord that Sars originally found the species growing on *Ascidia mentula* and on tubes of *Tubularia indivisa*”.

**Previous records from Chile.** Fjord Comau, Canal Fallos (polyp stage only) (Galea, 2007; Galea et al., 2007a,b).

### ***Bougainvillia pyramidata* (Forbes and Goodsir, 1853)**

(Figure S2)

**Material examined.** Puy5-20 (fertile erect colony on *Halecium fjordlandicum*, with *Obelia dichotoma* as epibiont), Puy10-15 (short stems on *Plumularia setacea*), Mag7-10 (colony bearing gonophores).

**Description.** Small colonies (usually monosiphonic, Figure S2: A,C), reaching at maximum 2 cm. Erect stems arising from a creeping, tubular stolon; branching quite straight and regular.

Pseudohydrotheca absent.

Hydranth elongated, terminal on branches and stems, with a whorl of filiform tentacles and a conical hypostome (Figure S2: B).

Gonophores (Figure S2: D,E) probably at early development stages; medusa buds sometimes in groups, owning a distinct short stalk (branched if more than one gonophore is present), borne on the pedicel of the hydranth or along the branches.

**Remarks.** Schuchert (2007) described the hydroid colonies of this species as polysiphonic. In the present material this habit has not been observed and this could be probably led back both to the scarcity and the bad preservation of the specimens and to the overall low abundance of Anthoathecata species.

Schuchert (2007) also underlined that *B. pyramidata* can be easily mistaken for *B. muscus*, but the former differs for the erectness and straightness of its stems, the straightness of its branches and the regularity of arrangement, accompanied by the unique feature of the branched pedicels of the medusa buds (Edwards, 1964).

The colony silhouette (i.e., shape and general pattern of the colony) actually observed can be easily reconducted to the pictures and the descriptions provided by Galea (2007) and Edwards (1964).

**World distribution.** Atlantic Ocean (European waters), in particular along the Western coast of British Isles (Ireland, West coast of England and Scotland) (Galea, 2007; Galea et al., 2007a,b).

**Previous records from Chile.** This species seems to be abundant from 42°10' S to 52°10' S; in particular, medusae were collected from fjord Comau by Galea 2007 (Galea et al., 2007a,b).

### **Family Hydractiniidae L. Agassiz, 1862**

This family includes 15 accepted genera (WoRMS, 2021).

Hydroids characterised by stolonal, polymorphic colonies that may bear chitinous or calcareous spines, usually epizootic (Daly et al., 2007; Bouillon et al., 2006). Hydrorhiza (which in some genera can contain ectodermal vesicles of unknown function) either as a reticulum or an encrusting mat of stolonal tubes (in some genera invested by a calcareous skeleton), which could be covered by a common layer of perisarc or with naked coenosarc. Polyps sessile and naked: (i) gastrozooids, with one whorl or with several closely alternating whorls of oral filiform tentacles or with scattered tentacles on the distal half of column, exceptionally with one or two tentacles; (ii) gonozooids, typically bearing gonophores, with or without oral tentacles and mouth (= blastostyles); (iii) dactylozooids, when present, with no tentacles (Bouillon et al., 2006).



## Hydractiniidae sp.

(Figure S3)

**Material examined.** Puy5-15 (sterile colony), Puy5-20 (sterile, stolonal colonies on *Lafoea dumosa* and on a polychaete tube).

**Description.** Stolonal, polymorphic colony, arising from polychaete tubes (where polyps are very abundant and tightly herded together, even reaching 6 mm in length) or growing on *Lafoea dumosa* (scattered distribution across the whole arborescent hydrocaulus, Figure S3:A). Creeping hydrorhiza, strictly attached to the substratum, reticulated, composed of a closely meshed network of perisarc-covered stolonal tubes; absence of spines.

Across the colony three types of polyps (all sessile and naked) can be distinguished (Figure S3:B,C,D,E): (i) gastrozooids, (ii) gonozooids, (iii) dactylozooids (probably tentaculozooids<sup>4</sup>). (i) Gastrozooids bigger than the others, characterised by a rounded-conical hypostome and bearing two whorls of tentacles (confined to a narrow region), equipped with well-visible rings of cnidocysts, especially at their tips. Gastrozooids claviform to tubular, slightly tapering at base, up to 6 mm high. (ii) Gonozooids smaller than gastrozooids,

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<sup>4</sup> Reduced dactylozooids similar to tentacle in structure, with a solid core of chordal endoderm and no mouth or gastric cavity, richly armed with cnidocysts and often with chemosensory receptors; very extensible and contractile (Bouillon et al., 2006). Cartwright et al., 2021 has pointed out that this kind of zooid only appears as a defence when another organism (non-hydractiniid) settles near the colony.

with an elongated hypostome. (iii) Few dactylozooids scattered across the colony, deeply armed with nematocysts, slender, with rounded tips, not swollen.

The collected material was sterile: no gonophores can be observed on gonozooids, not allowing us to distinguish male and female individuals.

Cnidome: microbasic euryteles present both on dactylozooids (8-10 x 3-4  $\mu\text{m}$ ) and tentacles of gastrozooids (8-11 x 3-4  $\mu\text{m}$ ); in the latter case, also abundant desmonemes can be observed (6-7 x 4  $\mu\text{m}$ ).

**Remarks.** The lack of gonophores has not allowed us to define the species or even the genus with certainty, so we preferred to be more conservative, leaving the specimens at the family level and naming it Hydractiniidae sp.

The present material resembles, from the morphological point of view, the pictures and the description given by Galea et al., 2007a,b about the Chilean record of the species *Hydractinia pacifica*. In fact, beyond the morphology, even the cnidome seems to correspond to that one described by Galea (2007). However, as underlined by Schuchert (2007), the nematocyst types of the Hydractiniidae are rather uniform and do not offer much help in reliably discriminating the species.

**Records from Chile.** The present material has been collected just from the station Puy 5, at 15 and 20 m depth. *Hydractinia pacifica*, *Hydractinia*

*parvispina*, *Podocoryna borealis*, *Podocoryna tenuis* are the main species belonging to the family Hydractiniidae recorded nowadays for the Chilean fjord region. Thus, our specimen probably belongs to the previous encountered *Hydractinia pacifica*.

### **Family Rhysiidae Brinckmann, 1965**

It is a monogeneric family, just with 3 valid species (WoRMS, 2021).

The family can be distinguished by dactylozooids covered with perisarc to the capitate apical tip and female gonozooids transforming into a sporosac-like structure (Daly et al., 2007): gonads are directly developed in the body wall of gonozooids, without forming special gonophores. The latter is the key-character which has allowed Brinckmann to erect this new taxonomic family as distinguished by other Anthoathecata groups (Hirohito, 1988).

Hydroids forming stolonial colonies, where the creeping hydrorhiza is formed by anastomosing stolons and covered with perisarc, showing polymorphism: (i) gastrozooids naked, columnar, with either one whorl of filiform tentacles or with cnidocyst clusters and a few thick filiform tentacles around a conical hypostome; (ii) gonozooids characterised by sexual dimorphism, with male hydranth bearing 3 or 4 filiform tentacles and female individuals with or without tentacles, transforming into a sporosac-like structure with the

endoderm forming a spadix feeding one egg, developing into a planula (Bouillon et al., 2006); (iii) dactylozooids, if present, perisarc-covered up to the capitate apical extreme (deeply armed with cnidocysts), which has no tentacles (Bouillon et al., 2004; Brinckmann, 1965; Bouillon et al., 2006).

### **Genus *Rhysia* Brinckmann, 1965**

#### ***Rhysia* sp.**

(Figure S4,S5; Table 3,4)

**Material examined.** Puy30-25m (on *Halecium fjordlandicum*).

**Description.** Polymorphic colony with gastrozooids, gonozooids and dactylozooids, rising from a creeping stolon (Figure S4). Polyps are connected through the hydrorhiza which forms a net of irregular mesh-size, covered by the perisarc. Even the thin whitish dactylozooids are covered by the perisarc, while gonozooids and gastrozooids are naked, yellowish and columnar. Gastrozooids (up to ~ 875 µm) are bigger than gonozooids (up to ~ 625 µm), characterised by a conical hypostome and owning one whorl of thick filiform tentacles, usually 10 and long up to ~ 450 µm, deeply armed with rings of cnidocysts. Dactylozooids' capitate apical extreme retracted within the perisarc, perhaps due either to the sample fixation or to a defence mechanism

(if observed at the microscope, the perisarc appears to be covered by cnidocysts which do not belong to this species).

Colony probably in an early stage of reproductive development; even if it is difficult to discern the sex of the gonozooids, probably in the present specimen only male individuals are present, resembling the description of *Rhysia autumnalis* provided by Brinckmann et al. (1993). Gonozooids not located in a restricted area of the colony; occurrence of dense clusters of nematocysts on the tentacle tips and the round hypostome (lacking mouth). Some gonozooids lack tentacles, most likely due to the preservation technique which could have induced the contraction of the tentacles or to the initial phase of development of the polyps.

**Table 3.** Cnidome composition and size ranges of nematocysts (length x width), in  $\mu\text{m}$ .

Nematocyst type	Undischarged	Discharged
Euryteles I	(8–12) x (5–8) $\mu\text{m}$	9 x 5 $\mu\text{m}$
Euryteles II	(18–21) x (7–8) $\mu\text{m}$	19 x 7 $\mu\text{m}$
Euryteles III	(26–31) x (11–14) $\mu\text{m}$	(27–31) x (12–14) $\mu\text{m}$
Desmonemes	(3–6) x (3–4) $\mu\text{m}$	-

**Table 4.** Distribution of nematocysts across the polymorphic colony.

Nematocyst type	Gastrozooids	Gonozooids	Dactylozooids
Euryteles I	+	+	+
Euryteles II	+	+	-
Euryteles III	+	+	+
Desmonemes	+	-	-

**Remarks.** The present material definitely differs from the current accepted three species belonging to the genus: (i) *Rhysia autumnalis*

Brinckmann, 1965; (ii) *Rhysia fletcheri* Brinckmann-Voss, Lickey and Mills, 1993; (iii) *Rhysia halecii* (Hickson and Gravely, 1907).

*R. autumnalis* (i) appears to be morphologically different from our specimen (this aspect could be affected by how the specimen has been preserved) and its distribution result to be restricted to the Western Mediterranean Sea. Concerning the cnidome, even though Brinckmann (1965) reported the presence of stenoteles in *R. autumnalis*, Schuchert (2008) indicated just the presence of desmonemes (4–5 x 3  $\mu\text{m}$ ) and three size classes of microbasic euryteles (29–31 x 11  $\mu\text{m}$ , 16 x 5–6  $\mu\text{m}$  and 8 x 4–5  $\mu\text{m}$ ) in the type material of this species; medium sized euryteles on the hypostome and smallest ones on tentacles (Cantero, 2015). According to the new description provided by Schuchert (2008), the cnidome of our specimen (Table 3,4, Figure S5) seems to be close to it. In any case, the environmental conditions experienced from this species in the Western Mediterranean (Boero, 1986; Brinckmann, 1965; Brinckmann et al., 1993) surely differ from those ones typifying the Chilean fjords and, thus, we can expect that our specimen is not co-specific to *R. autumnalis* due to the wide zoogeographic separation.

*R. fletcheri* (ii), described from Vancouver Island, British Columbia, Canada, and from Friday Harbor, Washington, U.S.A. (Brinckmann et al., 1993), is recognizable thanks to the lack of dactylozooids, even if Cantero (2015)

reported that “according to Schuchert, it can have tentaculozoids”. Once again, the cnidome of this species differs from that of our specimen (see table 1,2 for measures), having just desmonemes and two classes of euryteles (instead of three) (Brinckmann et al., 1993).

*R. halecii* (iii), whose occurrence has been reported for the Mediterranean Sea and the Antarctic Ocean (Hickson and Gravely, 1907, despite the species belongs to those very rare taxa which have been “missed” in the polar regions for the last 100 years, Ronowicz et al., 2019), is the most similar to our specimen morphologically speaking. However, it exhibits a different cnidome, where isorhizas can be observed (Cantero, 2015). Hirohito (1988) identified its specimen from Sagami Bay, Japan as belonging to *Stylactis halecii* (Hickson and Gravely, 1907), but Brinckmann et al. (1993) pointed out that the differences between the Antarctic and Sagami Bay in terms of environmental factors, such as temperature, can be the cause for which the Japanese species of *Rhysia* is conspecific with the Antarctic *R. halecii*.

In conclusion, the description of our specimen does not fit properly to any of the existing species, and possibly could be a species new for science; nevertheless, the early stage of reproductive structures has not allowed a fully detailed description of the gonozoids.

**Hydroid epibionts.** *Filellum serratum*.

**Records from Chile.** No members of the Rhysiidae family have been previously found in Chile and the present material was collected only from the Puy30 station, at 25 m depth.

### **Suborder Aplanulata Collins, Winkelman, Hadrys and Schierwater, 2005**

Capitate hydrozoans grouped by the synapomorphy of undergoing direct development without the ciliated planula stage that is typical of cnidarians (Petersen, 1990), thus forming a phylogenetically well-supported clade (Collins et al., 2005). It comprises 10 families (WoRMS, 2021).

### **Family Tubulariidae Goldfuss, 1818**

It includes 7 genera (WoRMS, 2021), and the monophyly of the family seems to be supported by both molecular data and morphological features, such as polyps having two sets of tentacles (an aboral and oral whorl, with gonophores developing in between), and medusae often owning a manubrium surrounded by gametogenic tissue (Daly et al., 2007).

Hydroid solitary or colonial. Hydrocaulus usually divided into a distal neck, covered by thin perisarc (secreted from a groove on the hydranth), and a proximal stem, of variable shape, with a basal disc or with stolons covered by thicker perisarc. Hydranth vasiform, characterised by the presence of oral (filiform to pseudofiliform, arranged in one to several closely set whorls) and



aboral tentacles (long, pseudofiliform or filiform, in one whorl). Gonophores as free medusae or fixed sporosacs, often giving rise to an actinula larva (Bouillon et al., 2006).

Some specimens are represented by scarce material; the bad preservation (especially concerning the coenosarc of the hydrocaulus) and the lack of gonophores have not allowed us to identify the species with confidence.

**Material examined.** Mag7-15 (single hydranth reaching 1.5 cm, without gonophores).

### **Genus *Hybocodon* L. Agassiz, 1860**

Hydroid usually solitary, with long stems and an irregularly branched hydrorhiza; tubular hydrocaulus, with open lumen, without parenchyma and longitudinal peripheral canals but weakly divided by eight or more longitudinal endodermic ridges (Bouillon et al., 2006). Perisarc inflated around the whole neck region of the hydranth and originating just below it (secreted from groove between hydranth and neck). Two closely set whorls of filiform to pseudofiliform oral tentacles, usually thicker than those ones forming the unique aboral whorl. Blastostyles bearing gonophores and developing in between oral and aboral tentacles, dichotomously branched (Bouillon et al., 2004; Bouillon et al., 2006).

***Hybocodon chilensis* Hartlaub, 1905**

(Figure S6,S7,S8; Table 5,6)

**Material examined.** Puy5-25 (fertile material, colony composed by 6 polyps and 12 empty hydrocauli), Puy10-15 (fertile material), Puy20-15 (fertile material), Puy26-30 (fertile material), Puy30-20 (fertile material), Mag7-25 (fertile material).

**Description.** Usually solitary polyps, just once a colony has been observed (reaching 5.5 cm in height, sample Puy5-25); in the latter case, hydrocauli are strictly aggregated in the basal part (some cauli adnate to adjacent ones with only the perisarc fused together), even surrounded by a polychaete tube.

Hydranth pear-shaped, with a rather broad base, born on the apex of a long, solitary hydrocaulus (Figure S6:A; Figure S7:A,D).

Hydrocaulus unbranched, tubular along the whole length (slightly enlarging distally), not becoming swollen toward the hydranth base, with a thick and smooth perisarc. Ridges visible through perisarc.

Tubular neck region characterised by a corrugated, annulated, wrinkled perisarc (Figure S6:B).

Tapering hypostome, surrounded by two close whorls of quite thick oral tentacles (up to 1.2 mm long, Figure S6:D, Figure S7:B) and one whorl of

thinner, filiform aboral tentacles, up to 22 (with a maximum observed length of 7 mm). Bases of aboral tentacles continuing as ridges over the basal part of hydranth body.

Gonophores (from which free medusae will be liberated) acorn-shaped, grouped in clusters, and arising between oral and aboral tentacles on unbranched blastostyles (max 8, long up to 2 mm) (Figure S6:C,E,F; Figure S7:B,C).

**Table 5.** Cnidome composition and ranges of dimensions of nematocysts (length x width), in  $\mu\text{m}$ .

Nematocyst type	Undischarged	Discharged
Stenoteles I	(7-9)x(6-8)	(8-9)x(6-8)
Stenoteles II	(11-15)x(10-15)	-
Anisorhizas	(9-13)x(9-13)	(12-13)x(10-11)
Desmonemes	(3-6)x(3-4)	(3-6)x(3-4)
Euryteles	(10-14)x(4-6)	(8-10)x4

**Table 6.** Distribution of nematocysts along the hydranth.

Nematocyst type	Aboral tentacles	Oral tentacles	Gonophores
Stenoteles I	+	+	+
Stenoteles II	- (*)	+	+
Anisorhizas	+	- (*)	- (*)
Desmonemes	+	+	-
Euryteles	+	+	- (*)

\*: possible occurrence due to contamination from the surrounding tissues.

**Remarks.** A detailed redescription of the species has recently been published by Galea (2006). Even though the author has suggested that the identification of species belonging to the genus *Hybocodon* should be based on the medusa stage due to the relative uniformity in hydroid morphology, the analysis of the cnidome (see table 5,6 for measures, Figure S8) has been of

crucial importance in the identification of the species, permitting to overcome the further difficulties given by the absence of fully developed gonophores. The relatively bad preserved material, especially regarding the endoderm of the hydrocauli, has not allowed us to observe clear transverse sections of the stems. In the colonial specimen, the basal portions of different hydrocauli could be loosely aggregated, sometimes adnate to adjacent ones with only the perisarc fused together.

The blastostyles resemble the drawings by Hartlaub (1905), where gonophores were probably in an early developmental stage too. The description of blastostyles fits with that one given by Petersen (1990).

The most developed gonophores are typified by a sort of “lid” at the apex, probably being the future one well-developed marginal tentacle, which characterises the species (Galea, 2006); a hint of the radial canals can be observed too.

It seems to be absent in the superficial brackish layer, being recorded only for depths below 15m.

**Hydroid epibionts.** *Obelia dichotoma*, *Modeeria rotunda*.

**World distribution.** As the etymology of the name suggests, the species has been described for the first time from the Chilean region; however, a New Zealand specimen that Schuchert (1996) ascribed to the species *Hybocodon*

*prolifer* L. Agassiz, 1862 seems instead, according to Galea (2006), belonging to *H. chilensis* on the basis of its cnidome and morphological description. This has determined an extension of the distribution to New Zealand.

**Previous records from Chile.** Calbuco (Hartlaub, 1905), Comau Fjord (Galea, 2006).

## **ORDER LEPTOTHECATA Cornelius, 1992**

The monophyly of Leptothecata is supported from both molecular and morphological phylogenetic analysis (Leclère et al., 2009). The theca, a skeletal covering on polyps (hydrotheca) and on gonophores (gonotheca), represents the synapomorphy of the group, even if in some analyses a theca-less taxon has been identified as the earliest diverging lineage of the group (thus, perhaps, the theca has evolved successively) (Daly et al., 2007).

Hydroids always colonial, provided with a single whorl of tentacles; medusae characterised by shallow bells with gametogenic tissue restricted to the radial canals (Daly et al., 2007).

Due to the lack of well-resolved phylogenetic relationships within the group, today the order is not divided into suborders anymore, even though some authors have tried to propose the establishment of new clades (WoRMS, 2021; Maronna et al., 2016).

### **Family Lafoeidae Hincks, 1868**

It comprises 6 genera (WoRMS, 2021); the family, which was assumed to be monophyletic based on morphological features (Collins et al., 2006), has instead resulted to be polyphyletic (Moura et al., 2011).

Colonial hydroids arising from a creeping hydrorhiza, with either an erect or stolonal pattern; hydrotheca from tubular to campanulate in shape, margin entire, usually without operculum (Bouillon et al., 2006).

Gonophores on fixed sporosacs; gonothecae of most species arranged closely packed in coppinia (Daly et al., 2007; Bouillon et al., 2006).

### **Genus *Filellum* Hincks, 1868**

Hydroid colonial, arising from a creeping filiform hydrorhiza, irregularly branched (usually growing as epibiont). Hydrotheca arising singly from the hydrorhiza; sessile, without diaphragm, tubular and adnate basally, curving upwards in varying degrees distally. Nematothecae or nematophores absent. Gonothecae arranged in coppinia (usually hermaphrodite, with or without hydrothecal protective tubes), closely packed, with lateral walls fused together, or weakly aggregated, not in close contact (Bouillon et al., 2006).

### ***Filellum serratum* (Clarke, 1879)**

(Figure S9, Table 7)

**Material examined.** Puy5-20 (on *Plumularia setacea*), Puy5-25, Puy26-20 (growing on *Halecium fjordlandicum*), Puy26-25, Puy26-30, Puy30-20 (well-structured, fertile colony growing on *Halecium fjordlandicum*), Puy30-25 (growing on *Obelia dichotoma*, *Symplectoscyphus* sp.), Puy30-30, Mag7-20, Mag7-25.

**Description.** Stolonal colony (able to reach even 15.5 mm in height, Figure S9:A) with creeping, irregularly branched, filiform, adhering hydrorhiza. Hydrorhizal tubes with anastomosed perisarc, forming a more or less tight mesh.

Hydrotheca (Figure S9:B) sessile, cylindrical, with basal part adnate to substratum, tubular or slightly flattened, and free part smooth, curving upwards forming different angles with substrate; upper side of the adnate part provided with numerous striae (transverse thickened ridges). Both the adnate adcauline side (clinging to the substratum from one quarter to three quarters of the total length of the theca) and the free adcauline side are very variable in length. Hydrothecal aperture rounded, rim even, usually everted; multiple renovations can be present (even more than 4).

Gonothecae, from which planulae larvae will be released, borne in “onion-shaped” coppiniae (Figure S9:C,D,E); They include a central mass of strictly

arranged, tubular gonothecae (rounded to polygonal in section, with lateral walls fused and distal end truncated), surrounded by an external fence of longer, slightly flattened defensive or accessory tubes. Tubes organized in a single concentric row. A somewhat thin external sheath is directly in contact with the exterior of the coppinia.

Most of gonothecae containing eggs or perhaps already fertilised eggs that were released once the section has been done.

*Table 7. Measurements of Filellum serratum (Clarke, 1879).*

Range		Present study	Galea, 2007	Vervoort, 1972a	Blanco, 1976	Calder, 1991	El Beshbeeshy, 1991	Peña Cantero et al., 2004
Hydrotheca	Free adcauline side	330-975	470-540	331-472	266-419	394-580	394-580	ca 264
	Adnate adcauline side	250-450	188-300	270-400	249-331	270-345	324-464	ca 320
	Abcauline side	230-500	581-675	-	-	-	-	ca 460
	Diameter at rim	80-180	146-153	160-200	136-168	74-130	162-191	ca 125

**Remarks.** The hydrotheca shows both adnate and free adcauline sides deeply variable in length (see table 7 for measures). As reported by Millard (1975), occasionally a few of the hydrothecae rise erect from the substratum with no adnate part.

The fertile colony of the sample Puy30-20 shows 7-8 coppiniae up to 2 mm wide and 1.2 mm high.



The first description of the coppinia of this species was by Ritchie (1911) where he stated that the accessory tubes stand out stiffly from the surface or lie closely arranged to each other, parallel to the surface of the coppinia.

The accessory tubes described by Galea (2007) were arranged in 2 concentric rows, while in the present material just a single row can be observed. Anyway, descriptions provided by Marques et al. (2011) and Galea (2007) mirror the situation provided by our specimen.

Even if *F. serratum* usually grows on other hydroids, its occurrence on polychaete tubes is quite common, but it seems able to colonise macroalgae, octocorals and egg cases (perhaps belonging to some gastropod mollusks) too. It has not been collected from 5 and 10 m depth, probably in relation to its epibiont habit and the availability of organism-substrate.

Since hydrothecae are identical in fertile and sterile colonies we decided to ascribe all the specimens to the same species.

**World distribution.** As Vervoort (2006: 231) and Peña Cantero et al. (1998) noted, *Filellum serratum* is generally conceived as a cosmopolitan species. However, since most of the records are based on inspection of sterile material its actual distribution is unknown.

**Previous records from Chile.** Strait of Magellan (Hartlaub, 1905), Golfo de Ancud (Leloup, 1974). Galea (2007) has collected this species between 42°10' S and 50°50' S.

### **Genus *Lafoea* Lamouroux, 1821**

Hydroid: colony occasionally stolonal but usually erect, branched, with polysiphonic hydrocaulus, terminal branches of hydrocaulus monosiphonic; hydrothecae irregularly arranged, tubular to deeply campanulate, radially to bilaterally symmetrical, pedicellate, usually free from stem or stolon, pedicel generally twisted, sometimes absent, not always well defined, diaphragm absent, hydrothecal base indistinctly separated from the pedicel by a ring of small desmocytes; gonophores as fixed sporosacs, gonothecae aggregated in coppinia with modified tubes (Bouillon et al., 2006).

### ***Lafoea dumosa* (Fleming, 1820)**

(Figure: S10, S27; Table 8)

**Material examined.** Puy5-15 (a fertile colony, on sponges), Puy5-20 (fertile colony), Puy10-15 (fertile colony), Puy14-15, Puy26-20 (fertile colonies growing on octocorals), Puy26-25 (fertile), Puy26-30, Puy30-15,

Puy30-25 (fertile), Mag7-15 (fragmented material), Mag7-20 (fertile), Mag7-25 (fertile).

**Description.** Colonies (Figure S10:A) usually characterized by monosiphonic stolons and/or erect polysiphonic stems (Figure S10:B), irregularly branched, composed of parallel tubes each bearing hydrothecae at irregular intervals, sometimes assuming a pseudo-verticillate arrangement.

Hydrothecae tubular, elongated, narrower basally and with a smooth perisarc, sometimes showing renovations (Figure S10:C); nearly straight shape, with almost parallel walls (usually with the adcauline wall slightly convex or curved downwards; circular rim, sometimes slightly everted.

Hydrothecal pedicels, if present, usually twisted and of variable length.

Gonothecae flask-shaped borne in coppiniae (Figure S10:D), usually surrounded by long defensive accessory tubules arranged in a chaotic manner. Gonothecae polygonal in dorsal view, closely packed with lateral walls fused each other; apical part with distal neck bearing a circular aperture, rim not even.

**Table 8.** *Measurements of Lafoea dumosa (Fleming, 1828).*

Range		Present study	Galea, 2007	Vervoort, 1972a	Rees and Vervoort, 1987 (Stn. 122)	El Beshbeeshy, 1991
Hydrotheca	Length	510-720	554–614	420–500	530–695	371–702
	Maximum width	130-170	143–154	145–150	-	116–139
	Diameter at rim	150-170	162–178	160–175	170–205	109–162
	Pedicel length	100-270	178–218	225–285	130–175	116–278
	Pedicel diameter	60-130	59-67	-	65-80	-
Coppinia	Gonotheca width	105-180	123-160	-	-	-

Gonotheca diameter aperture	30-45	34-38	-	-	-
Diameter auxiliary tubes	100-120	98-108	-	-	-

**Remarks.** *Lafoea dumosa* has rather constant dimensions (see table 8 for measures). Generally, it shows a very high amount of epibionts (Figure S27); in particular, microalgae like diatoms are abundant even in the inner layer of the perisarc. A lot of hydroid epibionts can be observed too, thanks to the diversified habitats created by the colony, increasing the fractal complexity of the environment and providing many different niches which could be exploited. Substrates can be various (*Halecium fjordlandicum*, sponges, polychaetes tubes, octocorals, egg cases probably belonging to some gastropods, bivalve mollusks, crustaceans, algae). Moreover, this species seems to prefer depth below 10 m, occurring in samples collected between 15 and 30 m. The present material morphologically matches the description provided by Galea (2007) and Vervoort (1972a,b).

**Hydroid epibionts.** *Clytia linearis*, *Hebella striata*, *Sertularella* sp., *Bougainvillia muscoides*, *Hydractinia pacifica*.

**World distribution.** *Lafoea dumosa* is widespread, “near-cosmopolitan, being widely distributed in Atlantic, Pacific, and Indian Oceans, penetrating both in Arctic and Antarctic regions (Vervoort and Watson 2003)” (Galea, 2007).

**Previous records from Chile.** Golfo de Ancud, Strait of Magellan (Leloup, 1974), and Trinidad Channel (Hartlaub 1905). Furthermore, Galea (2007) has recorded the presence of the species roughly between 42°10' S and 52°10' S as well.

### **Family Hebellidae Fraser, 1912**

It comprises 6 valid genera (WoRMS, 2021) and it is polyphyletic as demonstrated by Moura et al. (2011).

Daly et al. (2007) has, in fact, previously stressed the absence of diagnostic characters unique to the group.

Hydroid colonial, with campanulate and pedicellate hydrotheca arising from a creeping, tubular hydrorhiza; hydrothecal margin smooth, hydrothecal base marked by a more or less thick diaphragm and the possible presence of an annular perisarc thickening. Gonotheca solitary, arising from the hydrorhiza, sometimes operculate; gonophores as fixed sporosacs, or swimming gonophore, or eumedusoids, or free medusae (Bouillon et al., 2006).

### **Genus *Hebella* Allman, 1888**

Hydroids forming stolonial colony; pedicellate hydrotheca, campanulate to cylindrical in shape, usually with annular thickening and membranous or

perisarc-like diaphragm; gonophores either as liberable eumedusoids with mature “gonads” on radial canals, or as medusa already mature at liberation with 4 radial canals, each with a proximal gonad (Bouillon et al., 2006).

***Hebella striata* Allman, 1888**

(Figure S11, Table 9)

**Material examined.** Puy5-10, Puy14-15 (fertile, on *Symplectoscyphus*), Puy26-20 (on polychaete tubes, *Lafoea dumosa*), Puy 26-25, Puy30-15, Puy 30-25, Mag7-20 (on *Symplectoscyphus filiformis*).

**Description.** Stolonal colonies from a creeping, tubular, smooth hydrorhiza, usually growing on other hydroids (Figure S11:D).

Hydrotheca pedicellate, cylindrical, straight to somewhat bent, with walls almost parallel (Figure S11:A,F); rim circular, slightly everted. Renovations usually absent. Perisarc of the theca characterised by well-marked, closely set striations forming rings, which sometimes could be absent in the distal portion (appearing smooth in this case). Pedicel of variable length, separated from the hydrotheca by an internal peridermal ring; here the hydrotheca begins to widen gradually but distinctly, but without a swollen basal portion.

Gonotheca larger, broader and with less marked striae compared to the hydrotheca especially along the basal part; width increasing distally (Figure S11:B,C), but with walls almost parallel after the first basal third of the

gonotheca. A sort of operculum, composed by 4 flaps arising from a rim constituted by 4 pointed cusps, can be noticed.

*Table 9. Measurements of Hebella striata Allman, 1888.*

Range		Present study	Galea, 2007	Billard, 1914	Vervoort, 1972a	Millard, 1977	El Beshbeeshy, 1991
Hydrotheca	Length	650-1200	699-909	1050-1225	650-700	770-1100	788-1044
	Diameter at rim	200-270	188-233	280-300	190-215	240-310	185-255
	Pedicel length	160-2000	375-1080	260-610	130-335	440-870	139-1450
	Pedicel diameter	50-80	62-68	-	80	-	63-92
Gonotheca	Length	1800	-	-	-	-	-
	Diameter at rim	490	-	-	-	-	-

**Remarks.** Being a typical epibiont, it has been usually observed on other hydroids (*Symplectoscyphus filiformis*, *Obelia dichotoma*, *Lafoea dumosa*), but also on polychaete tubes.

The degree of striation of the hydrotheca is deeply variable, being quite reduced sometimes, especially on the distal portion. The general description of the hydrotheca provided by Vervoort (1972) fits well to our specimens (see table 9 for measures).

Fertile material has been observed just in the sample Puy14-15.

The only description found about *H. striata*'s gonothecae was that one provided by Hartlaub (1905) (here we report the translation from its original work written

in German): “Gonangium, which was still unknown to Allman, resembles that already described by Pictet (1893, 1.c.) with regard to its horn-like curved shape and its medusa formation, only that in *Hebella cylindrica* the curvature is not simply curled, but changes its ritual like a full horn. The gonangia I examined was of an adult; it has no clear stem and a very thick wall; the main curvature lies between the two proximal quarters. The very considerable width decreases towards the distal end. It has no external sculpturing. Its lower half contains the appendages of 4 medusas, the distal half is empty, presumably due to the completion of a fifth, ripe bud. The blastostyle lies close to the strongly curved inner side of the gonotheca, and the medusa buds face the opposite side. The most mature of the medusa buds is bell-shaped and has a fairly long manubrium. Sex products are not recognizable; at the edge of the bell sits a spherical appendage, perhaps a tentacle. The younger gonangium, which contains only a medusa bud, gives the impression that if it continued to grow it had become short, but not detached, stalked”.

The gonothecae of our specimen (table 9) appear to be different from Hartlaub’s material, mainly due to the presence of striae and the well-defined operculum; moreover, in the present material the medusa buds cannot be recognised probably in relation to the bad preservation.



Parasitic habit has been noticed in the sample Puy30-15 (Figure S11:E), with hydrotheca of *H. striata* arising from that one of *S. filiformis*, as previously reported by Galea (2007) (Chilean material, with colony growing in *S. filiformis* too) and El Beshbeeshy (2011) (hydroids collected from the Patagonian shelf, colony of *Hebella striata* growing in *S. subdichotomous*).

**World distribution.** *Hebella striata* shows both a sub-Antarctic and Antarctic distribution, being recorded from Argentine Patagonia (Vervoort 1972; El Beshbeeshy 1991), Tierra del Fuego, Falkland Islands, Peninsula Valdés, Kerguelen and Crozet Islands, Burdwood Bank, Magellan Strait, Pacific coast of Chile (Hartlaub 1905; Leloup 1974; Galea 2007), and Antarctica (El Beshbeeshy, 2011; Galea, 2007; Galea et al., 2007).

**Previous records from Chile.** Golfo de Ancud and Canal Calbuco (Leloup, 1974) probably representing the northern limit of the species; Smythe's Channel, Long Island and Puerto del Hambre (Tierra del Fuego, Hartlaub 1905) (Galea et al., 2014). Moreover, Galea (2007) and Galea et al., 2007a,b have recorded the species roughly from 43°50' S to 52°10' S.

### **Family Plumulariidae McCrady, 1859**

It comprises 12 genera (WoRMS, 2021) and its monophyly has been proved by molecular phylogenetic analysis (Leclère et al., 2007).

The main character distinguishing the family is represented by the attributes of the paired nematothecae, which are either absent or never fused with hydrothecae (Daly et al., 2007).

Hydroids forming upright stems, which could be more or less branched, arising from creeping, root-like or disc-shaped hydrorhiza; hydrocladia alternate, opposite or arranged in verticils. Hydrothecae (borne just on hydrocladia) typically small, uniseriate, at least partially adnate and with the possible presence of marginal cusps. Axillar, cauline or hydrothecal nematothecae usually bithalamic (two-chambered) and movable. Gonophores as fixed sporosacs; gonothecae solitary, without nematothecae, sometimes provided with phylactocarps (Bouillon et al., 2006).

### **Genus *Plumularia* Lamarck, 1816**

Hydroids forming erect colonies (stolonial when epizootic) from a creeping hydrorhiza or anchoring filaments. Hydrocauli usually monosiphonic, without hydrothecae, bearing alternate hydrocladia; the latter generally unbranched, divided into internodes and arranged pinnately or forming a gradual spiral.

Hydrothecae small and cup-shaped, partially or totally adnate, with a circular rim; three hydrothecal nematothecae, one median inferior and two lateral ones, being usually bithalamic and movable.

Gonophores as solitary, unprotected, fixed sporosacs, sometimes exhibiting a sort of “brood chamber” (= acrocyst) (Bouillon et al., 2004; Bouillon et al., 2006).

***Plumularia setacea* (Linnaeus, 1758)**

(Figure S12, Table 10)

**Material examined.** Puy5-10 (fertile), Puy5-15 (fertile), Puy5-20 (fertile, but with few and small gonothecae, probably at an early reproductive stage), Puy10-10, Puy10-15 (fertile), Puy10-20, Puy14-15, Puy20-10 (fertile), Puy20-15 (fertile), Puy20-20, Puy20-25, Puy20-30, Puy26-10, Puy26-15, Puy26-20 (very small colony), Puy26-30, Puy30-10 (fertile), Puy30-15, Puy30-20, Puy30-25, Puy30-30, Mag7-10 (very small colony), Mag7-15, Mag7-20, Mag7-25, Mag7-30.

**Description.** Erect colonies, with a main monosiphonic hydrocaulus from which several alternated hydrocladia arise (Figure S12:B). Hydrorhiza root-like shaped (Figure S12:D). Stem usually divided into internodes without hydrothecae, demarked by straight nodes. Hydrocladia alternate, neither arranged in verticils nor branched, bearing a distal apophysis. Axil of apophysis bearing a nematotheca; another nematotheca inserted on proximal-median part of the internode.

Hydrocladia divided into hydrothecate and non-hydrothecate internodes, the latter shorter than the former and bearing a single central nematotheca (Figure S12:C). Thecate internodes with one hydrotheca and three nematothecae: one mesial inferior and two lateral.

Gonothecae oblong, “leaf-shaped” (sex not clearly recognisable; general measures: 900-1300  $\mu\text{m}$  long, 200-400  $\mu\text{m}$  wide), inserted on apophyses through a short pedicel, sometimes narrowing distally into a neck of varied length with a circular, apical aperture (Figure S12:A).

**Table 10.** *Measurements of Plumularia setacea (Linnaeus, 1758).*

Range		Present study	Galea, 2007	Blanco, 1976	Ramil and Vervoort, 1992 (Stn. CP 149)	Medel and Vervoort, 1995	Vervoort and Watson, 2003 (Stn. B581)
Caulus	Internode length	600-1150	413–549	472–556	350–460	220–480	530–700
	Diameter at node	110-240	283–323	94–136	-	80–160	180–220
Cladium	Hydrothecate segment length	480-660	358–400	-	410–600	240–370	430–520
	Ahydrothecate segment length	200-370	149–185	-	210–320	110–260	225–250
	Diameter at node	50-90	74-93	-	-	50-70	-
Hydrotheca	Diameter lateral nematotheca	50-60	57–64	32–36	20–25	-	34–39
	Length lateral nematotheca	80-110	83–96	60–72	45–70	50–60 73–84	73–84
	Depth	70-150	95-116	-	-	80-110	-
	Diameter at rim	100-140	137–152	126–136	100–115	100–130	100–105

**Remarks.** The species is quite easily recognizable thanks to the pattern of distribution and the number of nematothecae along hydrocladia and hydrocaulus; its morphology varies just a little along the whole Puyuhuapi fjord. Sometimes the species can be found on polychaete tubes.

Gonothecae appearance perfectly resemble that one described by Agís et al., 2001.

No auto-epizootic/epizootic forms have been noticed, even if several authors have observed and described them (Agís et al., 2001; Calder, 1997; Galea and Leclère, 2007; Ramil and Vervoort, 1992; Millard 1973, Vervoort and Watson 2003).

It is widespread along the whole fjord. For measures see Table 10.

**Hydroid epibionts.** *Sertularella tenella* (Puy20-25), *Modeeria rotunda*.

**World distribution.** Cosmopolitan, except in purely Arctic and Antarctic waters (Calder 1997) (Galea, 2007).

**Previous records from Chile.** Guaitecas Islands, Talcahuano, Calbuco and from Tocopilla to Strait of Magellan. In addition, the species was collected roughly between 41°49' S and 50°50' S (Galea, 2007; Galea et al., 2007a,b).

### **Family Sertularellidae Maronna et al., 2016**

The family counts 26 valid genera (WoRMS, 2021).

Hydroids giving rise to erect colonies, which could be either polysiphonic or monosiphonic, branched or unbranched; hydrothecae typified by four marginal cusps and four triangular valves creating a pyramidal operculum (Maronna et al., 2016).

### **Genus *Sertularella* Gray, 1848**

Hydroids forming erect colonies, characterised by hydrocaulus and hydrocladia bearing two longitudinal rows of alternate, sessile hydrothecae. The latter showing a rim provided of 4 marginal cusps, sometimes even submarginal teeth can occur (the number of inner teeth can vary across the same colony); pyramidal operculum composed of 4 triangular flaps, creating a roof-like structure.

Abcauline caecum observed in retracted hydranth.

Gonophores as solitary fixed sporosacs, acrocyst present in some species (Bouillon et al., 2006).

**Remarks.** Species belonging to this genus have shown a distribution limited to the southern part of the fjord (from Mag7 to Puy30), probably because these stations are characterised by major inputs of salty water entering from the southern mouth. In fact, they have usually been found below 15 m depth, being absent in the superficial brackish layer (5-10m).

The material of some specimens was too scarce to be identified with confidence.

**Material examined.** Puy26-20 (a little stolonial colony, with an erect stem bearing 3 hydrothecae and other 2 stolonial pedicellate thecae), Puy26-25 (stolonial fragments bearing pedicellate hydrothecae, growing on *Lafoea dumosa*), Puy30-15 (an erect shoot constituted by 4 hydrothecae), Mag7-30 (a little stem bearing just 3 hydrothecae).

***Sertularella curvitheca* Galea and Schories, 2012**

(Figure S13, Table 11)

**Material examined.** Puy26-30m (an erect colonial fragment, with 2<sup>nd</sup>-order branching), Puy30-20 (many fragments of erect colonies), Puy30-25 (erect colony), Puy30-30 (erect branched colony), Mag7-25.

**Description.** Colonies formed by erect, monosiphonic stems, whitish, with an alternate and coplanar branching pattern (measuring up to 2 cm, Figure S13:A,B). First internode of hydrocladia longer than the others; internodes slightly zigzagging and delimited by somewhat marked nodes sloping in alternate directions, with a hydrotheca or a hydrotheca and a lateral apophysis held on the distal end. Usually, 5 hydrothecae between successive side branches.

Hydrothecae tubular, curving outwards, with the abaxial side mostly straight, becoming convex distally (Figure S13:C,D).

Adnate part of the adcauline side from 1/3 to more than 1/2 of the ordinary internode length.

Free part of the adcauline side quite straight, possibly showing a wavy perisarc, with 3 undulations (usually not visible on the abcauline side).

Rim with 4 pointed cusps separated by moderately deep, semi-circular embayments; pyramidal operculum composed by 4 triangular flaps characterised by many concentric, closely set striations, forming a roof-like structure. Absence of intrathecal, submarginal teeth.

None of the specimens was fertile, therefore gonothecae cannot be described.

*Table 11. Measurements of Sertularella curvitheca Galea and Schories, 2012.*

Range		Present study	Galea and Schories, 2012
Hydrotheca	Free adcauline side	400-600	410-450
	Adnate adcauline side	350-550	375-495
	Abcauline side	550-700	610-655
	Maximum width	360-450	340-395
	Diameter at rim	290-400	290-325
Stem	1° internode length	1650-3250	460-1930
	Internode length	350-1400	880-1320
	Internode diameter	180-390	-

**Remarks.** The present material is quite limited to describe the general pattern of a whole colony.



The absence of internal projections of perisarc constitute a relevant taxonomic diagnostic character, which have allowed us to carry out a preliminary helpful screening of the species belonging to the genus *Sertularella*.

The description given by Galea et al. (2017) fits well to our specimens: the peculiar shape of the hydrothecae (tubular and curving outwards) and the corresponding measures (see table 11 for measures) were crucial for the identification of the species.

**World distribution.** *S. curvitheca* seems to be endemic to the Southern Chilean Region.

**Previous records from Chile.** Región de los Lagos: Fjord Comau (Galea, 2007, as both *S. gayi* and *S. polyzonias*), Gulf of Ancud (Leloup, 1974, as *S. polyzonias*), Seno de Reloncaví (Galea and Schories, 2012). Región de Aysén: Canal Puyuhuapi (Galea et al., 2009, as *S. cf. gayi*); Isla Waller (Galea et al., 2017).

Región de Magallanes y de la Antártica Chilena: Canal Adalberto and Isla Camello (Galea, 2007, as *S. gayi*), Canal Fallos (Galea, 2007, as *S. polyzonias*).

### ***Sertularella tenella* (Alder, 1857)**

(Figure S14, Table 12)

**Material examined.** Puy20-25 (stolonial colony; substratum probably represented by an octocoral), Puy26-30 (a stolonial colony, on *Lafoea dumosa*),

Puy30-25 (stolonal colony growing on *Obelia longissima*,), Mag7-15 (stolonal colony on *Symplectoscyphus filiformis*,), Mag7-20 (stolonal colony on *S. filiformis*,), Mag7-25.

**Description.** Short, erect, monosiphonic, unbranched stems (reaching few centimetres in height, Figure S14:B,D) arising from a creeping hydrorhiza; possible presence of stolonal pedicellate hydrothecae. Colony not uniplanar, with slender, geniculate, and quite long internodes delimited by somewhat marked nodes sloping in alternate directions, with a hydrotheca held on the distal end.

Hydrothecae biseriate, alternated, coplanar; “flask-shaped”, long, characterised, especially in the stolonal form, by the presence of “rings”, visible in lateral view as 4-5 well-marked ribs (in the erect form, the ribs could be less noticeable, recognisable as undulations of the perisarc which could become less marked on the abcauline side)(Figure S14:A,C). Abcauline wall straight to convex, free part of adcauline side quite straight. Adnate part of the adcauline side reaching at maximum 1/3 of the internode length, but usually being much shorter. Absence of intrathecal, submarginal teeth.

Rim moderately everted, provided with 4 pointed cusps separated by deep, semi-circular embayments; pyramidal operculum composed by 4 triangular flaps characterised by concentric striations.

None of the specimens was fertile, therefore gonothecae cannot be described.

**Table 12.** Measurements of *Sertularella tenella* (Alder, 1856).

Range		Present study	Galea,2007
Hydrotheca	Free adcauline side	370-500	385–425
	Adnate adcauline side	250-450	285–385
	Abcauline side	320-650	560–640
	Maximum width	320-410	300–360
	Diameter at rim	270-320	260–300
	Number external ribs	3-4	-
Stem	Internode length	800-2150	785–2500
	Internode diameter	140-180	130-180

**Remarks.** The presence of stolonal hydrothecae, the absence of internal projections of perisarc, the recorded measures (see table 12 for measures), the geniculate pattern and the absence of basal internodal twists are key features which have allowed us to recognise the species as *S. tenella*.

**World distribution.** Near cosmopolitan (Schuchert 2001): European Waters (British Isles and North-West Europe), Gulf of Mexico, North-western Atlantic, Mediterranean Sea (inaccurate report). Scattered records also from New Zealand, Japan, Kerguelen Islands, Chile, Argentina, Western Canada, Venezuela, India (Bay of Bengal) (WoRMS, 2021; OBIS, 2021).

**Previous records from Chile.** Tocopilla (Leloup, 1974, here assigned to *S. geniculata* Hincks, 1874), Reloncaví Sound area (Galea and Schories, 2012).

**Family Symplectoscyphidae Maronna et al., 2016**

The family is divided into 3 accepted genera (WoRMS, 2021), all characterised by an hydrothecal rim constituted by three cusps bearing three valves forming an operculum (Maronna et al., 2016).

**Genus *Symplectoscyphus* Marktanner-Turneretscher, 1890**

Hydroids forming erect colonies, branched or unbranched, characterised by the absence of both a distinct stem and apophyses. Hydrocaulus and hydrocladia bearing alternate hydrothecae in two longitudinal rows.

Thecae sessile, provided with a rim constituted by 3 marginal cusps, usually an adcauline median and two latero-abcauline; 3 triangular flaps forming the operculum.

In some species, an oblique septum supporting the hydranth on the intrathecal wall at the base of hydrotheca can be observed; if the polyp is retracted, an abcauline caecum can be noticed too.

Gonophores as solitary fixed sporosacs; gonothecae normally having spiral or circular ribs, with distal tubular neck (Bouillon et al., 2006).

***Symplectoscyphus filiformis* (Allman, 1888)**

(Figure: S15,S27; Table 13)

**Material examined.** Puy5-10 (fertile), Puy14-15 (fertile), Puy30-15 (fertile), Mag7-10, Mag7-15 (fertile), Mag7-20 (fertile).

**Description.** Colony monosiphonic, branching dichotomously (with branching laying on the same plane), at irregular intervals; main stem not recognisable: branches inserted laterally below stem hydrothecae, thus becoming axillar and introducing a bend in longitudinal axis of stem, giving it a zigzag appearance. Transparent to white in colour.

Sometimes anastomosis between tips of branches of different colonies can be observed.

Nodes indicated by weak constrictions of perisarc, sometimes highlighted by alternated directly sloping lines; each internode bearing a single hydrotheca (or an hydrotheca and an apophysis) on the distal end.

Hydrothecae biseriate, alternate, on the same plane. Hydrotheca smooth (absence of transverse ridges, Figure S15:C), without internal submarginal projections of the perisarc; 3 hydrothecal cusps, 1 adcauline and 2 laterals, joined by deep embayments; operculum composed of 3 triangular flaps, creating a shallow roof-like structure; several renovations possibly present.

Hydrotheca slightly curving outwards, with the adnate part representing from 1/2 to 2/3 of the adcauline side (a distinct inflection point can be noticed where the adcauline wall becomes free); adcauline wall slightly convex, abcauline wall straight to concave (sometimes showing a basal swelling).

Sometimes a foramen can be observed below the hydrothecal base; in some hydrothecae, an oblique septum can be present too, usually recognisable as a row of desmocytes.

Gonothecae generally located below hydrothecae, characterised by transverse (not spirally arranged) frills, usually 8, curving upwards; adnate part flattened (Figure S15:D). Gonotheca joined to the colony through a basal pedicel, usually difficult to see. Terminal tube slender and cylindrical, aperture round on the distal end.

A sexual dimorphism seems to occur (Figure S15:A,B).

**Table 13.** *Measurements of Symplectoscyphus filiformis (Allman, 1888).*

Range		Present study	Galea,2007
Hydrotheca	Free adcauline side	220-400	177-280
	Adnate adcauline side	240-320	222-292
	Abcauline side	320-450	272-385
	Maximum width	200-270	185-220
	Diameter at rim	140-230	139-194
Internodes	Length	480-950	361-687
Gonotheca	Length	1030-1300	824-1028
	Maximum width	700-830	556-742
	Number of frills	8	7-9
	Tube length	150-250	200-300
	Tube diameter at rim	70-130	104-140

**Remarks.** This species usually shows high amounts of epibionts, both on the surface of the perisarc and on the inner layer, especially in the basal part of the colony (older thecae, Figure S27).

Both the shape of the hydrothecae and the morphology of the gonothecae suggest that the present material should belong to *S. filiformis*, even if the recorded tube length is shorter (see table 13 for measures).

In fact, a very important taxonomic diagnostic character for the genus *Symplectoscyphus* is represented by the gonotheca: the presence of a quite long, cylindrical, narrow, terminal tube at its apex have allowed researchers as Galea and Schories, 2012 to distinguish this species from the very similar *S. subdichotomous*.

**Hydroid epibionts.** *Phialella* cf. *quadrata*, *Filellum serratum*, *Modeeria rotunda*, *Bougainvillia pyramidata*, *Sertularella tenella*, *Hebella striata*.

**World distribution.** Even if Galea (2007a) has reported, as Hartlaub 1905 did, that the species is “probably endemic to Chilean Patagonia”, [OBIS \(2021\)](#) records its scattered occurrence from Burdwood Bank, Falklands and South Africa (Millard 1975), Antarctica, British Isles, Japan, New Zealand, North Pacific and along the North-eastern coast of the US as well.

**Previous records from Chile.** Puerto del Hambre (Hartlaub 1905) and roughly between 42°09' S and 43°56' S (H.R. Galea, 2007). Galea et al. 2007a,b hypothesize: “a transition [...] in two members of the genus *Symplectoscyphus*: *S. filiformis* was widely found between 42–44° S, while *S. subdichotomus* totally replaced the former southerly to 47–48° S. However, *S. filiformis* was

originally described from Puerto del Hambre (ca. 53° S, Allman 1888), and Leloup (1974) mentioned *S. subdichotomus* from Calbuco (ca. 41° S)”.

***Symplectoscyphus* sp.**

(Figure S16, table 14)

**Material examined.** Puy30-25 (sterile material, stolonial colony).

**Description.** Stolonial polysiphonic colony, with erect shoots (even longer than 2 cm, Figure S16:A,D) arising from a creeping, tubular hydrorhiza; branched stems without twists on the basal portion.

Internodes geniculate, bearing a hydrotheca on the distal end. Presence of an axillar hydrotheca at the branching point.

Hydrothecae biseriate, alternated and coplanar; elongated, tubular, narrow, with almost parallel walls (Figure S16:B,C). Free adcauline part straight to slightly convex, longer than the adnate side (always less than half of the whole length of the adcauline side). Abcauline side convex. Base of theca straight to oblique. Presence of 3 hydrothecal cusps, 1 adcauline and 2 lateral, separated by deep embayments; operculum composed by 3 smooth triangular flaps, converging in a shallow roof-like structure.

Hydrotheca markedly curving outwards; several renovations can be noticed (which deeply enhance the length of the walls), especially on thecae placed distally on branches.



Gonothecae absent.

*Table 14. Measurements of Symplectoscyphus sp.*

Range		Present study
Hydrotheca	Free adcauline side*	360-500
	Adnate adcauline side	150-300
	Abcauline side*	400-550
	Maximum width	210-270
	Diameter at rim	200-250
Internodes	Lenght	650-1000
	Diameter	150-220
*Measures take into account the renovations of the hydrotheca.		

**Remarks.** The material was sterile, but it significantly differs from the other identified species of the genus, *S. filiformis*, thanks to the geniculate internodes and the elongated and narrower shape of the hydrotheca, curving outwards with a longer free adcauline side and a shorter adnate part (see table 14 for measures).

The geniculate colony silhouette and the peculiar shape of the hydrotheca recall species such as *S. naumovi*, *S. paucicatillus*, *S. pedunculatus*, *S. fasciculatus*, *S. hesperides* (similar pattern, measures not available in literature); *S. johnstoni tropicus* and *S. anae* show an analogous morphology too, but their measures do not fit to our specimen.

Therefore, the lack of gonothecae has not allowed us to clearly identify the specimen: the features of the reproductive material are of key importance in the distinction of the species within the genus *Symplectoscyphus*. A general taxonomic revision about this genus could be very useful to point out all the

main differences, accompanied by a fully detailed and exhaustive redescription of each species.

**Hydroid epibionts.** *Modeeria rotunda*, *Filellum serratum*.

**Records from Chile.** It seems to be confined just to the station Puy30, where it has been collected at 25 m depth.

### **Family Tiarannidae Russell, 1940**

It comprises 7 genera (WoRMS,2021).

Hydroids forming erect or stolonal colonies, with the occurrence of deep, pedicellate or sessile thecae, usually asymmetric and tubular; characteristic operculum composed by “two pleated membranes which meet one another like a gabled roof, with straight ridges above and on the sides of hydrotheca, continuing up at each end, thus all imparting a bilateral symmetry to the distal part of hydrotheca” (Bouillon et al., 2004; Bouillon et al., 2006).

Gonophores as fixed sporosacs; gonothecae similar to hydrothecae, but usually larger (Bouillon et al., 2004; Bouillon et al., 2006).

### **Genus *Modeeria* Forbes, 1848**

Hydroids creating a stolonal, creeping colony, where polyps arise singly at short intervals from hydrorhiza; smooth pedicel of variable length, separated

from the theca through a very thin diaphragm, which could be even absent; hydrothecae smooth, deep and tubular, with margin produced on two sides; operculum of two longitudinally pleated membranes seated in the semi-circular embayments of the margin and meeting another like a gable; gonophores giving rise to free medusae and gonothecae similar to hydrothecae but larger, with or without a short pedicel, and containing up to 4 developing medusae (Bouillon et al., 2006).

***Modeeria rotunda* (Quoy and Gaimard, 1827)**

(Figure S17, Table 15)

**Material examined.** Puy5-20, Puy10-15 (fertile material, on *Lafoea dumosa*), Puy20-20, Puy26-15, Puy26-20 (on *Plumularia setacea*), Puy26-25, Puy26-30, Puy30-15, Puy30-20, Puy30-25 (on *Halopteris schucherti*, *Symplectoscyphus* sp., *Obelia longissima*), Puy30-30, Mag7-20.

**Description.** Stolonal, creeping, unbranched colonies usually showing an epizooic habit (Figure S17:C), especially on *Plumularia setacea*.

Hydrothecae arising at irregular intervals along the hydrorhiza; smooth, tubular with walls almost parallel or somewhat enlarging distally; operculum roof-shaped, articulating with the thecal wall along the curved line of the two-sided margin (Figure S17:A,B).

Hydranth separated from the pedicel (which is smooth and can become broader at the distal end, remaining straight or gently bending), through a thin diaphragm.

Gonotheca characterised by the same shape of the hydrotheca, containing more than one medusa bud.

*Table 15. Measurements of Modeeria rotunda (Quoy and Gaimard, 1827).*

Range		Present study	Galea, 2007	Edwards, 1973	El Beshbeeshy, 1991	Ramil and Vervoort, 1992 (Stn. DW132)	Vervoort, 2006 (Stn. 6062)
Hydrotheca	Length	700-1710	1177–1595	900–1760	250–812	1260–1365	1325–1375
	Width	180-480	284–371	250–380	232–290	345–390	300–325
	Pedicel length	180-1850	663–1860	200–234	670–1090	435–605	875–950
	Pedicel diameter	60-130	76-97	80-110	-	65-75	63-75
Gonotheca	Length	1400-1730	1680	2070–2340	-	2170	1625–1750
	Width	310-550	410	400-430	-	435	290-310

**Remarks.** The hydrothecal dimensions and the pedicel length vary greatly both within our samples and between different studies (see table 15 for measures).

The presence of a diaphragm separating the hydranth from the pedicel has not been reported by Edwards, 1973; as for the rest, the description provided by the author perfectly agrees with the present material.

As pointed out concerning *Filellum serratum*, *M. rotunda* has not been collected from 5 and 10 m depth, probably in relation to the fact that, being an

epibiont, more substrates (= more organisms) are available to be colonised below the superficial brackish layer.

**World distribution.** The species is spread worldwide, occurring in boreal, temperate, subtropical, and tropical parts of Atlantic, Pacific and Indian Oceans; the polyp phase has been able to colonise even Arctic and Antarctic regions (Vervoort 2006; Galea, 2007).

**Previous records from Chile.** Canal Chacao, Golfo de Ancud and Seno Reloncavi (Leloup, 1974) and roughly between 42°10' S and 50°50' S (Galea, 2007). The medusa stage has been recorded from the Strait of Magellan too (Pagès and Orejas 1999).

### **Family Haleciidae Hincks, 1868**

The family includes only 2 genera (WoRMS, 2021).

Hydroids forming stolonial or erect colonies, arising from a creeping hydrorhiza.

Hydrotheca, sessile or pedicellate, very shallow (the polyp, often robust, is not able to retract within it) and lacking of operculum. Hydrothecal rim usually even and flared, hydrothecal base defined by the presence of diaphragm and a ring of large, birefringent desmocytes; renovations common.

Gonophores generally as fixed sporosacs (some species bearing acrocyst), except for *Nemalecium* characterised by swimming gonophores; gonothecae solitary or grouped into a glomulus (Bouillon et al., 2006).

**Genus *Halecium* Oken, 1815**

Hydroids forming branched or unbranched, monosiphonic or polysiphonic colonies, arising from a creeping hydrorhiza; stem and branches divided into internodes, bearing an hydrotheca and a possible apophysis at the distal end. Hydrothecae alternate, shallow, usually with a rim everted and regenerated; basal part marked by the presence of a diaphragm and a ring of desmocytes. Hydranth characterised by “an annular bugle halfway up the gastric column” (Bouillon et al., 2006).

Gonophores as fixed sporosacs, sometimes showing acrocyst; gonothecae either solitary or aggregated into a glomulus, occasionally with gonophoral polyps or arising from within hydrothecae. Typically, a sexual dimorphism can be detected (Bouillon et al., 2006).

***Halecium fjordlandicum* Galea, 2007**

(Figure S18, table 16)

**Material examined.** Puy5-15, Puy5-20, Puy5-25, Puy20-15 (fertile with male gonothecae), Puy20-20, Puy20-25, Puy26-20 (male gonothecae), Puy30-

15 (fertile specimen, bearing both male and female gonothecae), Puy 30-20 (fertile, female gonotheca), Puy30-25, Puy30-30, Mag7-15 (fertile, with both female and male gonothecae), Mag7-20 (fertile), Mag7-25.

**Description.** Largest colony showing a basal polysiphonic stem and grading to monosiphonic at branches (reaching second-order branching)(Figure S18:A).

Internodes slightly geniculate and divided by somewhat oblique nodes. A hydrotheca is present at the distal end of each internode, alternately disposed and kind of pointing forward.

Perisarc of stems and branches relatively thin and transparent, sometimes diatoms or other microorganisms can be observed in the inner layer.

Branches, whose structure is similar to that of caulus, generally alternate, and borne on quite long stem apophyses originating below stem hydrothecae, the latter becoming thus axillar.

Hydrotheca very small and shallow, in which the polyp cannot retract (Figure S18:C); hydrotheca enlarging distally, basally characterised by a diaphragm and a ring of desmocytes, visible as refringent nodules; hydrotheca sometimes borne on short hydrophores diagonally directed. Rim circular and not everted. Renovations observed sometimes.

Hydranth exhibiting a basal ring of cnidocysts around the body.

Sexual dimorphism, with male and female gonothecae borne on different stems (monoecy): male gonotheca “club-shaped” and borne on short, annular pedicels (Figure S18:B,D); female gonotheca “kidney-shaped”, slightly compressed laterally and conical basally, with the "dorsal" side broadly rounded (Figure S18:E).

*Table 16. Measurements of Halecium fjordlandicum Galea, 2007.*

Range		Present study	Galea, 2007	Galea and Schories, 2012
Hydrotheca	Height of hydrotheca	30-50	26-36	-
	Diameter at rim	120-180	130-135	-
	Diameter at base	100-160	115-125	-
Stem internodes	Length	550-800	720–875	-
	Diameter at node	90-180	130–161	-
Branch internodes	Length	580-1040	775–825	-
	Diameter at node	90-130	94–125	-
Male gonotheca	Length	660-1220	-	1060–1315
	Width	240-250	-	200–230
Female gonotheca	Length	1150-1200	-	1165–1280
	Maximum width	550-600	-	410–450

**Remarks.** The pattern of the colony, the morphology of both hydrothecae and gonothecae (see table 16 for measures) and the hydranth shape (characterised by the occurrence of ~22 tentacles and of a nematocyst sheath around the body) strongly resemble those ones observable in the pictures and the descriptions of *H. fjordlandicum* provided by Galea, 2007; Galea et al., 2007a,b; Galea and Schories, 2012.



This species is quite abundant across the whole Puyuhuapi fjord, especially between 15 and 30 m depth. Its occurrence even in the inner part of the fjord (Puy5) may suggest the tolerance of a wide range of salinity, if compared with species such as *Sertularella* spp.

**Hydroid epibionts.** *Filellum serratum*, Bougainvillidae, *Clytia* sp., *Lafoea dumosa*, *Modeeria rotunda*.

**World distribution.** Probably restricted to the Chilean area.

**Previous records from Chile.** *H. fjordlandicum* is probably endemic to the Northern Patagonian zone, occurring from the Reloncaví Sound to Seno Magdalena (Galea and Schories, 2012). It has been collected along the fjord Comau as well (Galea, 2007).

***Halecium* sp. (d'Orbigny, 1842)**

(Figure S19, Table 17)

**Material examined.** Puy30-20 (fertile, polysiphonic, stolonial colony from which two little stems arise), Puy30-25 (fertile colony up to 15 mm, growing on a polychaete tube), Puy30-30 (a stolonial, monosiphonic colony growing on an octocoral).

**Description.** Monosiphonic colonies formed by stolonial hydrothecae or stems (not uniplanar) arising from a creeping, tubular hydrorhiza (Figure

S19:A). Nodes not visible, stem usually dichotomously branched at irregular intervals (Figure S19:C).

Strongly annulated perisarc when a hydrophore or a stem arises from the creeping hydrorhiza or at branching points; axillar hydrothecae usually absent. Each internode, generally quite straight and geniculate, bearing an hydrotheca on the distal end.

Hydrothecae shallow (but deeper if compared with those ones of *H. fjordlandicum*, Figure S19:D), flared, enlarging distally and basally marked with a ring of desmocytes above diaphragm; several renovations can be observed (up to 4). Rim everted and curved outwards. Hydrophores supporting regenerated hydrothecae gradually shorter distally.

Gonothecae, probably female ones, at early stage of development. In some of them, up to 5 little balls are visible within, maybe representing the future eggs (Figure S19:B,E). Gonothecae arising directly from the stolon, or on stems, at base of primary hydrophores on the side branches. Rounded to elliptical in shape, flattened in lateral view, and tapering basally into an elongated pedicel, sometimes covered with perisarc, which could be more or less annulated.

Occurrence of gonothecae at different stages on the same colony, sometimes showing a pore at the apex, probably in those cases where the reproductive development is in a more advanced stage.

*Table 17. Measurements of Halecium sp.*

Range		Present study
Hydrotheca	Height of hydrotheca	50-70
	Diameter at rim	140-170
	Diameter at base	80-100
Internodes	Length	700-1800
	Diameter at node	70-120
Gonothecae*	Length	650-1250
	Maximum width	290-770
*: probably female ones		

**Remarks.** The specimen is different from *Halecium fjordlandicum*, the other previously described species of the genus, mainly for the everted rim of the deeper hydrotheca (see table 17 for measures), the presence of numerous annulations along stems and branches, and for the morphology of gonothecae too.

Our material shows many affinities with the taxon inquirendum *Halecium tehuelchum* (d'Orbigny, 1842); d'Orbigny, 1835-1847 described the species as *Thoa tehuelcha* d'Orbigny, 1842: “Cette espèce est parfaitement caractérisée par ses rameaux filiformes très-déliés, formant des coudes alternatifs sur toute la longueur. De ces coudes partent de petits rameaux latéraux très-ramifiés, mais toujours courts. Les vésicules sont fixées à la base des derniers rameaux; leur figure est pyriforme, tout en se distinguant de l'espèce précédente par leur extrémité tronquée, sans former de tube terminal. Nous l'avons rencontrée jetée à la côte, en Patagonie, non loin de l'embouchure du Rio Negro”.

The present specimen seems to fit well to the description provided by d'Orbigny, 1835-1847 and Galea et al., 2014.

**Hydroid epibionts.** *Sertularella tenella*.

**Records from Chile.** Southernmost part of the Puyuhuapi fjord (site Puy30 at 20, 25 and 30 m depth).

### **Family Halopterididae Millard, 1962**

It is actually divided into 16 valid genera ([WoRMS, 2021](#)) and its monophyly appears to be supported by the molecular phylogenetic analysis conducted by Leclère et al., 2007. A taxonomic feature common to all the species belonging to the group (plesiomorphic character) is the presence of one median nematotheca and a pair of lateral nematotheca associated with each hydrotheca (Daly et al., 2007).

Hydroids showing either hydrocladia arising directly from hydrorhiza or erect hydrocauli (branched or unbranched, monosiphonic or polysiphonic) developing from a creeping or root-like hydrorhiza. Occurrence of hydrothecae on both cauli and cladia. Hydrocladial thecae typically large, with cusped or even rim; hydrocauline thecae well-developed too. Nematothecae present and variable in structure, one- or two-chambered, movable or immovable, usually not fused to hydrothecae or gonothecae (at least borne on the female ones).

Gonophores as fixed sporosacs contained in a simple gonotheca (frequently a sexual dimorphism can be observed); the latter usually solitary, arising from caulus or hydrocladia, neither aggregated nor protected by phylactocarps (Bouillon et al., 2006).

**Genus *Halopteris* Allman, 1877**

Colonies erect, typically forming pinnate cormoids, usually with a monosiphonic unbranched hydrocaulus arising from a creeping hydrorhiza. Hydrocladia alternate or in opposite pairs, or opposite basally and alternate distally, in one plane. Hydrothecae typically cup-shaped, present both on cauli and cladia, margin entire or with one median abcauline cusp; nematothecae polymorphic, movable or immovable, one- or two-chambered, lateral nematothecae typically borne on prominent peduncles adhering to hydrothecal wall. Gonophores as fixed sporosacs, gonothecae arising from hydrocaulus or hydrocladia, solitary, with or without nematothecae (Bouillon et al., 2006).

***Halopteris schucherti* Galea, 2006**

(Figure S20, Table 18)

**Material examined.** Puy20-20 (fertile), Puy20-30 (fertile), Puy26-25 (fertile), Puy30-25 (fertile), Mag7-15, Mag7-20, Mag7-25 (fertile).

**Description.** Colonies up to 2 cm (Figure S20:A), characterised by a feather-like shape, with monosiphonic stems arising from root-like hydrorhizae.

Erect hydrocauli, monosiphonic, unbranched, straight basally, slightly flexuous distally; usually the basal part of caulus devoid of hydrothecae and hydrocladia, while caulus above the basal part homomerously segmented into repeats by oblique nodes.

Some colonies showing branched hydrocladia, with branches arising from internode beside hydrotheca.

Internodes quite long and slender (especially those of hydrocladia), each one bearing an hydrotheca at the proximal end.

Apophysis alternately directed left and right, supporting hydrocladia, without nematothecae.

Hydrotheca cup-shaped, having a circular, straight, not everted rim (Figure S20:D). Abcauline and adcauline walls rather straight in side-view, almost parallel, slightly converging downwards. Adcauline wall adnate for about half of its length.

Cauline nematothecae. (i) One median inferior: below the hydrotheca, generally larger than the others and attached to frontal side of caulus. (ii) Two laterals: not reaching hydrothecal rim, placed on opposite side of caulus on

small apophyses adnate to hydrotheca. (iii) 6–8 above hydrotheca: one of these behind adcauline wall of hydrotheca, distal to axil and projecting above hydrothecal rim; either in median axis of caulus or displaced laterally, singly or in pairs.

Hydrocladial nematothecae (Figure S20:E). (i) One median inferior: below the hydrotheca, generally bigger than the others and attached to frontal side of caulus. (ii) Two laterals: not reaching hydrothecal rim, placed on opposite side of caulus on small apophyses adnate to hydrotheca. (iii) 4-5 above hydrotheca: one of these behind adcauline wall of hydrotheca, distal to axil and overtopping the hydrothecal rim; in one row, on upper side of hydrocladia.

Sometimes female and male gonothecae occurring on the same stem (dioecious colonies), arising laterally below hydrothecae and both showing 2 nematothecae at the level of the pedicel: female gonotheca S-shaped and bigger than male one, the latter slightly curved. Female gonothecae with distal end truncated transversely and provided with circular operculum; proximal end tapering towards base (Figure S20:C); male gonotheca ovate in shape, tapering toward base (Figure S20:B).

*Table 18. Measurements of Halopteris schucherti Galea, 2006.*

Range		Present study	Galea, 2006
Cladium	Diameter	60-120	61-72
	Length of segments	660-930	694-917
Caulus	Diameter	100-190	154–209
	Length of segments	810-1100	1010–1280

Cladial hydrotheca	Free adcauline side	80-160	67-100
	Abcauline side	170-260	167-211
	Diameter at rim	100-200	161-239
	Base width (*=depth)	80-180	*178-217
Cauline hydrotheca	Free adcauline side	80-150	75-100
	Abcauline side	150-260	173-192
	Diameter at rim	160-200	165-195
	Base width (*=depth)	80-160	*175-200
Female gonotheca	Length (diagonal)	650-780	730-790
	Width	350-420	333-394
	Diameter at aperture	210-330	217-256
Male gonotheca	Length	370-440	383-457
	Width	200-250	200-240

**Remarks.** The morphology of gonothecae, the number and pattern of distribution of nematothecae and the shape of hydrothecae have been of crucial importance to recognise the species (see table 18 for measures).

The present material perfectly agrees with the description and the pictures reported by Galea (2014).

The distribution of this species seems to be limited (as for the species belonging to the *Sertularella* genus) to the southern part of the fjord, from Mag7 to Puy30, and at deeper depths, below 15 m, probably in relation to the salinity gradient.

**Hydroid epibionts.** *Modeeria rotunda*.

**World distribution.** Known only from the Chilean fjord region.

**Previous records from Chile.** Fjord Comau, in particular from Punta Huinay (Galea, 2014).



### **Family Campanulariidae Johnston, 1836**

The family comprises 10 accepted genera (WoRMS, 2021), but its phylogenetic monophyly is not supported by molecular analysis (Govindarajan et al. 2006).

Species belonging to this family are morphologically characterised by the presence of a campanulate-shaped theca surrounding the polyp, the latter owning a peduncled hypostome, faired or globose, delimitating a “buccal cavity” (Daly et al., 2007; Bouillon et al., 2006).

Hydroids forming erect or stolonial colonies; hydrotheca generally pedicellate, provided with a rim which could be cusped and a basal diaphragm or an inward annular projection of perisarc.

Gonophores as free medusae, eumedusoids or sporosacs, in gonothecae (Bouillon et al., 2006).

### **Genus *Obelia* Péron and Lesueur, 1810**

Hydroids forming erect colonies, variably flexuous, with well-distinct stolons; internodes usually annulated proximally, supporting distally a pedicellate hydrotheca on apophysis. Hydrotheca bell-shaped to campanulate, showing a radial symmetry, a cusped or even margin and a basal diaphragm, usually oblique. Gonothecae inverted conical, with a raised or truncated apical aperture (Bouillon et al., 2006).

***Obelia dichotoma* (Linnaeus, 1758)**

(Figure: S21,S27; Table 19)

**Material examined.** Puy5-10 (fertile, on crustaceans), Puy5-15 (fertile), Puy5-20, Puy5-25, Puy5-30, Puy10-10 (fertile, growing on a sponge), Puy10-15 (fertile), Puy10-20 (fertile), Puy14-15 (fertile), Puy20-10 (fertile), Puy20-15 (fertile), Puy20-20 (fertile, probably at early-stage of reproductive development), Puy20-25, Puy26-5, Puy26-10 (fertile), Puy26-15 (fertile), Puy26-20 (material a bit ruined), Puy26-25 (fertile), Puy26-30, Puy30-10 (growing on Bryozoa and octocorals), Puy30-15, Puy30-20, Mag7-10 (fertile), Mag7-15 (fertile), Mag7-20, Mag7-25, Mag7-30 (fertile).

**Description.** Sympodial colonies (Figure S21:A,B), loosely fan-shaped, organized on erect, monosiphonic stems (which appear pale to mid brown), irregularly branched (even trichotomously), rising from tubular stolons usually firmly attached to the substratum.

Internodes of various length, usually slender, straight to somewhat geniculate, bearing a terminal annulated pedicellate hydrotheca and one or more apophysis (at the ramification level, supporting subsequent internodes) on the distal end; 5-7 rings present basally.

Pedical of the hydrotheca annulated, with smooth intermediate section if the pedicel length is quite great.

Hydrothecae “truncated cone-shaped”, with length and width variable, but generally flared, enlarging from the base to the rim (Figure S21:D,E). Circular aperture defined by a crenulate rim, with shallow, flat cusps (often difficult to observe).

Basal chamber rather large, separated from the hydrothecal cavity by a transverse or slightly oblique diaphragm if observed in lateral view.

Gonothecae borne on a pedicel marked by 5-8 rings, replacing an axillar hydrotheca; dimensions even more than twice bigger if compared with hydrothecae (Figure S21:C). Elongated conical shape; the rounded top of immature gonothecae becomes flattened with advancing of sexual development, showing a broad, ring-shaped aperture on a low collar.

**Table 19.** Measurements of *Obelia dichotoma* (Linnaeus, 1758).

Range		Present study	Galea, 2007	Gili et al., 1989	El Beshbeeshy, 1991	Cornelius, 1995b	Migotto, 1996	Vervoort and Watson, 2003 (Ralph's slide 2932)
Hydrotheca	Lenght	360-570	518–648	330–480	278–467	300–400	205–400	450–495
	Diameter at rim	270-520	355–501	280–380	255–406	200–250	172–305	280–310
	Pedicel length	300-1300	225–337	240–320	348–742	200–400	169–840	-
Gonotheca	Total length	850-1400	1100–1268	950–1100	-	800–1050	616–912	1150–1395
	Maximum width	240-340	282-310	-	-	230–290	223–320	295–310

Diameter at aperture	90-160	118-141	-	-	-	-	-
Collar length	70-150	130-150	-	-	-	-	-

**Remarks.** The absence of distinct nodes and of perisarc thickening has allowed us to distinguish the species from the similar *Obelia geniculata* and, in general, the morphology of the hydrotheca is crucial for the identification of the species (see table 19 for measures).

The silhouette of the whole colony is deeply variable across the different samples analysed.

The present material fits well to the description of the species given by Vervoort and Watson 2003.

*Obelia dichotoma* seems to be the most widespread species across the Puyuhuapi fjord, both from the bathymetric and the longitudinal point of view. The broad distribution is probably related to the wide tolerance range of environmental conditions and to the intrinsic adaptability of the species: in fact, it is present even in the innermost part of the fjord, characterised by lower salinity and higher sedimentation rates (Puy5, Puy10).

In some cases, the colonies show lots of epibionts (microorganisms like diatoms), both in the inner and on the outer layer of the perisarc.

It is able to colonize several substrates such as polychaetes tubes, crustaceans, sponges and even different hydroids (*Symplectoscyphus filiformis*, *Plumularia setacea*, *Lafoea dumosa*).

**Hydroid epibionts.** *Obelia longissima*.

**World distribution.** It is widespread, displaying a cosmopolitan distribution (Vervoort, 2006; Galea, 2007).

**Previous records from Chile.** Guaitecas Islands, Melinka , Tocopilla, Coquimbo Bay, San Vicente Bay, Seno Reloncavi, Golfo de Ancud (Leloup, 1974). Galea, 2007 has collected the species roughly from 42° to 52° S as well.

### ***Obelia longissima* (Pallas, 1766)**

(Figure S22, Table 20)

**Material examined.** Puy30-10 (fertile), Puy30-25.

**Description.** Sympodial colonies characterised by a long, monosiphonic stem (brown to black) and much shorter side branches, gradually shortening along stem (Figure S22:A,B). Internodes almost straight, long, slender and slightly geniculate, provided by few basal rings (usually 3); apophysis born on the distal end of the internode in case of branching.

Mode of branching quite variable, being even trichotomous.

Pedicel of the hydrotheca annulated, with smooth intermediate section if the pedicel is particularly long.

Hydrothecae campanulate, narrow, tapering toward the base and widening gradually towards the rim, with almost straight walls; aperture circular,

characterized by a hyaline, undulated or shallow castellate rim provided with low, rounded or blunt cusps (Figure S22:D).

Basal chamber fairly narrow, apically delimited by a straight or slightly oblique diaphragm.

Gonothecae borne on a ringed pedicel, replacing a terminal hydrotheca on internode (Figure S22:C); elongated conical, tapering toward the base and widening gradually towards the apex, where the top is flattened and characterised by the presence of a central collar with circular aperture.

*Table 20. Measurements of Obelia longissima (Pallas, 1766).*

Range		Present study	Vervoort and Watson, 2003
Hydrotheca	Length	350-520	280-350
	Diameter at rim	210-370	225-280
	Pedicel length	250-1700	-
Gonotheca	Total length	800-990	645-950
	Maximum width	300-340	195-325
	Diameter at aperture	120-140	110-135
	Collar length	80-110	-

**Remarks.** The hydrothecae of *Obelia longissima* are longer and narrower if compared with those ones of *O. dichotoma* (recalling the etymology of the species name itself, table 20), and recognizable thanks to differences in morphology, especially thanks to the structure of the hydrothecal cusps. The overall colony silhouette is different too.

The ratio “length/diameter at rim” of the hydrotheca is usually bigger than 1.5 considering older thecae (not the younger ones at the apex of the hydrocaulus), while this ratio in the case of *O. dichotoma* is generally lower than 1.5.

The present material well agrees with that provided by Vervoort and Watson 2003.

The species has been observed growing on polychaete tubes and on the congeneric *Obelia dichotoma*.

**Hydroid epibionts.** *Filellum serratum*, *Modeeria rotunda*, *Symplectoscyphus* sp.

**World distribution.** Near cosmopolitan (Vervoort and Watson 2003; Galea and Schories, 2012).

**Previous records from Chile.** Reloncaví Sound and gulfs of Ancud and Corcovado (Hartlaub, 1905; Galea and Schories, 2012; Leloup, 1974), Strait of Magellan (Hartlaub, 1905).

Galea and Schories, 2012 has underlined the fact that this species could be widespread along the whole Chilean coast.

**Genus *Clytia* Lamouroux, 1812**

Hydroids forming reptant, unbranched stolonal or erect branched, usually minute, monosiphonic or polysiphonic colonies; hydrorhiza branched but not anastomosing. Hydrothecae deep, campanulate, characterised by a sinuous or indented rim with clefts between round to sharply-pointed cusps and basally delimited by a diaphragm. Gonophores as free medusae; gonothecae conical and elongated (Bouillon et al., 2004; Bouillon et al., 2006).

***Clytia linearis* (Thorneley, 1900)**

(Figure S23, Table 21)

**Material examined.** Puy5-10, Puy5-15 (fertile), Puy5-20 (fertile), Puy5-25 (fertile), Puy5-30, Puy10-20, Puy14-15, Puy20-20, Puy20-25, Puy20-30, Puy26-10 (fertile), Puy26-20 (fertile, growing on *Lafoea dumosa*), Puy26-25, Puy30-30 (growing on octocorals), Mag7-15 (fertile), Mag7-20 (fertile), Mag7-25.

**Description.** Colonies usually monosiphonic, bearing erect pedicels unbranched or sub-sympodially branched; pedicels (of highly variable length) and branches ringed basally and distally, topped by hydrothecae, sometimes with a smooth intermediate section (Figure S23:A,B).

Hydrotheca very deep, cylindrical, narrow, not enlarging toward the rim, with walls almost straight and parallel, tapering basally (Figure S23:C). Circular aperture characterised by a rim not everted, composed by very pointed cusps



which determine the formation of slight longitudinal ridges along the upper part of the theca (Figure S23:D).

Basal chamber fairly narrow, defined by a thin, straight or slightly oblique diaphragm.

Gonothecae elongate-oval, truncate distally, narrow sub-distally and basally; usually axillar, borne on short and ringed pedicels.

*Table 21. Measurements of Clytia linearis (Thorneley, 1900).*

Range		Present study	Galea, 2007	Millard and Bouillon, 1973 (Praslin)	Calder, 1991	Migotto, 1996	Kelmo and Attrill, 2003	Schuchert, 2003
Hydrotheca	Lenght	550-970	665–870	500–940	736–1244	500–800	760–988	750–1000
	Diameter at rim	230-500	232–335	220–420	326–559	260–410	316–478	350
Gonotheca	Total length	1100-1550	966	1010–1320	1000	950–1110	960–989	1200
	Maximum width	400-560	343	330–430	400	330–400	-	400
	Diameter at aperture	250-400	280	-	325	280-330	330	-

**Remarks.** The ratio between length and diameter at rim of the hydrotheca is generally greater than 2 in the case of *Clytia linearis*, while is usually lower in the case of *C. reloncavia*. Furthermore, considering the theca size (see table 21 for measures), the basal chamber appears bigger than that one of *C. reloncavia*.

The description provided by Ramil and Vervoort, 1992 fits well to our specimens and the gonothecae perfectly resemble the description provided by Bouillon et al., 2004.

The numerous annulations at the base of the hydranth permit the flexure of the polyp, that actually has a curved look.

The species has been often observed on polychaete tubes, and are able to colonise octocorals and other hydroids too (*Plumularia setacea*, *Lafoea dumosa*). It is widespread along the whole fjord both from the latitudinal and the bathymetric points of view.

**World distribution.** Tropical and subtropical waters around the world (Galea 2007).

**Previous records from Chile.** Galea, 2007 has collected the abundant hydroid stage roughly from 42° to 52° S, representing the first report for Chile.

### ***Clytia reloncavia* Galea and Schories, 2012**

(Figure S24, Table 22)

**Material examined.** Puy5-30, Puy14-15, Puy26-20, Puy30-25, Mag7-20, Mag7-25, Mag7-30.

**Description.** Colonies monosiphonic (reaching even more than 2 cm in height, Figure S24:C), bearing erect pedicels unbranched or sub-sympodial

branched, arising from creeping hydrorhiza; pedicels (usually very long) and branches annulated basally and distally (rings shallow and tightly attached each other), topped by hydrothecae, sometimes with a smooth intermediate section and occasional annulations in between (Figure S24:A).

Hydrotheca very big, almost cylindrical, long and wide, not enlarging toward the rim, with walls almost straight and parallel, tapering basally (Figure S24:B,D). Circular aperture characterised by a characteristic rim, not everted and composed by shallow castellate cusps separated by rounded embayments. Basal chamber reduced, quite little (defined by a thin, straight or slightly oblique diaphragm), providing a small hydrothecal base.

Gonothecae not observed.

*Table 22. Measurements of Clytia reloncavia Galea and Schories, 2012.*

Range		Present study	Galea and Schories, 2012
Hydrotheca	Lenght	950-1750	1065–1640
	Diameter at rim	450-1100	475–835
	Pedicel length	1350-4700	-

**Remarks.** The species has been usually observed growing on polychaete tubes.

The present material (see table 22 for measures) well agrees with the description provided by Galea and Schories, 2012: “the habit of the colonies, the large size of the hydrothecae, their characteristic marginal cusps, and the

undulation of the thecal wall, make this species different from its congeners described previously”.

Its bathymetric distribution ranges between 15 and 30 m depth.

**World distribution.** Galea and Schories, 2012 have hypothesized that the species could be endemic to Southern Chile.

**Previous records from Chile.** Reloncaví Sound area and Gulf of Ancud (Galea and Schories, 2012; Leloup, 1974).

***Clytia* sp.**

(Figure S25, Table 23)

**Material examined.** Puy5-10 (fertile), Puy5-15, Puy5-20, Puy10-10, Puy10-15, Puy14-15, Puy20-10, Puy20-15, Puy20-20, Puy20-25 (growing on a polychaete tube), Puy26-15 (growing on octocorals), Puy26-20, Puy26-30, Puy30-15, Puy30-20 (growing on the hydrocaulus of a Tubulariidae, probably *Hybocodon chilensis*) Puy30-25, Mag7-10 (growing on foliose algae and probably on a Vermetidae mollusk shell), Mag7-20, Mag7-25.

**Description.** Colonies monosiphonic (Figure S25:A), bearing erect pedicels unbranched or sub-sympodial branched, arising from creeping hydrorhiza, but more often single stolonal hydrothecae have been found; pedicels and branches annulated basally and distally, topped by hydrothecae,

sometimes with a smooth intermediate section and occasional annulations in between.

Hydrotheca variable in shape, from cylindrical to conical, with walls parallel to slightly diverging distally, tapering basally; perisarc smooth (Figure S25:B).

Circular aperture characterised by a rim not everted, and composed by triangular cusps, with rounded but still pointed tips, separated by deep, rounded embayments (Figure S25:C).

Hydrothecal renovations never observed.

Basal chamber defined by a straight or slightly oblique diaphragm and providing a bigger hydrothecal base if compared with that one of *C. reloncavia*.

Only one gonotheca has been observed (total length: 1250 µm, maximum width: 380 µm, diameter at rim: 300 µm; collar length: 270 µm), similar to those one of *C. linearis*.

*Table 23. Measurements of Clytia sp.*

Range		Present study
Hydrotheca	Length	650-950
	Diameter at rim	250-600
	Pedicel length	570-2550

**Remarks.** The material belonging to this category is probably constituted by young specimens which are still not recognizable as *Clytia reloncavia* or *C. linearis*.

Furthermore, under the name of *Clytia* sp., all the material characterised by intermediate features between *C. reloncavia* and *C. linearis* has been accounted, concerning both the dimensions (see table 23 for measures) of the hydrothecae and the rim. Usually, the present specimens are characterized by thecae wider than *C. linearis*, but not being able to reach the size of *C. reloncavia*, with an intermediate type of rim (undulated but either not pointed or castellate).

In addition, the present material recalls the description of the specimens belonging to *Clytia* sp. provided by (Galea and Schories, 2012).

The specimens were growing on several substrates: polychaete tubes, algae, sponges, octocorals, rocks, and other hydroids (*Plumularia setacea*, *Halecium fjordlandicum*, hydrocaulus of a Tubulariidae).

**Records from Chile.** The present material comes from different stations along the Puyuhuapi Fjord.

### **Family Phialellidae Russell, 1953**

It is a monogeneric family ([WoRMS, 2021](#)). The questionable synapomorphies for the group are represented by “absence of marginal cirri from the medusa and a crease line at the base of the hydrothecal operculum” (Daly et al., 2007).

Hydroids forming erect or stolonal colonies, arising from a creeping hydrorhiza, sympodial. Hydrotheca persistent, pedicellate, tubular to campanulate and characterised by a cone-shaped operculum formed by separate triangular flaps demarcated or not from hydrothecal margin by a basal crease line; hydrotheca basally delimited by a diaphragm. Gonophores as free medusae, gonotheca usually stolonal but sometimes occurring on erect shoot (Bouillon et al., 2006).

**Genus *Phialella* Browne, 1902**

Hydroids forming stolonal or erect colonies; in the latter case, branching irregularly and with a flexuous pattern. Stem and pedicels annulated almost throughout, internodes are not recognisable.

Hydrotheca minute, campanulate, pedicellate and with diaphragm; operculum composed of triangular flaps. Hydranth extensile, owning amphicoronate tentacles. Gonophores as free medusae, gonothecae arising from short annulated pedicel on hydrorhiza or stem (Bouillon et al., 2006).

***Phialella* cf. *quadrata* (Forbes, 1848)**

(Figure S26, Table 24)

**Material examined.** Puy5-10, Puy5-15, Puy14-15 (fertile, erect colonies abundant on *Symplectoscyphus filiformis*), Puy26-15 (stolonial colony growing on octocorals), Mag7-15 (stolonial colony growing on *S. filiformis*)

**Description.** Colonies stolonial (Figure S26:A) or with erect shoots (showing a sympodial growth, reaching up to 0.5 cm, Figure S26:B) arising from a creeping, smooth hydrorhiza.

Perisarc annulated throughout stems and branches, especially at origin of branches, or with portions of smooth or slightly wrinkled perisarc.

Hydrotheca quite small and elongated, widest in the middle and characterised by thin, transparent, smooth walls which taper slightly basally and converge distally (Figure S26:D).

Distal third comprising membranous, conical pleated operculum, composed of several triangular, deep and acute convergent flaps, meeting centrally to form a pointed roof; operculum without crease-line basally (segments not clearly demarcated from the hydrothecal margin). Hydrotheca demarcated from the ringed pedicel through a thin diaphragm. Theca shorter than pedicel in erect stems.

Hydranth sometimes protruding tentacles outside the hydrotheca.



Gonothecae borne on stolon or at branching point on erect shoots, characterised by a short, ringed pedicel; gonothecae large and ovoid, smooth-walled, tapering basally and flattened apically (Figure S26:C).

*Table 24. Measurements of Phialella cf. quadrata (Forbes, 1848).*

Range		Present study	Galea, 2007	Ralph, 1957	Hamond, 1957	Millard and Bouillon, 1973
Hydrotheca	Total length	300-600	236-337	187-340	250	160-310
	Diaphragm to roof	190-420	196-216	-	-	-
	Max. width	100-160	110-163	140	100	80-110
	Roof height	50-200	65-98	-	-	-
	Diaphragm length	50-80	59-67	-	-	-
Pedicel	Length	80-1000	90-333	-	-	80-190
	Diameter	50-60	51-67	-	-	70-80
Gonotheca	Pedicel length	80-100	45	62	-	-
	Length	700-710	750-875	500-680	750	-
	Max. width	270-290	315-375	250	250	-

*Table 24. (continued)*

Range		Cornelius, 1995a	Naumov and Stepanjants, 1962	Vervoort, 1972a	Leloup, 1974	Millard, 1977	El Beshbeeshy, 1991	Blanco et al., 2000a
Hydrotheca	Total length	240-250	200-230	235-270	240-270	210-290	185-293	240-330
	Diaphragm to roof	-	-	-	150-180	-	-	-
	Max. width	100-130	-	90-100	110-120	110-140	69-116	80-120
	Roof height	-	40-42	-	70-100	-	40-92	-
	Diaphragm length	-	-	-	50-70	-	40-52	-
Pedicel	Length	-	-	-	70-100	-	-	-
	Diameter	-	-	-	50	-	-	-
Gonotheca	Pedicel length	-	100-160	-	200-300	-	-	-

Length	750	600-650	-	500-540	-	-	780-1000
Max. width	350-400	400-430	-	240-280	-	-	320-530

**Remarks.** The present material agrees with the redescription of the species provided by Galea, 2007.

The hydrotheca dimensions (see table 24 for measures) are more variable and with a wider range if compared with measures previously reported, probably influenced by the degree of compression of the theca itself. The length of the pedicel is strongly variable too. The stolonial hydrothecae seem to be bigger, probably representing the first thecae of possible future stems.

As pointed out by Galea, 2007, even if *Phialella quadrata* and *P. chilensis* appear to be quite identical from the morphological point of view, “only two medusae belonging to genus *Phialella* have been reported from South America, namely *P. quadrata* [...] and *P. falklandica* [...]”, therefore the present material has been assigned to the species of *P. quadrata*. However, molecular analysis should be carried out to ascertain that the two species (*P. quadrata* and *P. chilensis*) are genetically distinct.

A constant bathymetric pattern could be observed, with the occurrence at 10 or 15 m depth.

**World distribution.** Strait of Magellan, Antarctica, Auckland and Crozet Island, and Japan. Coastal waters of Atlantic and Indo-Pacific Oceans (Galea,

2007). Mediterranean and European waters (e.g., British Isles), New Zealand ([WoRMS, 2021](#)).

**Previous records from Chile.** Calbuco (Hartlaub, 1905), Coquimbo Bay, north of Golfo de Ancud, Strait of Magellan and Seno Ultima Esperanza (Leloup, 1974). Galea, 2007 collected the hydroid stage of the species roughly between 43° and 52° S, while the medusa stage of *P. quadrata* occurs along the entire Chilean coast (Fagetti 1973, Palma et al. 2007).

### *3.3. LITERATURE ANALYSIS*

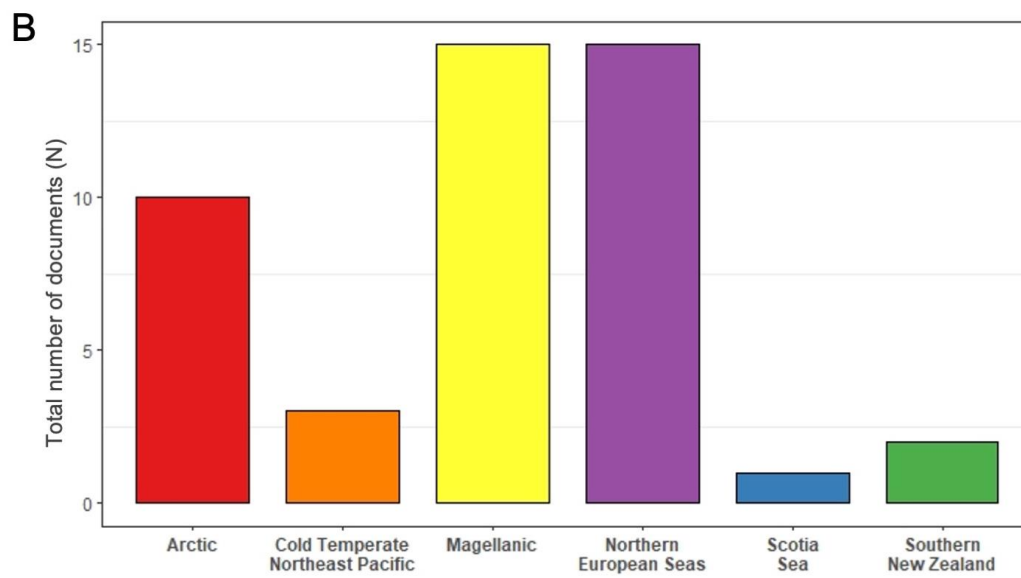
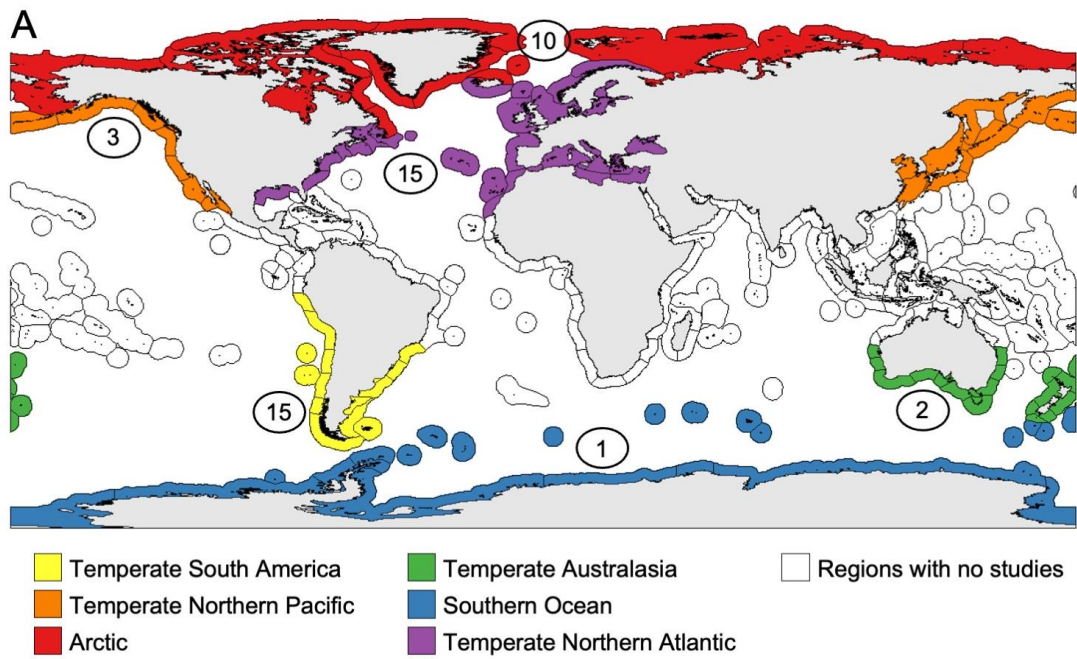
A total of 125 documents have been screened and analysed by reading the title and abstract, using the keywords specified in the Materials and Methods section. Those not following our eligibility criteria were removed, leading to 121 documents; after excluding duplicates, the final number of analysed works was 48 (Figure 1; Table S2).

Considering all the literature found, most of the works have been published from researchers with an affiliation in Chile (13) or Norway (11) (Figure 4). Many documents come from other countries belonging to the Continental Europe, such as Poland (5), Germany (3), France (2), Switzerland (2), Russia (2), Romania (1) and Iceland (1) (figure 2). Just 2 works have been reported for Australia and New Zealand, while a total of 5 articles comes from the North America (4 from USA and 1 from Canada) (Figure 4).



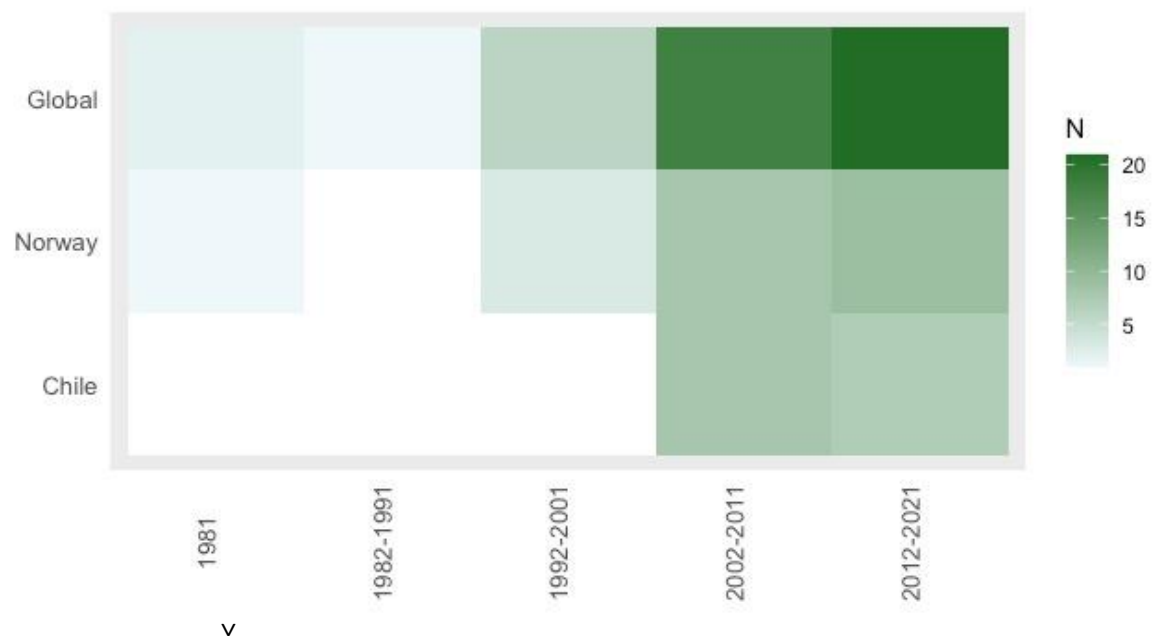
*Figure 4. Map displaying the total number of documents per first authors' affiliation country.*

Considering the marine realms, most of documents were carried out in the Temperate South America (15) and Temperate Northern Atlantic (15), followed by the Arctic (10), the Temperate Northern Pacific (3), the Temperate Australasia (2) and the Southern Ocean (1) (Figure 5A). Inside realms, the most studied provinces were the Magellanic (15), the Northern European Seas (15) and the Arctic (10) (Figure 5B).



*Figure 5. Total number of documents found for each marine realm (A) and province (B).*

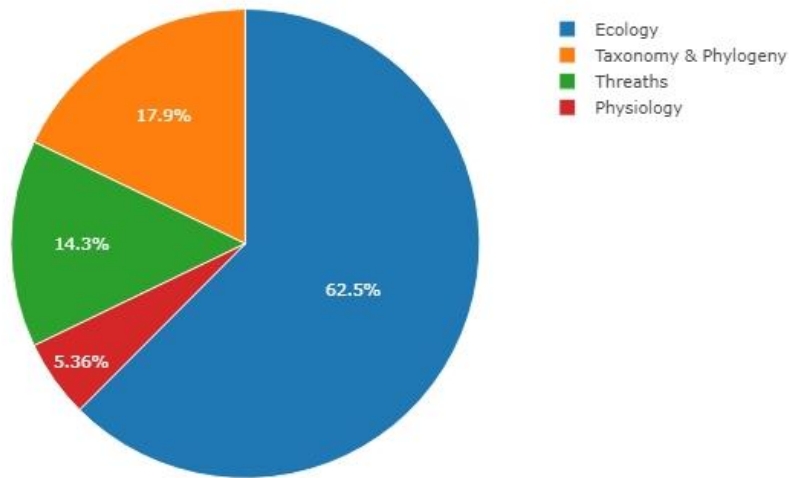
Generally, an increasing trend in the number of documents published through time can be noticed, with the highest number of documents (21) belonging to the last decade, 2012-2021 (Figure 6).



**Figure 6.** Number of documents per decade at global scale, in Norway and in Chile.

Concerning the application fields most of the documents focussed on the ecology (62.5%), especially regarding hydromedusae and Siphonophorae assemblages (Table S2); many other documents emphasize the importance of taxonomy phylogenetic studies (17.9%), while some authors have tried to deepen the knowledge about hydrozoan ecophysiology (5.36%) (Figure 7, Table S2). 14.3% investigates threats to which hydrozoans are usually subjected (Figure 7), involving both direct anthropogenic pressures, such as the harvesting of precious species of commercial interest or the mechanical destruction of animal forests created by habitat formers, and indirect impacts

like those ones due to climate change (in particular, global warming and ocean acidification) and eutrophication (Table S2).

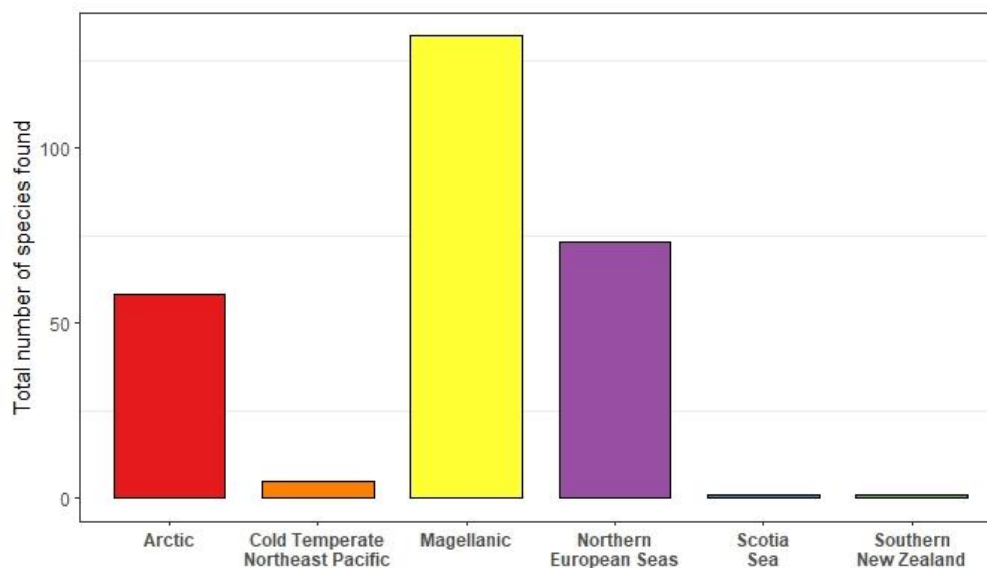


*Figure 7. Percentage contribution of each application field to the bibliographic research.*

From the literature, a total of 222 species belonging to five orders have been recorded, with Leptothecata group constituting the 53.6% of the total number of species found, divided into 24 families (Table S3). The remaining part was composed by Anthoathecata (29.7%, 20 families), Siphonophorae (14.4%, 13 families), Narcomedusae (1.35%, 2 families) and Limnomedusae (0.9%, 2 families) (Table S3). The most represented families for Leptothecata were Campanulariidae (with 25 species), Haleciidae (16), Sertularellidae (13) and Sertulariidae (12), while for Anthoathecata most of the species belonged to Bougainvilliidae (8), Hydractiniidae (7) and Eudendriidae (7). Regarding siphonophores, the Diphyidae family was represented by the highest number of species (8).



The total number of species found for each province reflects well the research effort that has been undertaken in these areas, with 132 species recorded for Magellanic, 73 for the Northern European Seas and 58 for the Arctic, whereas the Cold Temperate Northeast Pacific, the Scotia Sea and the Southern New Zealand count only 5, 1 and 1 species respectively (Figure 8).



*Figure 8. Total number of species per marine province.*

As mentioned in the Materials and Methods, only species listed for the Norwegian and the Chilean fjords were used for a deeper analysis. Concerning documents published over decades, similarly to the trend observed at a global scale, also for the Norwegian and Chilean fjord regions an increment in the number of works through time is detectable (figure 6). However, while for Norway, only in the decade 1982-1991 no documents were found, for Chile documents started to be published only from 2002 (figure 6).

The PERMANOVA analysis revealed significant differences between the two fjord regions (Table 25).

**Table 25.** Results of the one-way PERMANOVA. Analysis of variation in hydrozoan species listed the Norwegian and the Chilean fjords. *df* = degrees of freedom; *SS* = sum of squares; *MS* = mean squares; *Pseudo-F* = *F*-ratio; *P(perm)* = probability; *Up* = unique perms. Significant *p*-values ( $p < 0.05$ ) are given in bold.

Source	df	SS	MS	Pseudo-F	P(perm)	Up
Fi	1	27030	27030	99.273	<b>0.0001</b>	9913
Res	143	3.89E+09	2722.8			
Total	144	4.16E+09				

The average similarity is similar for the two fjord regions, being 10.50% for Chile and 10.15% for Norway (Table 26A). In the first case, the contribution was mainly given by *Errina antarctica* (19.42%), *Obelia dichotoma* (16.85%), *Bougainvillia pyramidata* (16.29%), *Plumularia setacea* (11.51%) and *Clytia linearis* (7.57%) (Table 26A). While, for Norway, a higher number of species contribute to the average similarity, primarily *Campanularia volubilis*, *Lafoea dumosa*, *Aglantha digitale*, *Obelia* spp., *Rathkea octopuntata* and *Symplectoscyphus tricuspoidatus* with values ranging from 9.01% to 5.26% (Table 26B).

**Table 26.** Results of SIMPER analyses (cut-off 70%) used to identify taxa that mostly contribute to hydrozoan faunal similarity within (A) Chilean and (B) Norwegian fjords. *Av.Abund* = mean abundance; *Av.Sim* = mean similarity; *Sim/SD* = similarity/standard deviation; *Contrib%* = contribution relative to single taxon; *Cum%* = cumulative contribution.

Group	Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
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A		Sim%				
Chile	<i>Errina antarctica</i>	0.15	2.04	0.14	19.42	19.42
10.50%	<i>Obelia dichotoma</i>	0.34	1.77	0.32	16.85	36.27
	<i>Bougainvillia pyramidata</i>	0.28	1.71	0.23	16.29	52.56
	<i>Plumularia setacea</i>	0.24	1.21	0.19	11.51	64.06
	<i>Clytia linearis</i>	0.25	0.80	0.23	7.57	71.64

B		Diss%				
Group	Species	Av.Abund	Av.Sim	Sim/SD	Contrib%	Cum.%
Norway	<i>Campanularia volubilis</i>	0.38	0.92	0.38	9.01	9.01
10.15%	<i>Lafoea dumosa</i>	0.34	0.78	0.34	7.64	16.66
	<i>Aglantha digitale</i>	0.28	0.70	0.24	6.86	23.51
	<i>Obelia</i> spp.	0.28	0.70	0.24	6.86	30.37
	<i>Rathkea octopunctata</i>	0.28	0.70	0.24	6.86	37.23
	<i>Symplectoscyphus tricuspidatus</i>	0.31	0.53	0.30	5.26	42.49
	<i>Lensia conoidea</i>	0.24	0.50	0.20	4.96	47.45
	<i>Gonothyraea loveni</i>	0.28	0.47	0.25	4.60	52.05
	<i>Filellum serpens</i>	0.28	0.46	0.26	4.50	56.55
	<i>Orthopyxis integra</i>	0.28	0.40	0.27	3.97	60.52
	<i>Nanomia cara</i>	0.21	0.32	0.17	3.18	63.70
	<i>Sertularia argentea</i>	0.24	0.29	0.23	2.84	66.54
	<i>Sertularella rugosa</i>	0.24	0.28	0.23	2.73	69.27
	<i>Sympagohydra tuuli</i>	0.07	0.25	0.05	2.43	71.70

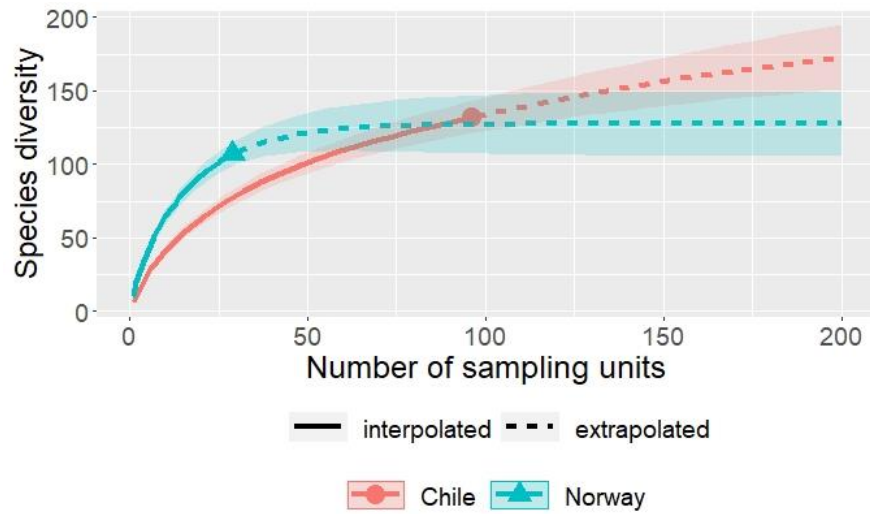
In addition, the SIMPER analysis revealed high dissimilarity in the assemblages associated to the two fjord regions, reaching the 98.72% (Table 27). The dissimilarity was given by various species, but mainly related to *Obelia dichotoma* (3.12%), *Bougainvillia pyramidata* and *Errina antarctica* (2.88% each), and *Plumularia setacea* (2.40%) (Table 27). A large part of the species contributed to between-sites dissimilarity at the analysed fjords, being absent in one of the two (Table 27).

**Table 27.** Results of SIMPER analyses (cut-off 70%) used to identify taxa that mostly contribute to hydrozoan faunal dissimilarity within Chilean and Norwegian fjords. *Av.Abund* = mean abundance; *Av.Diss* = mean dissimilarity; *Diss/SD* = dissimilarity/standard deviation; *Contrib%* = contribution relative to single taxon; *Cum%* = cumulative contribution.

Group	Species	Av.Abund	Av.Abund	Av.Dis	Diss/S	Contrib	Cum.
Diss%		Group	Group	s	D	%	%
		Chile	Norway				
Norway vs. Chile	<i>Obelia dichotoma</i>	0.34	0.03	3.08	0.53	3.12	3.12
98.72%	<i>Bougainvillia pyramidata</i>	0.28	0.00	2.84	0.42	2.88	5.99
	<i>Errina antarctica</i>	0.15	0.00	2.84	0.30	2.88	8.87
	<i>Plumularia setacea</i>	0.24	0.00	2.40	0.38	2.43	11.30
	<i>Lafoea dumosa</i>	0.10	0.34	2.26	0.67	2.29	13.59
	<i>Obelia</i> spp.	0.03	0.28	2.19	0.53	2.21	15.81
	<i>Aglantha digitale</i>	0.00	0.28	2.15	0.52	2.18	17.99
	<i>Rathkea octopunctata</i>	0.00	0.28	2.15	0.52	2.18	20.17
	<i>Lensia conoidea</i>	0.07	0.24	2.07	0.51	2.10	22.27
	<i>Campanularia volubilis</i>	0.00	0.38	2.07	0.69	2.10	24.37
	<i>Sympagohydra tuuli</i>	0.00	0.07	1.92	0.23	1.95	26.31
	<i>Modeeria rotunda</i>	0.17	0.07	1.85	0.29	1.87	28.18
	<i>Clytia linearis</i>	0.25	0.00	1.83	0.45	1.86	30.04
	<i>Gonothyraea loveni</i>	0.00	0.28	1.80	0.40	1.83	31.87
	<i>Ptychogena crocea</i>	0.00	0.10	1.59	0.23	1.61	33.48
	<i>Hybocodon chilensis</i>	0.22	0.00	1.56	0.36	1.58	35.06
	<i>Symplectoscyphus tricuspoidatus</i>	0.00	0.31	1.52	0.62	1.54	36.60
	<i>Nanomia cara</i>	0.00	0.21	1.51	0.42	1.53	38.13
	<i>Filellum serpens</i>	0.00	0.28	1.50	0.54	1.52	39.65
	<i>Orthopyxis integra</i>	0.00	0.28	1.32	0.57	1.34	40.99
	<i>Grammaria abietina</i>	0.03	0.21	1.18	0.46	1.19	42.18
	<i>Phialella quadrata</i>	0.14	0.07	1.14	0.42	1.16	43.34
	<i>Apolemia uvaria</i>	0.00	0.10	1.13	0.19	1.15	44.49
	<i>Sertularia argentea</i>	0.00	0.24	1.10	0.53	1.12	45.61
	<i>Symplectoscyphus filiformis</i>	0.14	0.00	1.07	0.30	1.09	46.70
	<i>Halecium</i> spp.	0.03	0.17	1.07	0.45	1.08	47.78
	<i>Dimophyes arctica</i>	0.06	0.14	1.07	0.38	1.08	48.86
	<i>Sertularella rugosa</i>	0.00	0.24	1.06	0.54	1.07	49.93
	<i>Campanulina pumila</i>	0.01	0.21	1.05	0.44	1.06	51.00
	<i>Calycella syringa</i>	0.02	0.21	1.04	0.49	1.05	52.05
	<i>Hydractinia pacifica</i>	0.11	0.00	1.00	0.26	1.01	53.06
	<i>Halecium arcticum</i>	0.00	0.21	0.96	0.48	0.98	54.04

<i>Halecium mirabile</i>	0.00	0.21	0.96	0.48	0.98	55.01
<i>Tesserogastris musculosa</i>	0.00	0.03	0.96	0.16	0.97	55.99
<i>Laomedea flexuosa</i>	0.00	0.10	0.95	0.29	0.97	56.95
<i>Obelia longissima</i>	0.01	0.17	0.92	0.43	0.93	57.88
<i>Mitrocomella polydiademata</i>	0.00	0.14	0.89	0.31	0.90	58.78
<i>Lafoeina maxima</i>	0.00	0.07	0.84	0.20	0.85	59.63
<i>Cordagalma ordinatum</i>	0.01	0.14	0.84	0.33	0.85	60.48
<i>Eutonina indicans</i>	0.00	0.14	0.79	0.32	0.80	61.29
<i>Halitholus cirratus</i>	0.00	0.07	0.79	0.25	0.80	62.08
<i>Halecium fjordlandicum</i>	0.10	0.00	0.75	0.25	0.76	62.85
<i>Ectopleura dumortierii</i>	0.09	0.00	0.75	0.22	0.76	63.61
<i>Hebella striata</i>	0.13	0.00	0.74	0.33	0.75	64.36
<i>Symplectoscyphus subdichotomus</i>	0.09	0.00	0.71	0.25	0.72	65.08
<i>Eudendrium annulatum</i>	0.00	0.17	0.68	0.45	0.69	65.76
<i>Sertularia cupressoides</i>	0.00	0.17	0.68	0.45	0.69	66.45
<i>Halopteris schucherti</i>	0.09	0.00	0.67	0.21	0.68	67.13
<i>Clytia</i> spp.	0.07	0.03	0.67	0.28	0.68	67.81
<i>Candelabrum phrygium</i>	0.00	0.10	0.65	0.32	0.65	68.47
<i>Sarsia tubulosa</i>	0.00	0.10	0.64	0.23	0.65	69.12
<i>Earleria panicula</i>	0.00	0.07	0.63	0.19	0.64	69.75
<i>Sertularella quasiplana</i>	0.09	0.00	0.58	0.28	0.59	70.34

The extrapolation curves (figure 9) indicate that the sampling effort applied by now to the Chilean region is about more than 3 times bigger than that one carried out in the Norwegian fjords. However, in the latter case, the number of species found per sampling unit is quite high and just a little bit smaller than the value recorded for the other country (figure 9). The extrapolated part of the rarefaction curve representing Norwegian species diversity per sampling unit is almost asymptotic, conversely the sampling effort for the Patagonian zone seems to be still not enough (figure 9).



*Figure 9. Rarefaction curve estimating the captured species diversity for the two analysed countries. Shaded areas represent a confidence interval of 90-95%.*

## Chapter 4

### 4. DISCUSSION

From the present study 26 species typical of hard bottom assemblages were identified (Galea, 2006; Galea et al., 2007; Galea et al., 2007a,b,c, 2014; Galea and Schories, 2012; Galea, 2014). If compared with the work carried out by Galea (2007) based on material collected along almost the entire Chilean fjord region, where the author reported the presence of 63 species, the number of species identified here represents a great number for a quite small sampling area, suggesting a high beta biodiversity in Puyuhuapi Channel.

The most represented species belong to Campanulariidae and Sertulariidae families, in agreement with the observation of Galea et al. (2007a) in the fjord region of southern Chile. In addition, most of the recorded species are cosmopolitan or near-cosmopolitan (Galea, 2007b), while two species are confined to the southern hemisphere: *Hybocodon chilensis*, recorded both in Chile and New Zealand, and *Hebella striata*, showing a Sub-Antarctic and Antarctic distribution (Galea, 2007).

Some of the species identified in this study (*Bougainvillia muscoides*, *Filellum* sp., *Halecium fjordlandicum*, *Hybocodon chilensis*, *Hydractinia* spp., *Modeeria rotunda*, *Obelia dichotoma*, *Plumularia setacea*) were already recorded in Puyuhuapi Channel by Galea et al. (2009), while 16 species

(*Bougainvillia pyramidata*, *Clytia linearis*, *Clytia reloncavia*, *Clytia* spp., *Filellum serratum*, *Halecium* sp., *Halopteris scucherti*, *Hebella striata*, *Lafoea dumosa*, *Obelia longissima*, *Phialella* cf. *quadrata*, *Rhysia* sp., *Sertularella curvitheca*, *Sertularella tenella*, *Sertularella* sp., *Symplectoscyphus filiformis*, *Symplectoscyphus* sp.) were new records for the area. Apart from *Rhysia* sp., which represented also a new record for the Patagonian region, all the other species can be easily found in other Chilean fjords, suggesting that the observed species composition could be influenced by the assemblages of adjacent areas (Galea, 2007; Galea et al., 2007a,b). Currents have a predominant role in structuring benthic communities' composition, thus possibly promoting larval dispersion (Cowen and Sponaugle, 2009). The water column of fjords and channels of Chilean Patagonia is shaped by complex interactions between freshwater run-off and intrusions of the Subantarctic Surface Water (Crawford et al., 2021), which can also influence the connection between adjacent fjords through water movements. However, no detailed hydrographic study, considering also the ecological and genetic connectivity of organisms, has been published so far, making our considerations mere suggestions.

Various species were found settled on polychaete tubes, while species generally belonging to *Obelia* or *Clytia* spp. were observed colonising also bivalves, crustaceans and egg cases (perhaps of some gastropods). Mobile substrates



have an advantage over stable microhabitats, by providing protection against sediment and supplying better water flow conditions for suspension feeders, especially concerning food availability and waste evacuation (Ronowicz et al., 2008). Nonetheless, epizoism on other hydroids was very common, with *Modeeria rotunda*, *Hebella striata*, *Filellum serratum*, *Phialella* cf. *quadrata*, species belonging to genus *Sertularella* and to family Bougainvilliidae and Hydractiniidae growing as epibionts. Algae, octocorals (e.g., *Primnoella chilensis* or *Thouarella* spp.) and bryozoans, considered valuable habitat formers in fjords ecosystems, represented other important secondary substrates (Forsterra et al., 2017), even though more frequently bryozoans have been observed growing on hydroids, as also described by Kukliński and Barnes (2005). The epibiotic habit of hydroids can be seen as an adaptation to face the competition for the space when the primary substrate is already occupied by other organisms, since they compete poorly with other benthic sessile species (Roveta et al., 2022).

A latitudinal-longitudinal gradient in the number of species along the fjord axis was not discernible, in line for what observed for fjords without tidal glaciers (Carney et al., 1999), as the Puyuhuapi Channel is. In fact, it has been demonstrated that, in non-glacial fjords, a lack of a gradient in suspended sediments and water clarity can be found, thus making communities along the

fjords similar to each other (Carney et al., 1999). On the other hand, in fjords with actively retreating tide-water glaciers, suspended sediment levels can be extremely high at the heads and exponentially lower at the mouths, with changes in species composition that are directly correlated to the gradient of water transparency (Carney et al., 1999). This pattern also determines that the highest biodiversity is recorded in sites located furthest from the glacier (Ronowicz et al., 2008, 2011, 2018). However, herein the highest number of species were recorded in the outer station (Puy30), an analogous situation was also observed by Ronowicz et al. (2011) in the benthic hydrozoan fauna of Hornsund, at the Svalbard Islands.

The low sedimentation rates of non-glacier fjords can also help to explain why, contrary to Ronowicz et al. (2011), who highlighted the presence of less-tolerant species belonging to the order Anthoathecata mainly in the outer parts, in Puyuhuapi Channel Anthoathecata species (i.e., *Bougainvillia muscoides*, *Bougainvillia pyramidata*, *Bougainvillia* sp., *Hybocodon chilensis*, Hydractiniidae sp.) were found in the inner sites as well.

Another feature underlining the importance of the distinction between glacier and non-glacier fjords has been provided by Ronowicz et al. (2008): authors observed that sexual reproduction seemed to be inhibited by glacier-derived disturbance, with fertile species at the “clearest” sites bearing fixed

gonophores. The main advantage of this reproductive strategy could be related to the increasing possibilities of keeping subsequent generations near to a favourable habitat (Ronowicz et al., 2008). Instead, along the Puyuhuapi Channel, species in their reproductive period has also been collected from the inner sampling stations, even displaying gonophores developing into free medusae, as demonstrated by the presence of specimens belonging to the genus *Bougainvillia*.

The vertical distribution of hydroids within fjords is well described in the literature (e.g., Smith and Witman, 1999; Voronkov et al., 2010; Ronowicz et al., 2018), and it can be mainly related to the influence of the superficial brackish layer, where generally euryhaline and/or eurythermal species occur (Betti et al., 2017). In fact, in the present study a clear bathymetric gradient can be discerned. In particular, between 0 and 5 m depth just species with a wide tolerance to low salinities, like *Obelia dichotoma* and specimens belonging to the Bougainvillidae family, have been recorded. In general, the euryhaline affinity of species belonging to *Obelia*, *Clytia* and *Bougainvillia* genera are well-known and numerous studies from different geographic areas have underlined this aspect (Calder and Mayal, 1998; Palma et al., 2007; Vannucci et al., 1961), further highlighting their possible threatening role as introduced species easily adaptable to the new local conditions (Ferrapeira, 2011).

However, below the superficial brackish layer, other factors can be involved in shaping the vertical zonation of hydroid assemblages, especially light and water movement, which can deeply affect the shallow water communities (Boero and Fresi 1986; Di Camillo et al. 2008; Puce et al. 2009; Gonzalez-Duarte et al. 2014). As pointed out in other geographical areas (e.g., Gonzalez-Duarte et al., 2014; Roveta et al., 2022), some species occur in a narrow bathymetric range. This pattern is evident also in our study, with the exclusive presence of some hydroids at specific depths: in fact, 2 species (*Bougainvillia muscoides* and Tubulariidae sp.) were limited to the 15 m depth, and other 2 species (*Rhysia* sp. and *Symplectoscyphus* sp.) were exclusively found at 25 m depth.

The seasonal effect is quite clear concerning ice-covered fjords at high latitudes where the glacial melting induced by the sun radiation of the polar summer brings to the release of high freshwater amounts within fjords, determining phytoplankton blooms. In fact, sea ice conditions affect the hydrography and the primary production regime (Weydmann et al., 2013; Wiedmann et al., 2016) and most of the organisms exploits and depends upon this event to grow rapidly and reproduce (Węśławski et al., 1988). However, even non-glacier fjords can be influenced by physical-chemical factors changing during the year, especially concerning freshwater inputs, whose control on coastal temperature and salinity is more evident during winter. (Castillo et al., 2016). The reduced

light radiation during this season may lower the primary production, which in turn will influence the whole food chain leading to a decreased trophic availability. Thus, completely diverse food webs can be observed according both to the temporal and the spatial scale (González et al., 2011). However, this general pattern could be different between the considered areas, showing also a latitudinal gradient, in relation to photoperiods and occurrence of glaciers (González et al., 2011). In addition, other stressors may concur to modify the environmental conditions experienced by fjords' organisms in different seasons, such as the wind direction or the geomorphology of the inlets, having a great relevance in shaping the mixing along the water column (Castillo et al., 2016).

It is known, especially for temperate latitudes, that temperature, light, salinity, sedimentation and competition for the substrate can play an important role in hydroids' seasonality (Bavestrello et al., 2006; Puce et al., 2009; Roveta et al., 2022). Moreover, considering also the pelagic stage, conditions experienced by polyps may be significant in determining the magnitude of medusa production, influencing the benthic-pelagic coupling (Knutsen et al., 2018).

Considering previous studies on the surrounding area, between Corcovado Gulf and Puerto Aysen, all were conducted in the same season of our study (February/March) (Galea et al., 2007a,b, 2009; Galea, 2007), thus allowing a

comparison among datasets. A total of 13 species belonging to Campanulariidae (3), Plumulariidae (1), Tubulariidae (1), Bougainvillidae (2), Haleciidae (1), Tiarannidae (1), Hebellidae (1), Phialellidae (1), Symplectoscyphidae (1) and Lafoeidae (1) were shared between our study and previous species lists.

It is recognized that *Obelia dichotoma* and *Clytia linearis* are perennial species, which could be encountered all over the year, and *Filellum serratum* and *Plumularia setacea* shows a similar pattern too.

For other species the seasonality is known, as reported by Bouillon et al., 2004 for the Mediterranean area, such as spring for *Modeeria rotunda* and summer and autumn for *Phialella quadrata*. However, most of the species in common with the adjacent areas have been just recently discovered (e.g., *Halecium fjordlandicum*, *Clytia reloncavia*) and/or seem to be endemic to the Chilean region, and their ecology is still poorly investigated for this reason.

Concerning the species listed from the literature analysis, hydromedusae of *Obelia* spp., *Clytia* spp. and *Bougainvillia* spp. usually show a wide spatial distribution in both the hemispheres and the abundance they can achieve may be relevant (Bravo et al., 2011; Palma et al., 2014; Sigurðsson et al., 2021). Many families, such as Campanulariidae, Haleciidae, Symplectoscyphidae and Eudendriidae, display congeneric species in southern and northern hemisphere

(e.g., *Halecium arcticum* in Hornsund, Svalbard (M. Ronowicz et al., 2008) and *Halecium fjordlandicum* in Chilean fjords (Galea, 2007)). Instead, other species have been recorded from fjords of both the hemisphere, as happened for *Modeeria rotunda*, *Phialella* cf. *quadrata*, *Obelia longissima*, *Bougainvillia muscoides*, *Lafoea dumosa*, *Sertularella tenella* (Halsband et al., 2018; Hosia and Båmstedt, 2007; Knutsen et al., 2018; M. Ronowicz et al., 2008; A. Voronkov et al., 2010).

From the literature analysis, it has been observed that there is an unbalanced distribution of the studies across the different realms and associated provinces. The pattern can be explained looking at the affiliation of authors investigating the topic: the most studied provinces were the Magellanic, the Northern European Seas and the Arctic, and most of the works have been published from researchers coming from Chile or Norway. A possible explanation can be the growing interest in exploiting fjords as shelter and productive places to set aquaculture facilities, typically present in the most studied regions. In fact, most of the research focused on zooplankton communities (e.g., hydromedusae, siphonophores) has been undertaken to evaluate the possibilities of installing this kind of structures in the investigated areas or to gather baselines for evaluating environmental changes caused by the aquaculture itself (Sigurðsson

et al., 2021). Furthermore, the effects that will arise from the predicted massive expansion of aquaculture in the next few years, mainly toward the Central Patagonian Zone, are noteworthy and must be evaluated (e.g., impacts on *Errina antarctica* assemblages), considering that nowadays the local densities of fish farms are much more higher if compared to Norway (Forsterra et al., 2017). In addition, especially along Norwegian coasts, the occurrence of biofouling communities on kelps (within which hydroids represent one of the main components) is of great concern in macroalgal cultivation, a sector that is gaining interest in Europe due to a general need for ingredients in a number of products such as food, fish diets, cosmetics, pharmaceuticals, biofuel, etc. (Matsson et al., 2019).

However, additional efforts should be made to explore the biodiversity of fjords in the remnant geographic areas (e.g., Alaska, New Zealand) in order to be able to protect them.

It is quite clear the existence of an increasing annual trend concerning publications about the study of the hydrozoan fauna of fjord ecosystems. The growing interest on these communities can be related to: (i) the increased awareness on the importance of having baselines to detect future changes in species composition, richness or abundance overtime (Włodarska-Kowalczyk et al., 2009; Palma et al., 2011; Knutsen et al., 2018); (ii) their noteworthy



ecological and functional role in the benthic-pelagic coupling, able to alter biogeochemical cycles (Di Camillo et al., 2017; Forsterra et al., 2017; Grange et al., 2017).

Several studies spoke about “hydrozoan turf” (see Table S2 for references), focusing their attention at the phylum-level biodiversity, even if it is well-known that responses to changing conditions often take place on species-level (e.g., Algueró-Muñiz et al., 2017), making clear that the taxonomic analysis of hydrozoan communities should be deepened worldwide. Studies focussing on the systematic hydrozoan diversity of fjords have been carried out especially on samples collected along the Patagonian region (Galea et al., 2007a,b,c, 2009, 2014; 2019; Galea, 2006, 2007, 2014; Galea and Schories, 2012), contributing providing detailed descriptions of hydroids and hydromedusae, finding new species, many of which endemic to the region. On the other hand, most of systematic works did not present any ecological information, leading to a reduction in value and attractiveness, with all the useful information on species distribution and diversity often lost (Di Camillo et al. 2018).

Most of the works have an ecological approach (62.5%), especially focused on zooplankton assemblages. The role of gelatinous carnivores (i.e., medusae, siphonophores, ctenophores and organisms belonging to the phylum Urochordata) is increasing day by day, due to the possible impacts on the

trophic chain. In fact, planktonic cnidarians are tactile predator, highly efficient in terms of energy use. They are significant consumers of zooplankton and ichthyoplankton, competing directly and indirectly with fish larvae or juvenile fish, some of which are of commercial interest (Palma et al., 2018) and thus inducing relevant trophic cascading effects as well (Hosia and Båmstedt, 2007). However, aggregations of jellies have also other socio-economic costs and may: (i) clog water intakes of power and desalination plants; (ii) cause a problem for the tourism industry; (iii) negatively impact or hinder fisheries reducing fish catch; (iv) hamper aquaculture production (Båmstedt et al., 1998; Halsband et al., 2018; Knutsen et al., 2018; Matsson et al., 2019).

In many of the ecological documents, lists of species have been provided without specifying useful information like the collection site(s) or depth(s). This aspect avoids the construction of detailed datasets regarding pattern of species richness and distribution, and do not allow a better understanding of organisms' natural history. As already pointed out by Ajala-Batista et al. (2020), studies providing this kind of geographical/temporal data not only improve the data quality, but also facilitate the literature analysis for other researchers (e.g., timesaving in data compilation).

Few documents have investigated how the physiology of different hydrozoan organisms varies according both to natural factors and anthropic influence. The

main faced threats involve both direct anthropogenic pressures, such as the harvesting of precious species of commercial interest (i.e., stylasterid corals) or the mechanical destruction of animal forests (Forsterra et al., 2017; Häussermann et al., 2016; Miller et al., 2004), and indirect impacts like those ones due to climate change (in particular, global warming and ocean acidification) and eutrophication (table S4)(Al-Habahbeh et al., 2020; Algueró-Muñiz et al., 2017; Arai, 2001; Forsterra et al., 2017; Grange et al., 2017; Langer et al., 2017; Ronowicz et al., 2011; Sigurðsson et al., 2021).

Although hydrozoans represent one of the most common groups (e.g., Palma and Silva, 2004; M. Ronowicz et al., 2018), information on Hydrozoa inhabiting fjords ecosystems is scant, fragmentary, and sparse in the literature. This issue led to not consider in statistical analysis most of the fjord regions of the world (Algueró-Muñiz et al., 2017; Carney et al., 1999; Grange et al., 2017; Hartill et al., 2020; Langer et al., 2017; Miller et al., 2004; Schuchert and Reiswig, 2006; Sigurðsson et al., 2021; Smith and Witman, 1999; Zelickman et al., 1969).

The evident difference between Norwegian and Chilean fjords in terms of species composition and number of hydrozoan species is also observed in the formal statistical analyses and underlined by a high average dissimilarity

between the two regions. These results can be explained not only on the bases of environmental filters, but mainly by the distance which separates these ecosystems, being located in opposite hemispheres. The influence of historical biogeographic constraints in determining actual organisms' distribution and regional communities structure may be relevant, leading to speciation events and local adaptations (Leibold et al., 2010; Sanmartín, 2012).

Concerning physical-chemical features, Syvitski and Shaw, 1995 has distinguished between Norwegian mainland and Svalbard fjords. The latter experiences an “arctic desert” climate, with a lower basin water temperature and a lower river discharge, but with a more relevant role of glaciers. On the other hand, Chilean and Norwegian mainland fjords seem to be similar, both subjected to temperate or subarctic maritime climate, higher freshwater amounts and higher temperatures. However, the sedimentation rate appears to have a major role in the Chilean region (Syvitski and Shaw, 1995).

An important contribution in the within group dissimilarity was given by species exclusively found on one of the two fjord regions (see Table 26,27). However, some species have been listed for both areas. Many examples are provided by siphonophores, such as *Muggiaea atlantica*, *Agalma elegans*, *Cordagalma ordinatum*, *Dimophyes arctica* and *Lensia conoidea*. Hydromedusae belonging to *Modeeria rotunda*, *Leuckartiara octona*, *Obelia*

*geniculata*, *O. dichotoma*, *Obelia* spp., *Clytia* spp., *Proboscidactyla stellata*, *Laodicea undulata*, *Euphysa aurata*, *Hydractinia* spp., *Coryne eximia*, *Bougainvillia muscoides*, *Bougainvillia* spp. and *Podocoryna borealis* result to be shared between these regions. All these species show a cosmopolitan or near-cosmopolitan distribution, and their occurrence within inner waters can be linked to the influence of surrounding sea currents and to their possible establishment in the inlets with a permanent population (e.g., *Lensia conoidea* in Norwegian fjords, Pagès et al., 1996).

Low within-group average similarities highlighted by the SIMPER analysis may be also because documents are focused mainly on the benthic or on the pelagic compartment, and this involves the use of completely different sampling strategies, bringing to the collection of almost totally different species (Table 26,27). For instance, siphonophores are not included in studies carried out on benthos, while some hydromedusae can be present under the form of hydroid stage. In addition, within each group both temperate (Norway and Northern-Central Chile) and subpolar/polar fjords (Svalbard and Southern Chile) have been considered, whose different physical characteristics could further increase the variation in terms of species composition (Pearson et al., 1980).

The extrapolated part of the rarefaction curve representing Norwegian species diversity per sampling unit is almost asymptotic, even if the sampling effort applied by now to the Chilean region is about more than 3 times bigger than that one carried out in the Norwegian fjords (Figure 9). Conversely the sampling effort applied to the Patagonian region seems to be still not enough, and this could be explained by the huge extension and complexity of the Patagonian fjords' ecosystem (Forsterra et al., 2017). Beyond the problem linked to the large area which should be investigated, the existence of cryptic species may hamper the goal of reaching a sampling effort able to adequately estimate the actual biodiversity.

Lastly, being fjords enclosed basins, they are more easily subjected to anthropogenic stress and pollution, which could hamper the balance of these delicate ecosystems and monitoring through sentinel species should be constant in order to evaluate their health status and distinguish between natural and induced fluctuations. Hence, these transition environments, between terrestrial ecosystems and the open ocean, should be considered as an Aquatic Critical Zone (ACZ), a sensitive system needing intensive investigation, as proposed by Bianchi et al., 2020.

## Chapter 5

### 5. *CONCLUSIONS*

In conclusion, this work is the first trying to find a correlation between the hydrozoan fauna of different fjords around the world and it represents a major advancement compared to the fragmentary and scattered information previously available, based mostly on local observations. Therefore, we have tried to stress this point, not restricting the research to the mere analysis of Patagonian fjords' hydrozoans but pointing out possible redundant relationships between species diversity/composition and typical fjords' environment, mainly driven by natural factors and/or anthropogenic disturbances. Sedimentation and depth seem to be the most relevant factors in determining species composition and abundance along horizontal and vertical gradients, respectively.

Moreover, the new data from the taxonomic report about hydroids collected along the Puyuhuapi Channel (Aysen region, Chile) contribute to fill a gap of knowledge about the hydroid distribution in the study area, adding new records. As resulted from the species diversity rarefaction curves, the sampling effort applied since now to the Chilean region seems to be still not enough to properly represent the actual biodiversity, with the need of further studies where different kinds of techniques (e.g., plankton and trawl nets, acoustic and optical

investigations, taxonomic and molecular analyses, phylogenetic studies based on DNA barcoding) should be integrated to gather a more comprehensive and holistic point of view based on an ecosystem-approach.

Future research should be focused not only on the quality but even on the quantity of the species present within a study area, because often the species composition of the hydrozoan community could be the same in different periods or between sampling sites, although showing fluctuations concerning biomass. Moreover, impacts can determine specie-specific reactions, which could not be detected at phylum level.

Few investigations have been conducted with the aim of detecting seasonal patterns of fjords' hydroids. It is important to consider that the conditions experienced by the polyps (e.g., increase in temperatures, enhanced food availability) may be significant in determining the magnitude of medusa production with the subsequent determination of possible blooms (Knutsen et al., 2018; Zelickman et al., 1969).

Benthic stages can also colonise buoys and submerged structures of aquaculture facilities, which provide themselves a suitable artificial substrate for the settlement, even of species that can be dangerous and cause fish mortality (Halsband et al., 2018). Large accumulations of gelatinous zooplankton in the fjords may have negative impacts on both fisheries and aquaculture, with mass



occurrence of siphonophores having downsides for local fishermen that depend on the local fjord stocks of fish and shrimps (Knutsen et al., 2018).

Furthermore, protection of the biodiversity within fjords is still challenging and the “formal” establishment of marine reserves is not adequate if it causes the further deterioration of the ecosystems worthy of conservation (e.g., diving activities affecting *Errina novazelandiae* assemblages in Fiordland, New Zealand) (Miller et al., 2004).

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**TABLE S1** - Dataset of the identified species and information about the collection sites.

Site	Latitude	Longitude	Depth (m)	Bougainvillidae sp.	Bougainvillia muscoides	Bougainvillia pyramidata	Hydractiniidae sp.	Rhysia sp.	Tubulariidae sp.	Hybocodon chilensis	Filellum serratum	Lafoea dumosa	Hebella striata	Plumularia setacea	Sertularella sp.	Sertularella curvitheca
Puy5	44° 28' 46" S	072° 39' 11" W	10	1	0	0	0	0	0	0	0	0	1	1	0	0
Puy5	44° 28' 46" S	072° 39' 11" W	15	1	0	0	1	0	0	0	0	1	0	1	0	0
Puy5	44° 28' 46" S	072° 39' 11" W	20	0	0	1	1	0	0	0	1	1	0	1	0	0
Puy5	44° 28' 46" S	072° 39' 11" W	25	1	0	0	0	0	0	1	1	0	0	0	0	0
Puy5	44° 28' 46" S	072° 39' 11" W	30	1	0	0	0	0	0	0	0	0	0	0	0	0
Puy10	44° 35' 01" S	072° 44' 02" W	10	0	0	0	0	0	0	0	0	0	0	1	0	0
Puy10	44° 35' 01" S	072° 44' 02" W	15	0	1	1	0	0	0	1	0	1	0	1	0	0
Puy10	44° 35' 01" S	072° 44' 02" W	20	0	0	0	0	0	0	0	0	0	0	1	0	0
Puy14	44° 38' 34" S	072° 47' 50" W	15	1	0	0	0	0	0	0	0	1	1	1	0	0
Magd7	44° 40' 05" S	072° 47' 55" W	10	0	0	1	0	0	0	0	0	0	0	1	0	0
Magd7	44° 40' 05" S	072° 47' 55" W	15	0	0	0	0	0	1	0	0	1	0	1	0	0
Magd7	44° 40' 05" S	072° 47' 55" W	20	1	0	0	0	0	0	0	1	1	1	1	0	0
Magd7	44° 40' 05" S	072° 47' 55" W	25	1	0	0	0	0	0	1	1	1	0	1	0	1
Magd7	44° 40' 05" S	072° 47' 55" W	30	1	0	0	0	0	0	0	0	0	0	1	1	0
Puy20	44° 45' 01" S	072° 44' 51" W	10	0	0	0	0	0	0	0	0	0	0	1	0	0
Puy20	44° 45' 01" S	072° 44' 51" W	15	0	0	0	0	0	0	1	0	0	0	1	0	0
Puy20	44° 45' 01" S	072° 44' 51" W	20	0	0	0	0	0	0	0	0	0	0	1	0	0
Puy20	44° 45' 01" S	072° 44' 51" W	25	1	0	0	0	0	0	0	0	0	0	1	0	0
Puy20	44° 45' 01" S	072° 44' 51" W	30	0	0	0	0	0	0	0	0	0	0	1	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	5	1	0	0	0	0	0	0	0	0	0	0	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	10	0	0	0	0	0	0	0	0	0	0	1	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	15	1	0	0	0	0	0	0	0	0	0	1	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	20	1	0	0	0	0	0	0	1	1	1	1	1	0
Puy26	44° 51' 53" S	072° 55' 33" W	25	1	0	0	0	0	0	0	1	1	1	0	1	0
Puy26	44° 51' 53" S	072° 55' 33" W	30	0	0	0	0	0	0	1	1	1	0	1	0	1
Puy30	44° 54' 59" S	073° 08' 51" W	10	0	0	0	0	0	0	0	0	0	0	1	0	0
Puy30	44° 54' 59" S	073° 08' 51" W	15	1	0	0	0	0	0	0	0	1	1	1	1	0
Puy30	44° 54' 59" S	073° 08' 51" W	20	1	0	0	0	0	0	1	1	0	0	1	0	1
Puy30	44° 54' 59" S	073° 08' 51" W	25	1	0	0	0	1	0	0	1	1	1	1	0	1
Puy30	44° 54' 59" S	073° 08' 51" W	30	1	0	0	0	0	0	0	1	0	0	1	0	1



**TABLE S1 – continued.**

Site	Latitude	Longitude	Depth (m)	Sertularella tenella	Symplectoscyphus filiformis	Symplectoscyphus sp.	Modeeria rotunda	Halecium fjordlandicum	Halecium sp.	Halopteris schucherti	Obelia dichotoma	Obelia longissima	Clytia linearis	Clytia reloncavia	Clytia spp.	Phialella cf. quadrata
Puy5	44° 28' 46" S	072° 39' 11" W	10	0	1	0	0	0	0	0	1	0	1	0	1	1
Puy5	44° 28' 46" S	072° 39' 11" W	15	0	0	0	0	1	0	0	1	0	1	0	1	1
Puy5	44° 28' 46" S	072° 39' 11" W	20	0	0	0	1	1	0	0	1	0	1	0	1	0
Puy5	44° 28' 46" S	072° 39' 11" W	25	0	0	0	0	1	0	0	1	0	1	0	0	0
Puy5	44° 28' 46" S	072° 39' 11" W	30	0	0	0	0	0	0	0	1	0	1	1	0	0
Puy10	44° 35' 01" S	072° 44' 02" W	10	0	0	0	0	0	0	0	1	0	0	0	1	0
Puy10	44° 35' 01" S	072° 44' 02" W	15	0	0	0	1	0	0	0	1	0	0	0	1	0
Puy10	44° 35' 01" S	072° 44' 02" W	20	0	0	0	0	0	0	0	1	0	1	0	0	0
Puy14	44° 38' 34" S	072° 47' 50" W	15	0	1	0	0	0	0	0	1	0	1	1	1	1
Magd7	44° 40' 05" S	072° 47' 55" W	10	0	1	0	0	0	0	0	1	0	0	0	1	0
Magd7	44° 40' 05" S	072° 47' 55" W	15	1	1	0	0	1	0	1	1	0	1	0	0	1
Magd7	44° 40' 05" S	072° 47' 55" W	20	1	1	0	1	1	0	1	1	0	1	1	1	0
Magd7	44° 40' 05" S	072° 47' 55" W	25	1	0	0	0	1	0	1	1	0	1	1	1	0
Magd7	44° 40' 05" S	072° 47' 55" W	30	0	0	0	0	0	0	0	1	0	0	1	0	0
Puy20	44° 45' 01" S	072° 44' 51" W	10	0	0	0	0	0	0	0	1	0	0	0	1	0
Puy20	44° 45' 01" S	072° 44' 51" W	15	0	0	0	0	1	0	0	1	0	0	0	1	0
Puy20	44° 45' 01" S	072° 44' 51" W	20	0	0	0	1	1	0	1	1	0	1	0	1	0
Puy20	44° 45' 01" S	072° 44' 51" W	25	1	0	0	0	1	0	0	1	0	1	0	1	0
Puy20	44° 45' 01" S	072° 44' 51" W	30	0	0	0	0	0	0	1	0	0	1	0	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	5	0	0	0	0	0	0	0	1	0	0	0	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	10	0	0	0	0	0	0	0	1	0	1	0	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	15	0	0	0	1	0	0	0	1	0	0	0	1	1
Puy26	44° 51' 53" S	072° 55' 33" W	20	0	0	0	1	1	0	0	1	0	1	1	1	0
Puy26	44° 51' 53" S	072° 55' 33" W	25	0	0	0	1	0	0	1	1	0	1	0	0	0
Puy26	44° 51' 53" S	072° 55' 33" W	30	1	0	0	1	0	0	0	1	0	0	0	1	0
Puy30	44° 54' 59" S	073° 08' 51" W	10	0	0	0	0	0	0	0	1	1	0	0	0	0
Puy30	44° 54' 59" S	073° 08' 51" W	15	0	1	0	1	1	0	0	1	0	0	0	1	0
Puy30	44° 54' 59" S	073° 08' 51" W	20	0	0	0	1	1	1	0	1	0	0	0	1	0
Puy30	44° 54' 59" S	073° 08' 51" W	25	1	0	1	1	1	1	1	0	1	0	1	1	0
Puy30	44° 54' 59" S	073° 08' 51" W	30	0	0	0	1	1	1	0	0	0	1	0	0	0

**TABLE S2** - List of selected papers referring to the hydrozoan fauna of fjords, with all details.

Publication year	Authors	Title	DOI/reference	Realm	Ecoregion	Country	Document type	Application field	Analysed level of biodiversity
2021	Sigurðsson G.M., Lüskow F., Gislason A., Svavarsson J.	Summer phenology of the sub-surface gelatinous zooplankton assemblage in two North-Western Icelandic fjords	10.1007/s00300-021-02947-9	Temperate Northern Atlantic	Northern European Seas	Iceland	Article	Ecology, Threats	Species-level
2020	Al-Hababbeh A.K., Kortsch S., Bluhm B.A., Beuchel F., Gulliksen B., Ballantine C., Cristini D., Primicerio R.	Arctic coastal benthos long-term responses to perturbations under climate warming: Climate change impact on Arctic benthos	10.1098/rsta.2019.0355	Arctic	Arctic	Norway	Article	Ecology, Threats	Phylum-level (hydrozoan turf)
2020	Hartil E.C., Walle R.G., Aust P.J.	Deep coral habitats of Glacier Bay National Park and Preserve, Alaska	10.1371/journal.pone.0236945	Temperate Northern Pacific	Cold Temperate Northeast Pacific	Alaska	Article	Ecology	Phylum-level (hydrozoan turf)
2019	Matsson S., Christie H., Fieler R.	Variation in biomass and biofouling of kelp, <i>Saccharina latissima</i> , cultivated in the Arctic, Norway	10.1016/j.aquaculture.2019.03.068	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level
2019	Galea H.R., Schories D., Holtheuer J.	Three new records of hydroids (Cnidaria: Hydrozoa) from southern Chile	10.5281/zenodo.3463457	Temperate South America	Magellanic	Chile	Article	Taxonomy	Species-level
2018	Palma S., Cabello F.,	Siphonophores of the Chiloé Inland Sea: biodiversity, spatial	10.1007/s12526-017-0662-y	Temperate South America	Magellanic	Chile	Article	Ecology	Species-level

	Silva N., Canepa A.	distribution and environmental association							
2018	Pérez-Santos I., Castro L., Ross L., Niklitschek E., Mayorga N., Cubillos L., Gutierrez M., Escalona E., Castillo M., Alegría N., Daneri G.	Turbulence and hypoxia contribute to dense biological scattering layers in a Patagonian fjord system	10.5194/os-14- 1185-2018	Temperate South America	Magellanic	Chile	Article	Ecology	Phylum-level (plankton assemblages)
2018	Martell L., Tandberg A.H.S., Hosia A.	The illusion of rarity in an epibenthic jellyfish: Facts and artefacts in the distribution of <i>Tesserogastria muscolosa</i> (Hydrozoa, Ptychogastridae)	10.1186/s10152- 018-0515-5	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Taxonomy & phylogeny	Species-level
2018	Ronowicz M., Kukliński P., Włodarska- Kowalczyk M.	Diversity of kelp holdfast- associated fauna in an Arctic fjord - inconsistent responses to glacial mineral sedimentation across different taxa	10.1016/j.ecss.201 8.01.024	Arctic	Arctic	Norway	Article	Ecology	Species-level
2018	Knutsen T., Hosia A., Falkenhaug T., Skern- Mauritzen R., Wiebe P.H., Larsen R.B., Aglen A., Berg E.	Coincident mass occurrence of gelatinous zooplankton in Northern Norway	10.3389/fmars.20 18.00158	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level

2018	Halsband C., Majaneva S., Hosia A., Emaus P.A., Gaardsted F., Zhou Q., Nøst O.A., Renaud P.E.	Jellyfish summer distribution, diversity and impact on fish farms in a Nordic fjord	10.3354/meps122 74	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level
2018	Marquardt M., Majaneva S., Pitusi V., Søreide J.E.	Pan-Arctic distribution of the hydrozoan <i>Sympagohydra tuuli</i> ? First record in sea ice from Svalbard (European Arctic)	10.1007/s00300- 017-2219-8	Arctic	Arctic	Norway	Article	Taxonomy & phylogeny	Species-level
2017	Meyer K.S., Sweetman A.K., Kuklinski P., Leopold P., Vogedes D., Berge J., Griffiths C., Young C.M., Renaud P.E.	Recruitment of benthic invertebrates in high Arctic fjords: Relation to temperature, depth, and season	10.1002/Ino.1060 2	Arctic	Arctic	Norway	Article	Ecology	Species-level
2017	Langer J.A.F., Sharma R., Schmidt S.I., Bahrtdt S., Horn H.G., Algueró- Muñiz M., Nam B., Achterberg E.P., Riebesell U., Boersma M.,	Community barcoding reveals little effect of ocean acidification on the composition of coastal plankton communities: Evidence from a long- term mesocosm study in the Gullmar Fjord, Skagerrak	10.1371/journal.p one.0175808	Temperate Northern Atlantic	Northern European Seas	Sweden	Article	Physiology, threats	Phylum-level (plankton assemblages)

	Thines M., Schwenk K.								
2017	Schuchert P., Hosia A., Leclère L.	Identification of the polyp stage of three leptomedusa species using DNA barcoding	10.5281/zenodo.322675	Temperate Northern Atlantic	Northern European Seas	Norway	Review	Taxonomy & phylogeny	Species-level
2017	Grange L.J., Smith C.R., Lindsay D.J., Bentlage B., Youngbluth M.J.	High abundance of the epibenthic trachymedusa <i>Ptychogastris polaris</i> Allman, 1878 (Hydrozoa, Trachylina) in subpolar fjords along the West Antarctic Peninsula	10.1371/journal.pone.0168648	Southern Ocean	Scotia Sea	Antarctica	Article	Taxonomy & phylogeny, Ecology	Species-level
2017	Algueró-Muñiz M., Alvarez-Fernandez S., Thor P., Bach L.T., Esposito M., Horn H.G., Ecker U., Langer J.A.F., Taucher J., Malzahn A.M., Riebesell U., Boersma M.	Ocean acidification effects on mesozooplankton community development: Results from a long-term mesocosm experiment	10.1371/journal.pone.0175851	Temperate Northern Atlantic	Northern European Seas	Sweden	Article	Ecology, Physiology, Threats	Species-level
2017	Försterra G., Häussermann V., Laudien J.	Animal forests in the Chilean fjords: Discoveries, perspectives, and threats in shallow and deep waters	10.1007/978-3-319-21012-4_3	Temperate South America	Magellanic	Chile	Book chapter	Ecology, Threats	Species-level

2016	Palma S., Retamal M.C., Silva N., Canepa A.	Siphonophores in fjords and channels in southern Patagonia: Biodiversity, spatial distribution and environmental association	10.1017/S0025315416001302	Temperate South America	Magellanic	Chile	Article	Ecology	Species-level
2014	Palma S., Córdova P., Silva N., Silva C.	Biodiversity and spatial distribution of medusae in the Magellan Region (Southern Patagonian Zone) [Biodiversidad y distribución especial de las medusas en la región Magallánica (Zona Patagónica Austral)]	10.3856/vol42-issue5-fulltext-21	Temperate South America	Magellanic	Chile	Article	Ecology	Species-level
2014	Palma S., Retamal M.C., Silva N., Silva C.	Horizontal and vertical distributions of siphonophores in relation to oceanographic conditions in Chilean Patagonian fjords [Distribución horizontal y vertical de los sifonóforos en relación con las condiciones oceanográficas en fiordos patagónicos chilenos]	10.3989/scimar.03966.04B	Temperate South America	Magellanic	Chile	Article	Ecology	Species-level
2011	Ronowicz M., Włodarska-Kowalczyk M., Kukliński P.	Patterns of hydroid (Cnidaria, Hydrozoa) species richness and distribution in an Arctic glaciated fjord	10.1007/s00300-011-0999-9	Arctic	Arctic	Norway	Article	Ecology, Threats	Species-level
2011	Bravo V., Palma S., Silva N.	Seasonal and vertical distribution of medusae in Aysén region, southern Chile [Distribución estacional y vertical de	10.3856/vol39-issue2-fulltext-17	Temperate South America	Magellanic	Chile	Article	Ecology	Species-level

		medusas en la región de Aysén, sur de Chile]							
2011	Palma S., Silva N., Cristina Retamal M., Castro L.	Seasonal and vertical distributional patterns of siphonophores and medusae in the Chiloé Interior Sea, Chile	10.1016/j.csr.2010.04.007	Temperate South America	Magellanic	Chile	Article	Ecology	Species-level
2010	Voronkov A., Stepanjants S.D., Hop H.	Hydrozoan diversity on hard bottom in Kongsfjorden, Svalbard	10.1017/S0025315409991573	Arctic	Arctic	Norway	Article	Ecology	Species-level
2009	Galea H.R., Häussermann V., Försterra G.	New additions to the hydroids (Cnidaria: Hydrozoa) from the fjords region of Southern Chile	10.11646/zootaxa.2019.1.1	Temperate South America	Magellanic	Chile	Article	Taxonomy	Species-level
2009	Włodarska-Kowalczyk M., Kukliński P., Ronowicz M., Legeżyńska J., Gromisz S.	Assessing species richness of macrofauna associated with macroalgae in Arctic kelp forests (hornsund, svalbard)	10.1007/s00300-009-0590-9	Arctic	Arctic	Norway	Article	Ecology	Phylum-level (hydrozoan turf)
2008	Ronowicz M., Włodarska-Kowalczyk M., Kuklinski P.	Factors influencing hydroids (Cnidaria: Hydrozoa) biodiversity and distribution in Arctic kelp forest	10.1017/S0025315408001495	Arctic	Arctic	Norway	Article	Ecology	Species-level
2008	Hosia A., Båmstedt U.	Seasonal abundance and vertical distribution of siphonophores in western Norwegian fjords	10.1093/plankt/fbn045	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level

2007	Hosia A., Båmstedt U.	Seasonal changes in the gelatinous zooplankton community and hydromedusa abundances in Korsfjord and Fanafjord, western Norway	10.3354/meps07148	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level
2007	Galea H.R., Försterra G., Häussermann V.	Additions to the hydroids (Cnidaria: Hydrozoa) from the fjords region of southern Chile	10.11646/zootaxa.1650.1.4	Temperate South America	Magellanic	Chile	Article	Taxonomy	Species-level
2007	Galea H.R.	Hydroids and hydromedusae (Cnidaria: Hydrozoa) from the fjords region of southern Chile	<a href="https://www.scopus.com/inward/record.uri?eid=2-s2.0-35448968724&amp;partnerID=40&amp;md5=be2cd01afba7f1c7321157a371437379">https://www.scopus.com/inward/record.uri?eid=2-s2.0-35448968724&amp;partnerID=40&amp;md5=be2cd01afba7f1c7321157a371437379</a>	Temperate South America	Magellanic	Chile	Review	Taxonomy	Species-level
2007	Häussermann V., Försterra G.	Extraordinary abundance of hydrocorals (Cnidaria, Hydrozoa, Stylasteridae) in shallow water of the Patagonian fjord region	10.1007/s00300-006-0207-5	Temperate South America	Magellanic	Chile	Article	Physiology, Threats	Species-level
2006	Galea H.R.	Rediscovery and redescription of <i>Hybocodon chilensis</i> Hartlaub, 1905 (Cnidaria: Hydrozoa) from Comau Fiord, southern Chile	<a href="https://www.scopus.com/inward/record.uri?eid=2-s2.0-33746365865&amp;partnerID=40&amp;md5=2e29c662e0565aceab4cd7b252c49ad3">https://www.scopus.com/inward/record.uri?eid=2-s2.0-33746365865&amp;partnerID=40&amp;md5=2e29c662e0565aceab4cd7b252c49ad3</a>	Temperate South America	Magellanic	Chile	Article	Taxonomy	Species-level



2006	Schuchert P., Reiswig H.M.	Brinckmannia hexactinellidophila, n. gen., n. sp.: A hydroid living in tissues of glass sponges of the reefs, fjords, and seamounts of Pacific Canada and Alaska	10.1139/Z06-031	Temperate Northern Pacific	Cold Temperate Northeast Pacific	Alaska, Canada	Article	Taxonomy & phylogeny	Species-level
2005	Kukliński P., Barnes D.K.A.	Microhabitat diversity of Svalbard Bryozoa	10.1080/0022293 0400001350	Arctic	Arctic	Norway	Article	Ecology	Phylum-level (hydrozoan turf)
2004	Palma S., Silva N.	Distribution of siphonophores, chaetognaths, euphausiids and oceanographic conditions in the fjords and channels of southern Chile	10.1016/j.dsr2.20 04.05.001	Temperate South America	Magellanic	Chile	Conference paper	Ecology	Species-level
2004	Miller K.J., Mundy C.N., Chadderton W.L.	Ecological and genetic evidence of the vulnerability of shallow- water populations of the stylasterid hydro coral Errina novaezelandiae in New Zealand's fiords	10.1002/aqc.597	Temperate Australasia	Southern New Zealand	New Zealand	Conference paper	Physiology, Threats	Species-level
2003	Birkely S.- R., Gulliksen B.	Feeding ecology in five shrimp species (Decapoda, Caridea) from an arctic fjord (Isfjorden, Svalbard), with emphasis on Sclerocrangon boreas (Phipps, 1774)	10.1163/1568540 03322381513	Arctic	Arctic	Norway	Article	Ecology	Phylum-level (hydrozoan turf)
2001	Arai M.N.	Pelagic coelenterates and eutrophication: A review	10.1023/A:10118 40123140	-	-	-	Conference paper	Ecology	Species-level

2000	Gorsky G., Flood P.R., Youngbluth M., Picheral M., Grisoni J.-M.	Zooplankton distribution in four western Norwegian fjords	10.1006/ecss.1999.0540	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Phylum-level (plankton assemblages)
1999	Carney D., Oliver J.S., Armstrong C.	Sedimentation and composition of wall communities in Alaskan fjords	10.1007/s003000050388	Temperate Northern Pacific	Cold Temperate Northeast Pacific	Alaska	Article	Ecology	Phylum-level (hydrozoan turf)
1999	Smith F., Witman J.D.	Species diversity in subtidal landscapes: Maintenance by physical processes and larval recruitment	10.1890/0012-9658(1999)080[0051:SDISLM]2.0.CO;2	Temperate Australasia	Southern New Zealand	New Zealand	Article	Ecology	Phylum-level (hydrozoan turf)
1998	Båmstedt U., Fosså J.H., Martinussen M.B., Fosshagen A.	Mass occurrence of the physonect siphonophore <i>apolemia uvaria</i> (lesueur) in norwegian waters	10.1080/00364827.1998.10413673	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level
1996	Pagès F., González H.E., González S.R.	Diet of the gelatinous zooplankton in Hardangerfjord (Norway) and potential predatory impact by <i>Aglantha digitale</i> (trachymedusae)	10.3354/meps139069	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level
1980	Gulliksen B.	The macrobenthic rocky-bottom fauna of Borgenfjorden, North-Trøndelag, Norway	10.1080/00364827.1980.10431479	Temperate Northern Atlantic	Northern European Seas	Norway	Article	Ecology	Species-level
1969	Zelickman E.A., Gelfand V.I., Shifrin M.A.	Growth, reproduction and nutrition of some Barents Sea hydromedusae in natural aggregations	10.1007/BF00393889	Temperate Northern Atlantic	Northern European Seas	Russia	Article	Ecology	Species-level

**TABLE S3** - List of the species (with order and family to which they belong) recorded in fjords all over the world.

Order	Family	Species	Chile	Norway	Svalbard	New Zealand	Antarctica	Iceland	Sweden	Alaska	Canada	Russia
Leptothecata	Sertulariidae	Abietinaria pulchra	0	0	1	0	0	0	0	0	0	0
Siphonophorae	Abylidae	Abylopsis tetragona	1	0	0	0	0	0	0	0	0	0
Leptothecata	Aequoreidae	Aequorea coerulescens	1	0	0	0	0	0	0	0	0	0
Leptothecata	Aequoreidae	Aequorea globosa	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Agalmatidae	Agalma elegans	1	1	0	0	0	0	0	0	0	0
Trachymedusae	Rhopalonematidae	Aglantha digitale	0	1	1	0	0	1	1	0	0	0
Anthoathecata	Pandeidae	Amphinema rugosum	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Amphisbetia operculata	1	0	0	0	0	0	0	0	0	0

Trachymedusae	Rhopalonematidae	Amphogona apicata	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Apolemiidae	Apolemia spp.	0	1	0	0	0	0	0	0	0	0
Siphonophorae	Apolemiidae	Apolemia uvaria	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Bougainvilliidae	Bimeria vestita	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Bougainvilliidae	Bougainvillia superciliaris	0	0	0	0	0	1	0	0	0	0
Anthoathecata	Bougainvilliidae	Bougainvillia macloviana	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Bougainvilliidae	Bougainvillia muscoides	1	1	0	0	0	0	0	0	0	0
Anthoathecata	Bougainvilliidae	Bougainvillia muscus	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Bougainvilliidae	Bougainvillia pyramidata	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Bougainvilliidae	Bougainvillia spp.	1	1	0	0	0	0	0	0	0	0

Anthoathecata	Bythotiaridae	Brinckmannia hexactinellidop hila	0	0	0	0	0	0	0	0	1	1	0
Anthoathecata	Bythotiaridae	Bythotiara murrayi	0	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulinidae	Calycella syringa	1	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Bythotiaridae	Calycopsis simplex	0	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Campanularia agas	1	0	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Campanularia hincksii	1	0	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Campanularia lennoxensis	1	0	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Campanularia spp.	0	0	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Campanularia volubilis	0	0	1	0	0	0	0	0	0	0	0

Leptothecata	Campanulinidae	Campanulina pumila	1	0	1	0	0	0	0	0	0	0
Anthoathecata	Candelabridae	Candelabrum phrygium	0	0	1	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Chelophyes appendiculata	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia gracilis	1	0	1	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia hemisphaerica	0	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia islandica	0	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia linearis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia paulensis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia reloncavia	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia simplex	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Clytia spp.	1	1	0	0	0	0	1	0	0	0

Siphonophorae	Cordagalmatidae	Cordagalma ordinatum	1	1	0	0	0	0	0	0	0	0
Anthoathecata	Cordylophoridae	Cordylophora caspia	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Corymorphidae	Corymorpha nutans	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Corynidae	Coryne eximia	1	1	0	0	0	0	0	0	0	0
Anthoathecata	Corynidae	Coryne spp.	1	0	0	0	0	0	0	0	0	0
Narcomedusae	Cuninidae	Cunina octonaria	0	0	0	0	0	0	0	0	0	0
Narcomedusae	Cuninidae	Cunina peregrina	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulinidae	Cuspidella procumbens	0	0	1	0	0	0	0	0	0	0
Leptothecata	Campanulinidae	Cuspidella spp.	0	0	1	0	0	0	0	0	0	0
Leptothecata	Mitrocomidae	Cyclocanna producta	0	1	0	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Dimophyes arctica	1	1	0	0	0	0	0	0	0	0

Leptothecata	Dipleurosomatidae	Dipleurosoma typicum	0	1	0	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Dynamena pumila	0	1	0	0	0	0	0	0	0	0
Leptothecata	Mitrocomidae	Earleria panicula	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Tubulariidae	Ectopleura dumortierii	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulinidae	Egmundella gracilis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulinidae	Egmundella magellanica	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Stylasteridae	Errina antarctica	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Stylasteridae	Errina novazelandiae	0	0	0	1	0	0	0	0	0	0
Anthoathecata	Stylasteridae	Errina spp.	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Eudendriidae	Eudendrium annulatum	0	0	1	0	0	0	0	0	0	0



Anthoathecata	Eudendriidae	Eudendrium nambuccense	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Eudendriidae	Eudendrium rameum	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Eudendriidae	Eudendrium ramosum	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Eudendriidae	Eudendrium scotti	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Eudendriidae	Eudendrium spp.	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Eudendriidae	Eudendrium vaginatum	0	0	1	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Eudoxoides spiralis	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Corymorphidae	Euphysa aurata	1	1	0	0	0	0	0	0	0	0
Anthoathecata	Corymorphidae	Euphysa tentaculata	0	1	0	0	0	0	0	0	0	0
Leptothecata	Eirenidae	Eutonina indicans	0	1	0	0	0	1	0	0	0	0

Leptothecata	Lafocidae	Filellum magnificum	1	0	0	0	0	0	0	0	0	0
Leptothecata	Lafocidae	Filellum serpens	0	0	1	0	0	0	0	0	0	0
Leptothecata	Lafocidae	Filellum serratum	1	0	0	0	0	0	0	0	0	0
Leptothecata	Lafocidae	Filellum spp.	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Bougainvilliidae	Garveia spp.	0	0	1	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Gonothyraea loveni	0	0	1	0	0	0	0	0	0	0
Limnomedusae	Olindiidae	Gossea brachymera	1	0	0	0	0	0	0	0	0	0
Leptothecata	Lafocidae	Grammaria abietina	1	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium arcticum	0	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium beanii	1	0	0	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium curvicaule	0	0	1	0	0	0	0	0	0	0

Leptothecata	Haleciidae	Halecium cymiforme	1	0	0	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium delicatulum	1	0	0	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium fjordlandicum	1	0	0	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium fraseri	1	0	0	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium halecinum	0	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium labrosum	0	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium minutum	0	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium mirabile	0	0	1	0	0	0	0	0	0	0

Leptothecata	Haleciidae	Halecium muricatum	0	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium speciosum	0	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium spp.	1	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium tenellum	1	0	1	0	0	0	0	0	0	0
Leptothecata	Haleciidae	Halecium textum	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Pandeidae	Halitholus cirratus	0	0	1	0	0	0	0	0	0	0
Leptothecata	Mitrocomidae	Halopsis ocellata	1	0	0	0	0	0	0	0	0	0
Leptothecata	Halopterididae	Halopteris enersis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Halopterididae	Halopteris schucherti	1	0	0	0	0	0	0	0	0	0
Leptothecata	Hebellidae	Hebella dispolians	1	0	0	0	0	0	0	0	0	0

Leptothecata	Hebellidae	<i>Hebella striata</i>	1	0	0	0	0	0	0	0	0	0
Trachymedusae	Halicreatidae	<i>Homoeonema platygonon</i>	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Tubulariidae	<i>Hybocodon chilensis</i>	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Tubulariidae	<i>Hybocodon prolifer</i>	0	0	0	0	0	1	1	0	0	0
Anthoathecata	Tubulariidae	<i>Hydocodon unicus</i>	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Hydractiniidae	<i>Hydractinia carica</i>	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Hydractiniidae	<i>Hydractinia pacifica</i>	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Hydractiniidae	<i>Hydractinia</i> spp.	1	1	0	0	0	0	0	0	0	0
Leptothecata	Kirchenpaueriidae	<i>Kirchenpaueria curvata</i>	1	0	0	0	0	0	0	0	0	0
Leptothecata	Lafoeidae	<i>Lafoea dumosa</i>	1	0	1	0	0	0	0	0	0	0
Leptothecata	Campanulinidae	<i>Lafoeina longithecata</i>	1	0	0	0	0	0	0	0	0	0

Leptothecata	Campanulinidae	Lafoeina maxima	0	0	1	0	0	0	0	0	0	0
Leptothecata	Laodiceidae	Laodicea pulchra	1	0	0	0	0	0	0	0	0	0
Leptothecata	Laodiceidae	Laodicea undulata	1	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Laomedea flexuosa	0	0	1	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Lensia conoidea	1	1	0	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Lensia meteori	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Lensia subtilis	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Pandeidae	Leuckartiara octona	1	1	0	0	0	1	0	0	0	0
Limnomedusae	Geryoniidae	Liriope tetraphylla	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Rathkeidae	Lizzia blondina	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Margelopsidae	Margelopsis hartlaubii	0	1	0	0	0	0	0	0	0	0
Leptothecata	Melicertidae	Melicertum octocostatum	0	1	0	0	0	0	0	0	0	0

Leptothecata	Mitrocomidae	Mitrocomella polydiademata	0	1	0	0	0	0	0	0	0	0
Leptothecata	Tiarannidae	Modeeria rotunda	1	1	0	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Muggiaea atlantica	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Diphyidae	Muggiaea bargmannae	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Agalmatidae	Nanomia cara	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Pandeidae	Neoturris brevicornis	0	0	0	0	0	1	0	0	0	0
Anthoathecata	Pandeidae	Neoturris pileata	0	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Obelia bidentata	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Obelia dichotoma	1	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Obelia geniculata	1	1	0	0	0	0	0	0	0	0

Leptothecata	Campanulariidae	<i>Obelia longissima</i>	1	0	1	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	<i>Obelia</i> spp.	1	1	0	0	0	1	1	0	0	0
Leptothecata	Malagazziidae	<i>Octophialucium funerarium</i>	0	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulinidae	<i>Opercularella lacerata</i>	0	0	1	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	<i>Orthopyxis crenata</i>	1	0	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	<i>Orthopyxis integra</i>	0	0	1	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	<i>Orthopyxis mollis</i>	1	0	0	0	0	0	0	0	0	0
Leptothecata	Thyroscyphidae	<i>Parascyphus repens</i>	1	0	0	0	0	0	0	0	0	0
Leptothecata	Teclaiidae	<i>Parateclaiia norvegica</i>	0	1	0	0	0	0	0	0	0	0



Leptothecata	Syntheceiidae	Parathuiaria polycarpa	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Pericladium mirabilis	0	0	1	0	0	0	0	0	0	0
Leptothecata	Phialellidae	Phialella belgicae	1	0	0	0	0	0	0	0	0	0
Leptothecata	Phialellidae	Phialella falklandica	0	0	0	0	0	0	0	0	0	0
Leptothecata	Phialellidae	Phialella quadrata	1	0	1	0	0	0	1	0	0	0
Siphonophorae	Physophoridae	Physophora hydrostatica	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Boreohydridae	Plotocnide borealis	0	1	0	0	0	0	0	0	0	0
Leptothecata	Plumulariidae	Plumularia setacea	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Hydractiniidae	Podocoryna areolata	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Hydractiniidae	Podocoryna borealis	1	1	0	0	0	1	0	0	0	0

Anthoathecata	Hydractiniidae	Podocoryna carnea	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Hydractiniidae	Podocoryna tenuis	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Rathkeidae	Podocorynoide s minima	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Prayidae	Praya dubia	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Proboscidactylidae	Proboscidactyl a mutabilis	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Proboscidactylidae	Proboscidactyl a ornata	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Proboscidactylidae	Proboscidactyl a stellata	1	1	0	0	0	0	0	0	0	0
Anthoathecata	Bythotiaridae	Protiaropsis minor	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Bythotiaridae	Protiaropsis spp.	1	0	0	0	0	0	0	0	0	0
Trachymedusae	Ptychogastridae	Ptychogastria polaris	0	0	0	0	1	0	0	0	0	0

Leptothecata	Laodiceidae	<i>Ptychogena crocea</i>	0	1	1	0	0	0	0	0	0	0
Siphonophorae	Pyrostephidae	<i>Pyrostephos vanhoeffeni</i>	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Rathkeidae	<i>Rathkea formosissima</i>	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Rathkeidae	<i>Rathkea octopunctata</i>	0	1	0	0	0	0	1	0	0	1
Leptothecata	Campanulariidae	<i>Rhizocaulus verticillatus</i>	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Oceaniidae	<i>Rhizogeton nudus</i>	0	0	1	0	0	0	0	0	0	0
Trachymedusae	Rhopalonematidae	<i>Rhopalonema funerarium</i>	1	0	0	0	0	0	0	0	0	0
Trachymedusae	Rhopalonematidae	<i>Rhopalonema velatum</i>	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Rhysiidae	<i>Rhysia</i> spp.	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Prayidae	<i>Rosacea plicata</i>	1	0	0	0	0	0	0	0	0	0

Anthoathecata	Corynidae	Sarsia lovenii	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Corynidae	Sarsia spp.	0	0	1	0	0	0	0	0	0	0
Anthoathecata	Corynidae	Sarsia tubulosa	0	1	1	0	0	1	1	0	0	0
Leptothecata	Sertularellidae	Sertularella antarctica	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella clausa	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella curvitheca	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella fuegonensis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella gayi	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella implexa	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella polyzonias	1	0	0	0	0	0	0	0	0	0

Leptothecata	Sertularellidae	Sertularella quasiplana	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella rugosa	0	0	1	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella sanmatiasensis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella spp.	1	0	1	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella tenella	1	0	1	0	0	0	0	0	0	0
Leptothecata	Sertularellidae	Sertularella valdiviae	1	0	0	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Sertularia albimaris	0	0	1	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Sertularia argentea	0	0	1	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Sertularia cupressoides	0	0	1	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Sertularia fabricii	0	0	1	0	0	0	0	0	0	0

Leptothecata	Sertulariidae	Sertularia schmidti	0	0	1	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Sertularia similis	0	0	1	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Sertularia spp.	0	0	1	0	0	0	0	0	0	0
Leptothecata	Sertulariidae	Sertularia tenera	0	1	0	0	0	0	0	0	0	0
Leptothecata	Campanulariidae	Silicularia rosea	1	0	0	0	0	0	0	0	0	0
Trachymedusae	Rhopalonematidae	Sminthea eurygaster	1	0	0	0	0	0	0	0	0	0
Narcomedusae	Solmundaeginidae	Solmundella bitentaculata	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Sphaerocorynidae	Sphaerocoryne cocometra	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Sphaeronectidae	Sphaeronectes fragilis	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Sphaeronectidae	Sphaeronectes irregularis	1	0	0	0	0	0	0	0	0	0

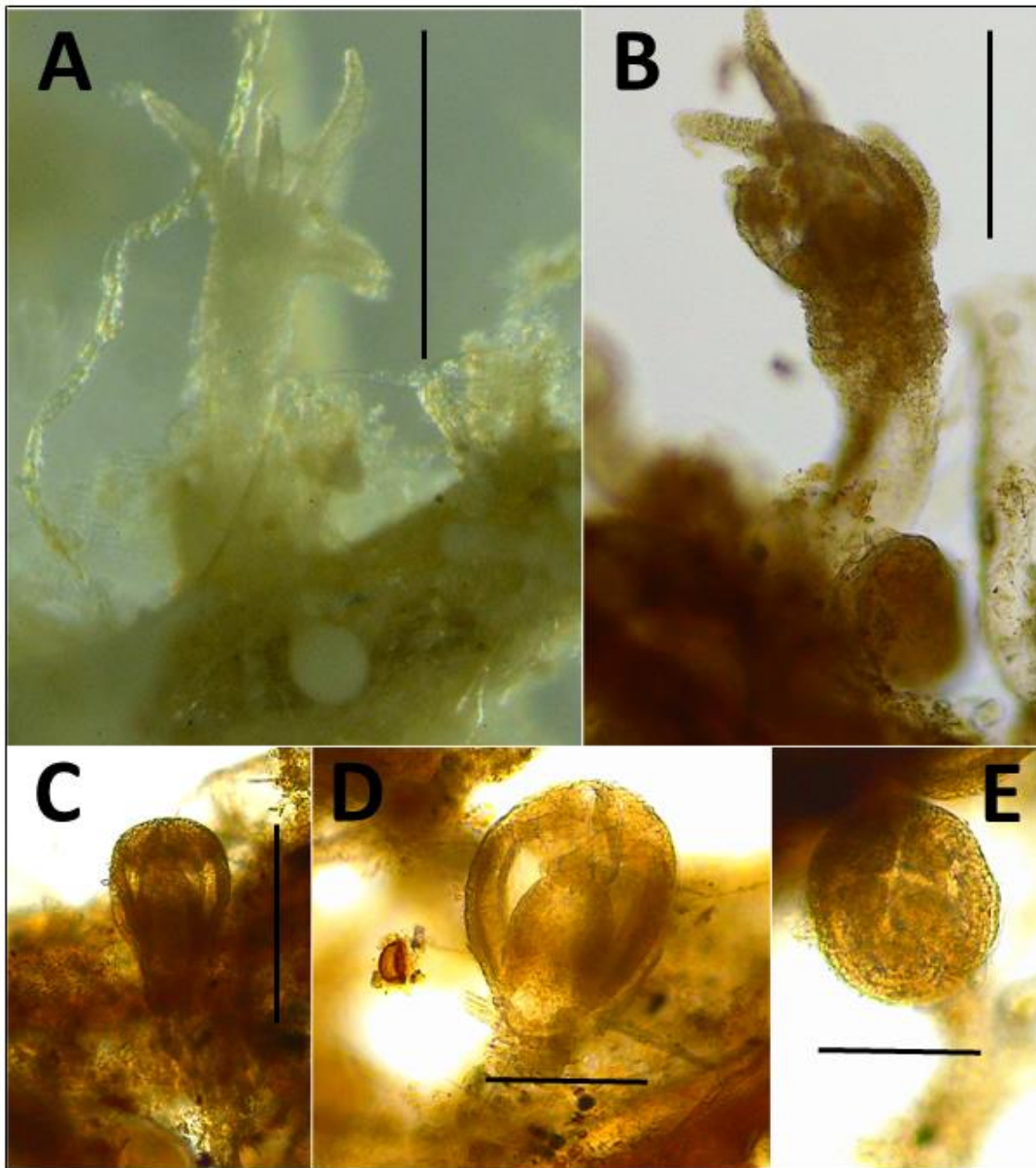
Siphonophorae	Sphaeronectidae	Sphaeronectes koellikeri	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Sphaeronectidae	Sphaeronectes spp.	0	1	0	0	0	0	0	0	0	0
Anthoathecata	Corynidae	Stauridiosarsia gemmifera	0	1	0	0	0	0	0	0	0	0
Leptothecata	Laodiceidae	Staurostoma mertensii	0	1	0	0	0	1	0	0	0	0
Leptothecata	Laodiceidae	Staurostoma mertensii	0	0	0	0	0	0	0	0	0	0
Anthoathecata	Protohydridae	Sympagohydra tuuli	0	0	1	0	0	0	0	1	1	0
Leptothecata	Symplectoscyphidae	Symplectoscyphus filiformis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Symplectoscyphidae	Symplectoscyphus leloupi	1	0	0	0	0	0	0	0	0	0

Leptothecata	Symplectoscyphidae	Symplectoscyphus magellanicus	1	0	0	0	0	0	0	0	0	0
Leptothecata	Symplectoscyphidae	Symplectoscyphus marionensis	1	0	0	0	0	0	0	0	0	0
Leptothecata	Symplectoscyphidae	Symplectoscyphus milneanus	1	0	0	0	0	0	0	0	0	0
Leptothecata	Symplectoscyphidae	Symplectoscyphus spp.	1	0	0	0	0	0	0	0	0	0
Leptothecata	Symplectoscyphidae	Symplectoscyphus subdichotomus	1	0	0	0	0	0	0	0	0	0
Leptothecata	Symplectoscyphidae	Symplectoscyphus tricuspидatus	0	0	1	0	0	0	0	0	0	0
Leptothecata	Synthechiidae	Synthecium protectum	1	0	0	0	0	0	0	0	0	0
Trachymedusae	Ptychogastridae	Tesserogastria musculosa	0	1	0	0	0	0	0	0	0	0

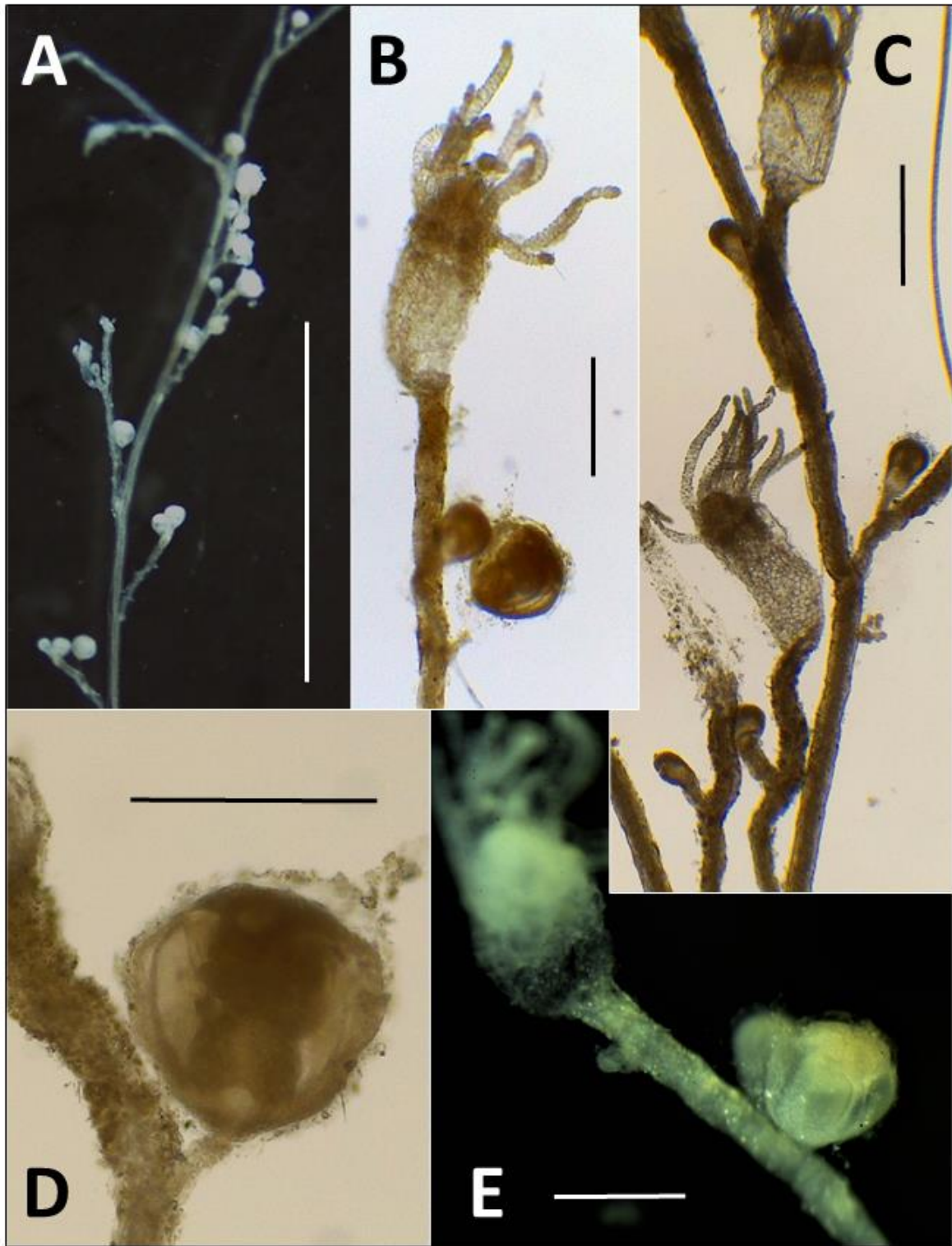


Leptothecata	Tiaropsidae	Tiaropsis multicirrata	0	1	0	0	0	0	0	0	0	1
Anthoathecata	Tubulariidae	Tubularia sp.	0	0	0	0	0	0	0	1	0	0
Anthoathecata	Oceaniidae	Turritopsis spp.	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Hippopodiidae	Vogtia pentacantha	1	0	0	0	0	0	0	0	0	0
Siphonophorae	Hippopodiidae	Vogtia serrata	1	0	0	0	0	0	0	0	0	0
Anthoathecata	Zancleidae	Zanclea spp.	0	1	0	0	0	0	0	0	0	0
<b>Total species found</b>		<b>222</b>	<b>132</b>	<b>54</b>	<b>58</b>	<b>1</b>	<b>1</b>	<b>11</b>	<b>6</b>	<b>3</b>	<b>2</b>	<b>2</b>

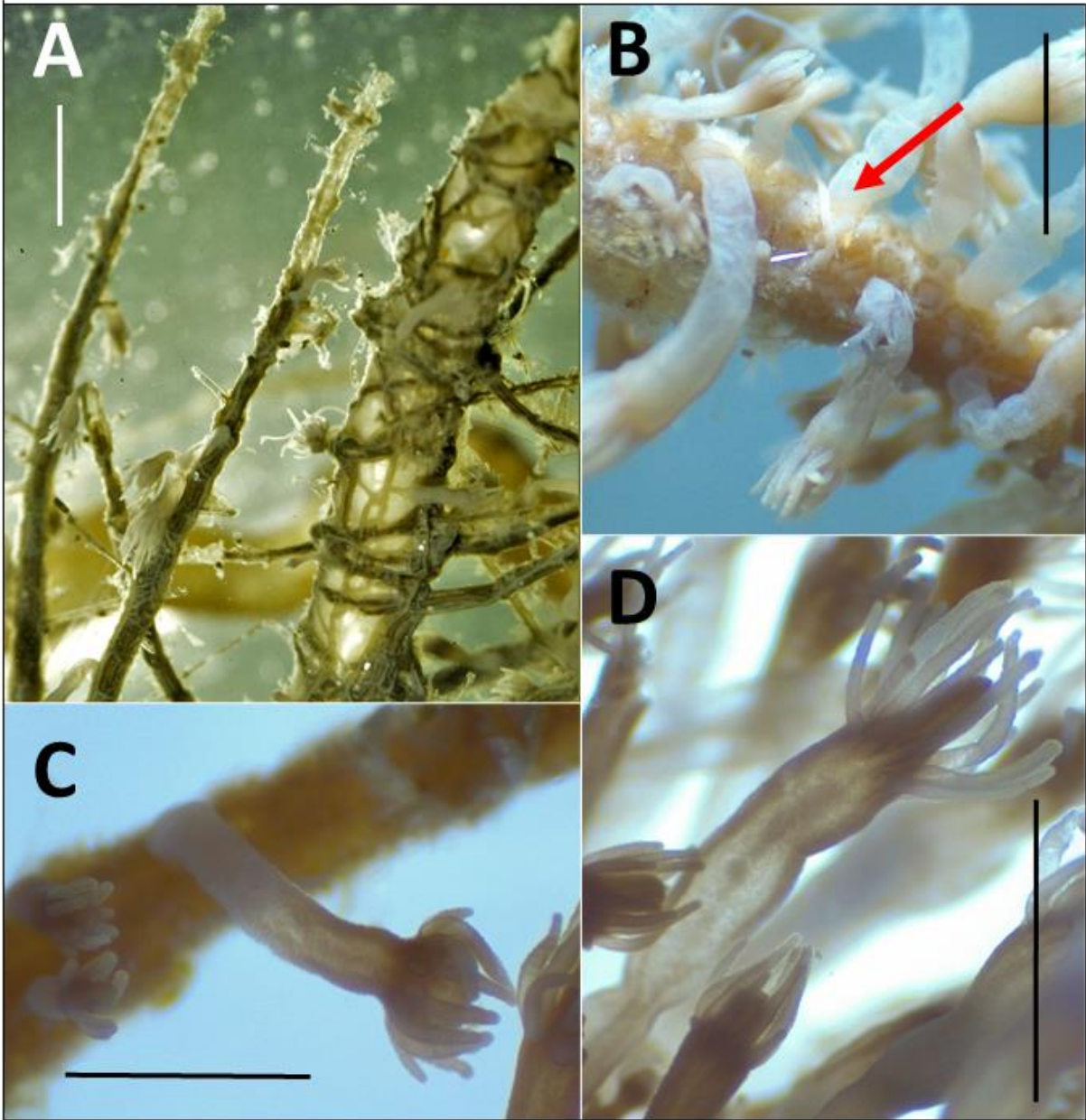
SUPPLEMENTARY MATERIAL – TAXONOMIC REPORT



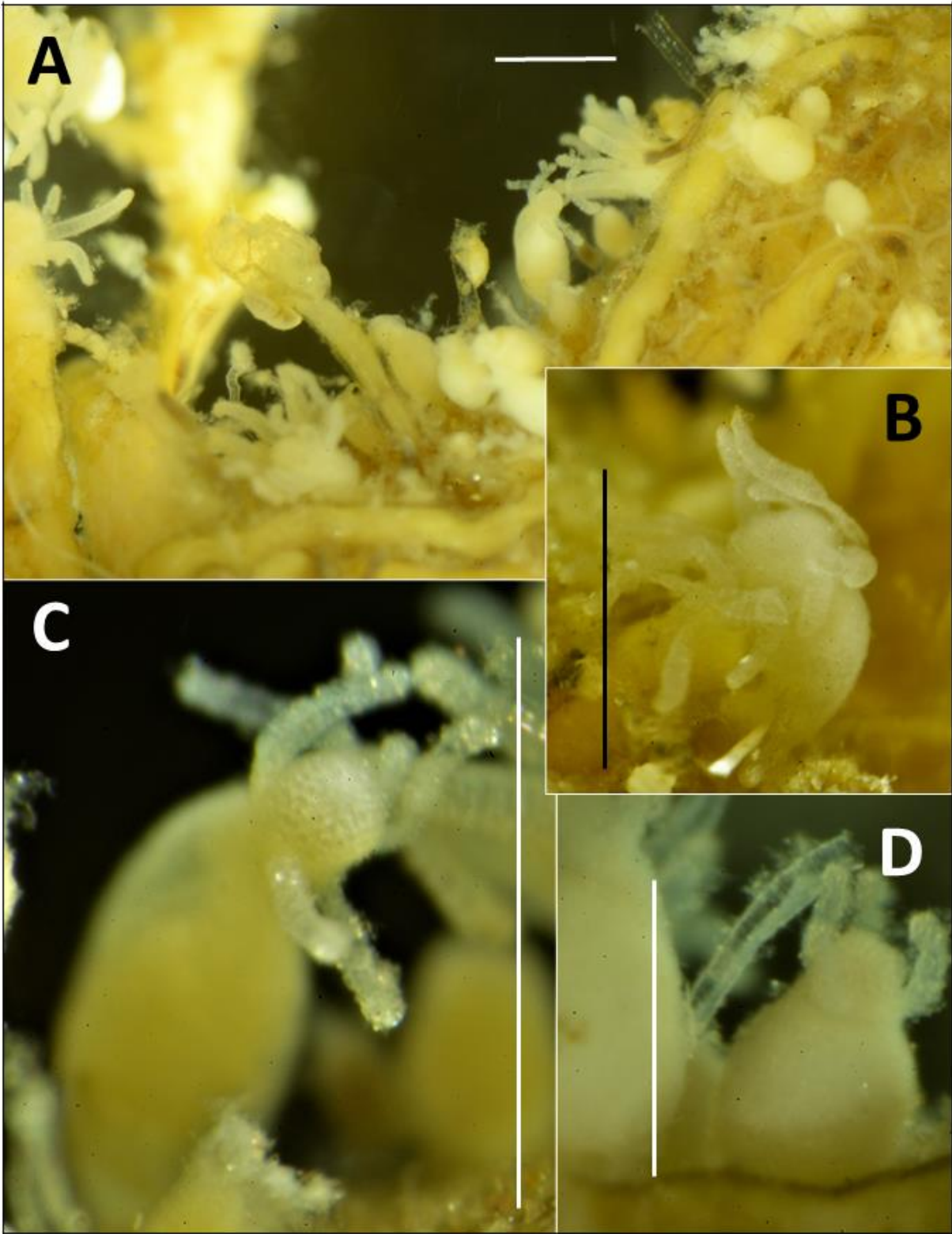
**Figure S1.** *Bougainvillia muscoides*: hydranth (A,B) and gonophore (C,D,E). Scale bars: 500  $\mu\text{m}$  (A,B); 400  $\mu\text{m}$  (C); 300  $\mu\text{m}$  (D,E).



**Figure S2.** *Bougainvillia pyramidata*: colony detail (A,C), hydranth (B) and gonophore (D,E). Scale bars: 1 cm (A); 1 mm (B,C,D,E).



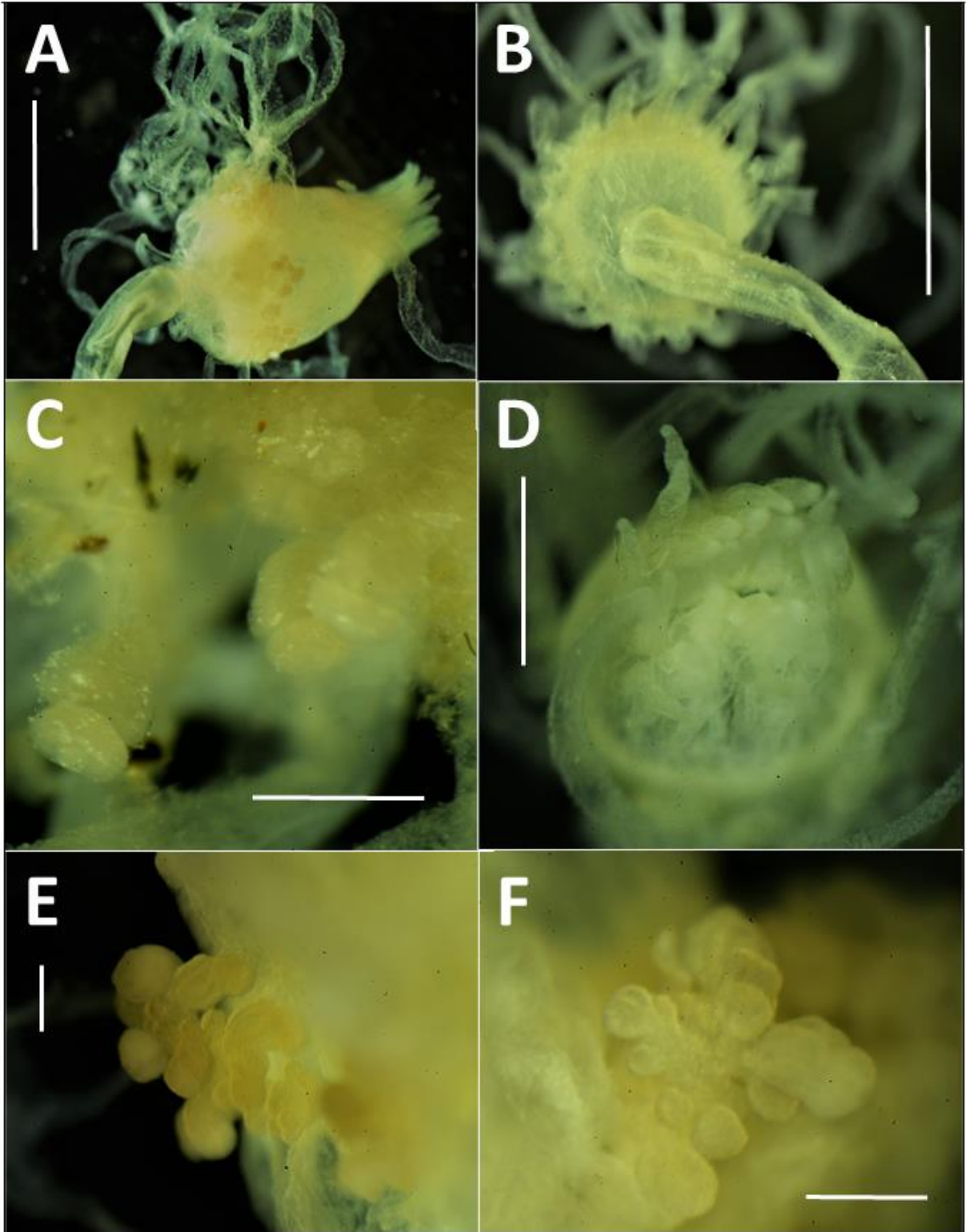
**Figure S3.** *Hydractiniidae* sp.: colony detail (A), dactylozoid (B), gastrozoid (C), gonozoid (D,E). Scale bars: 3 mm (A,B,C,D).



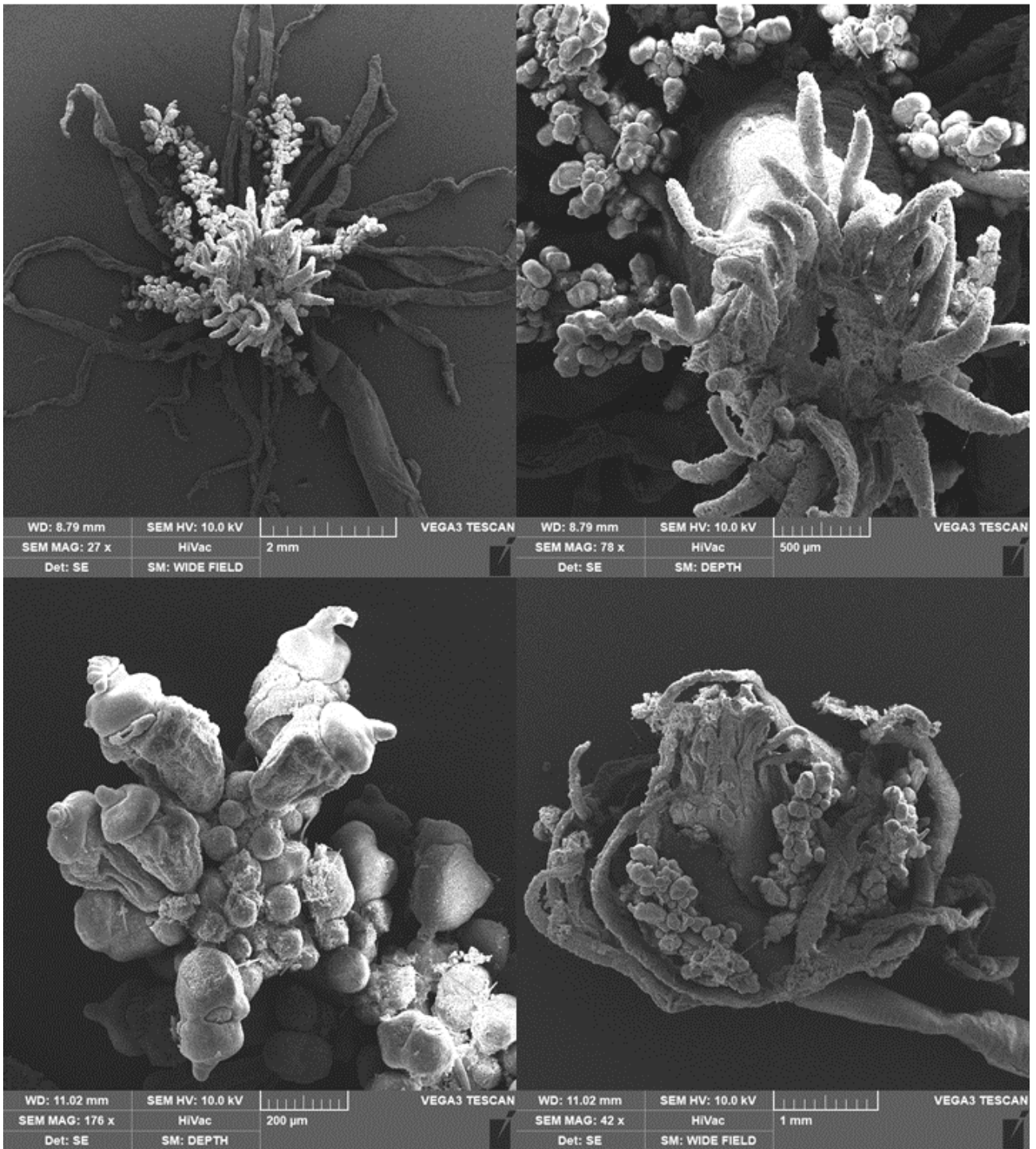
**Figure S4.** *Rhysia* sp.: colony detail (A), gastrozoid (B), gonozoid (C), dactylozoid (D). Scale bars: 850  $\mu$ m (B), 625  $\mu$ m (A,C); 450  $\mu$ m (D).



**Figure S5.** Cnidome of *Rhysia* sp.: eurytele III (A), eurytele II undischarged (B) and discharged (C), desmoneme (D,E) eurytele I (F). Scale bars: 30  $\mu$ m (A); 20  $\mu$ m (B,C); 5  $\mu$ m (D,E); 10  $\mu$ m (F) .

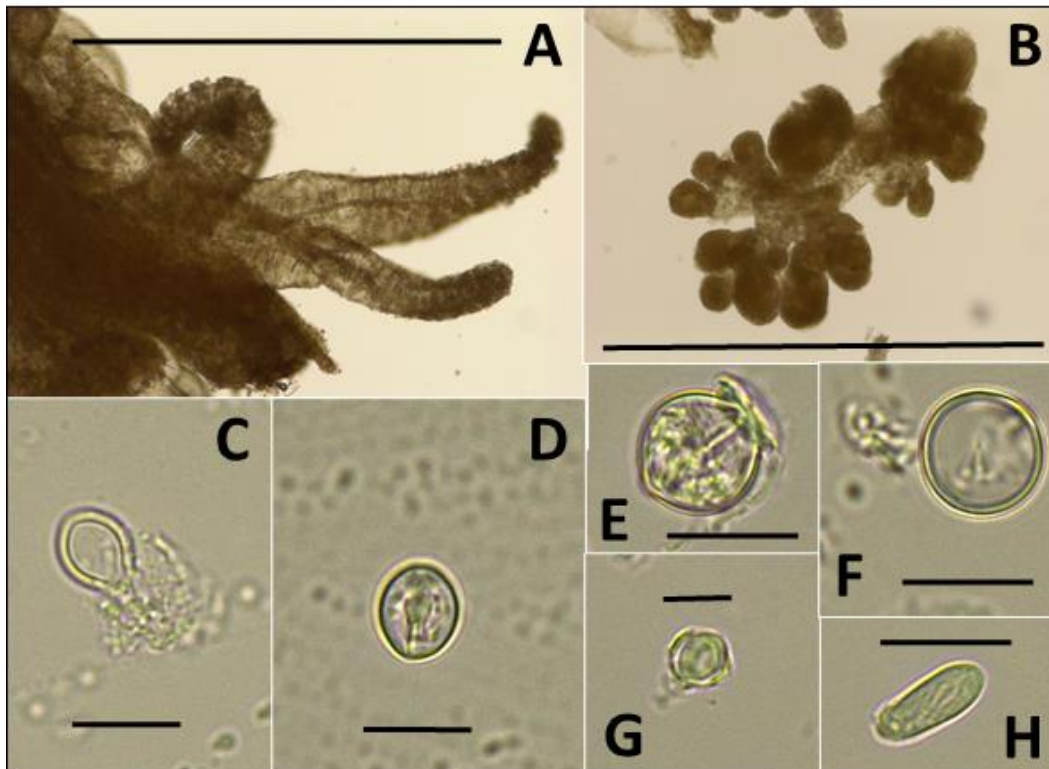


**Figure S6.** *Hybocodon chilensis*: hydranth (A) with details of the neck region (B) and the mouth surrounded by oral tentacles (D); gonophores (C, E, F). Scale bars: 2.5 mm (A,B); 300  $\mu\text{m}$  (C,E,F); 1 mm (D).

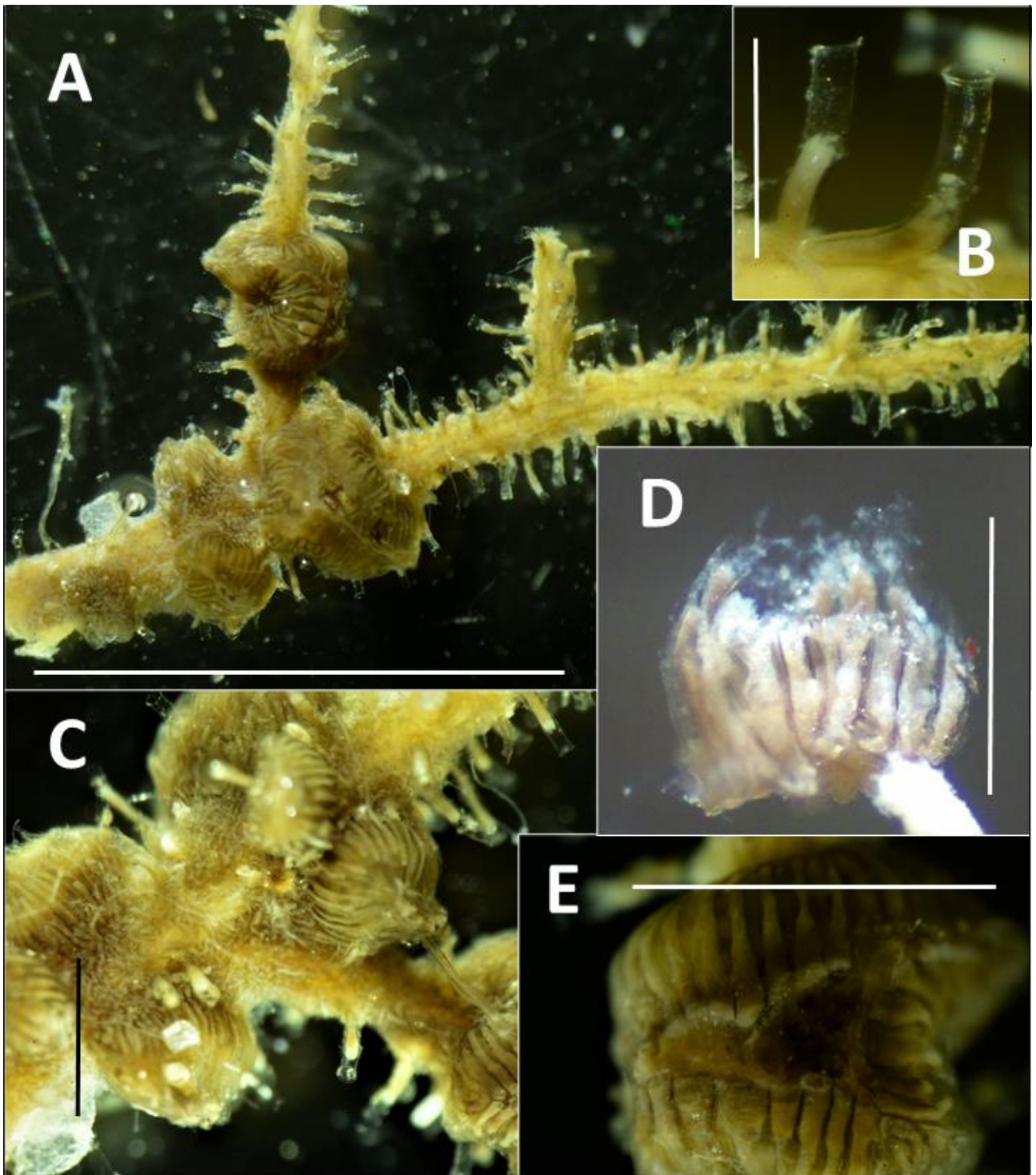


**Figure S7.** *Hybocodon chilensis* (SEM pictures): mature hydranth (A) with a detail of the mouth surrounded by oral tentacles and blastostyles (B); gonophores at the apex of a blastostyle (C); lateral view of a mature hydranth (D).

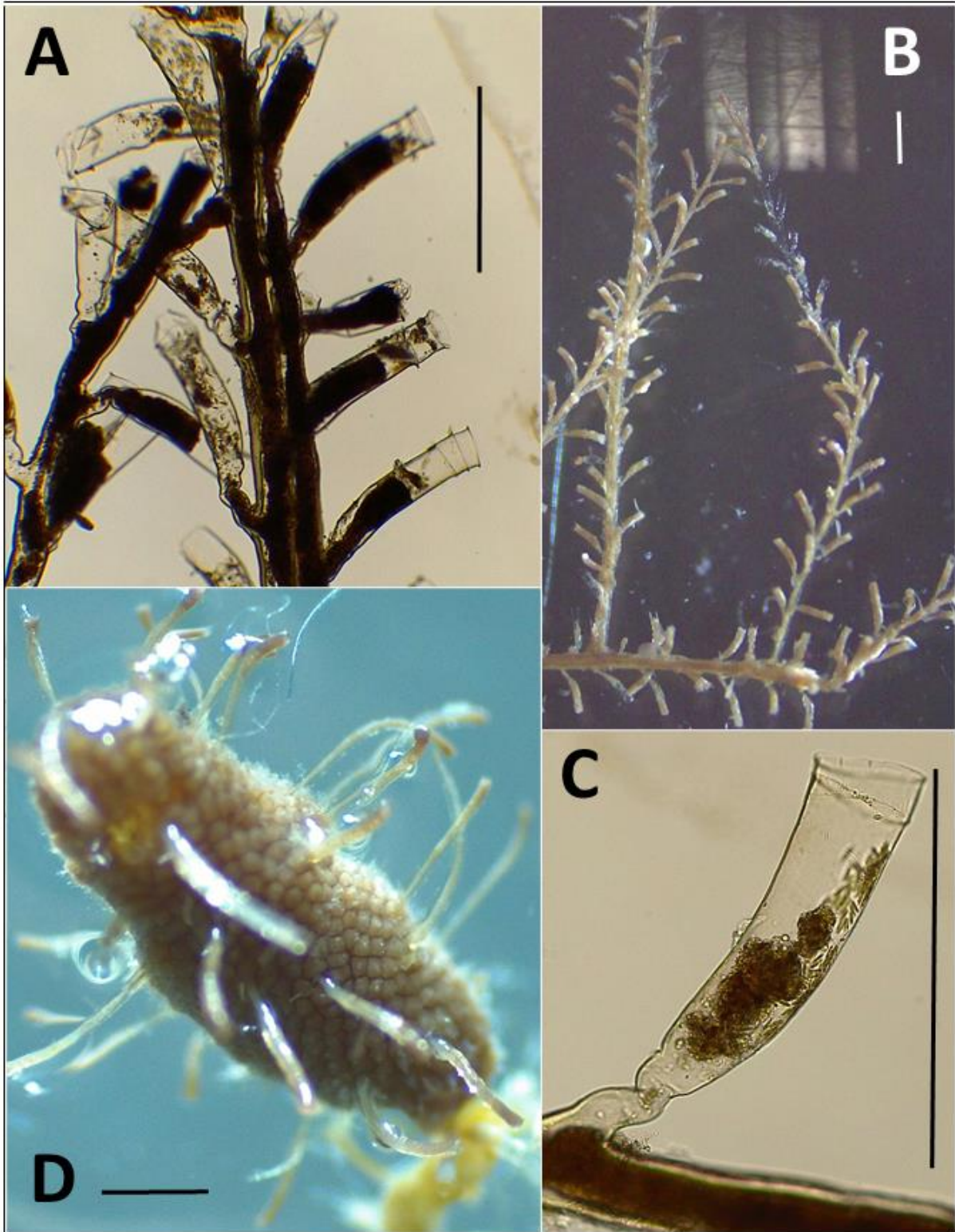




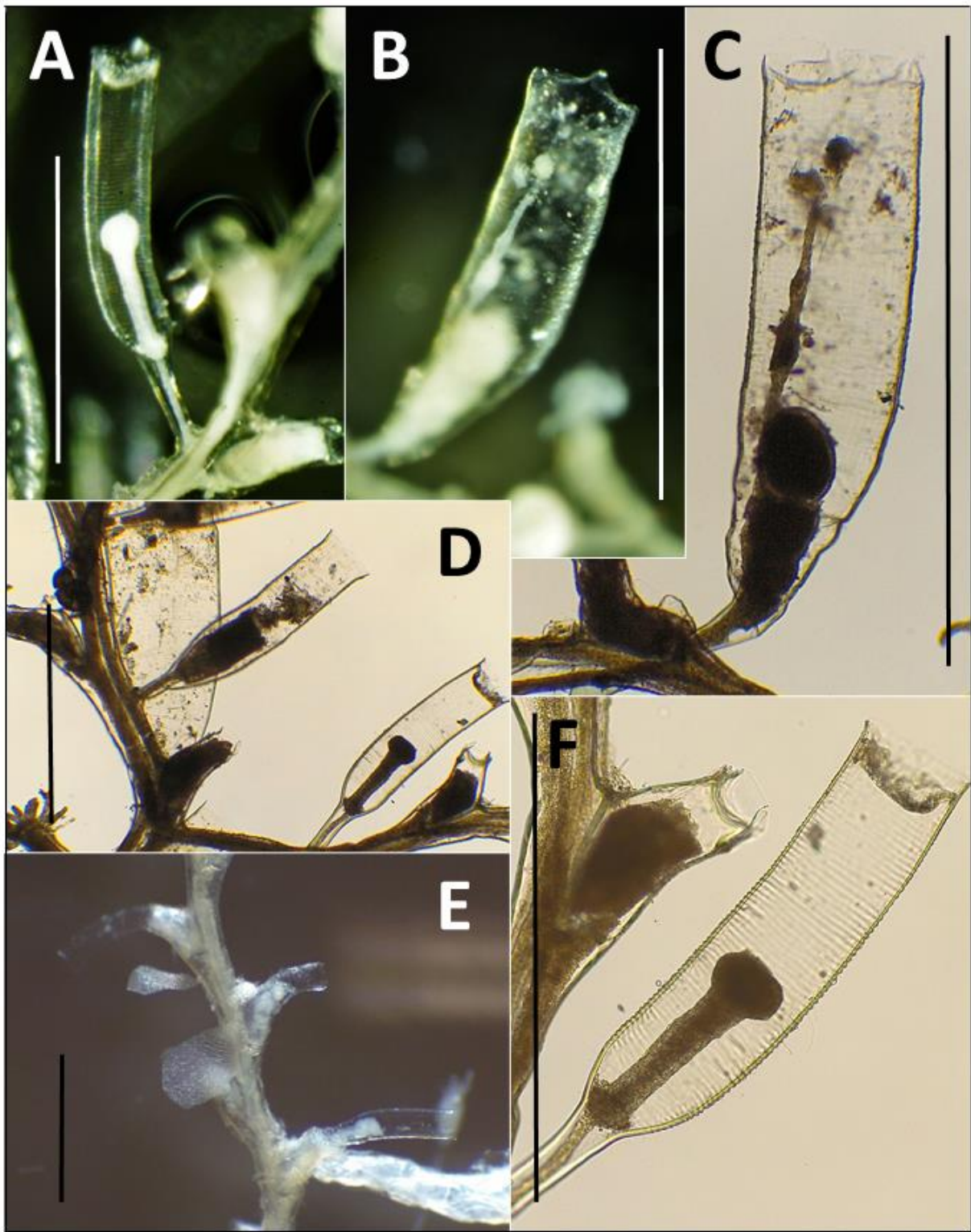
**Figure S8.** *Hybocodon chilensis*: detail of the oral tentacles (A); detail of the blastostyle (B). Cnidome: stenotele I discharged (C) and undischarged (D), stenotele II (E), anisorhiza (F), desmoneme (G), eurytele (H). Scale bars: 1 mm (A,B); 8  $\mu\text{m}$  (C,D); 12  $\mu\text{m}$  (E,F,H); 5  $\mu\text{m}$  (G).



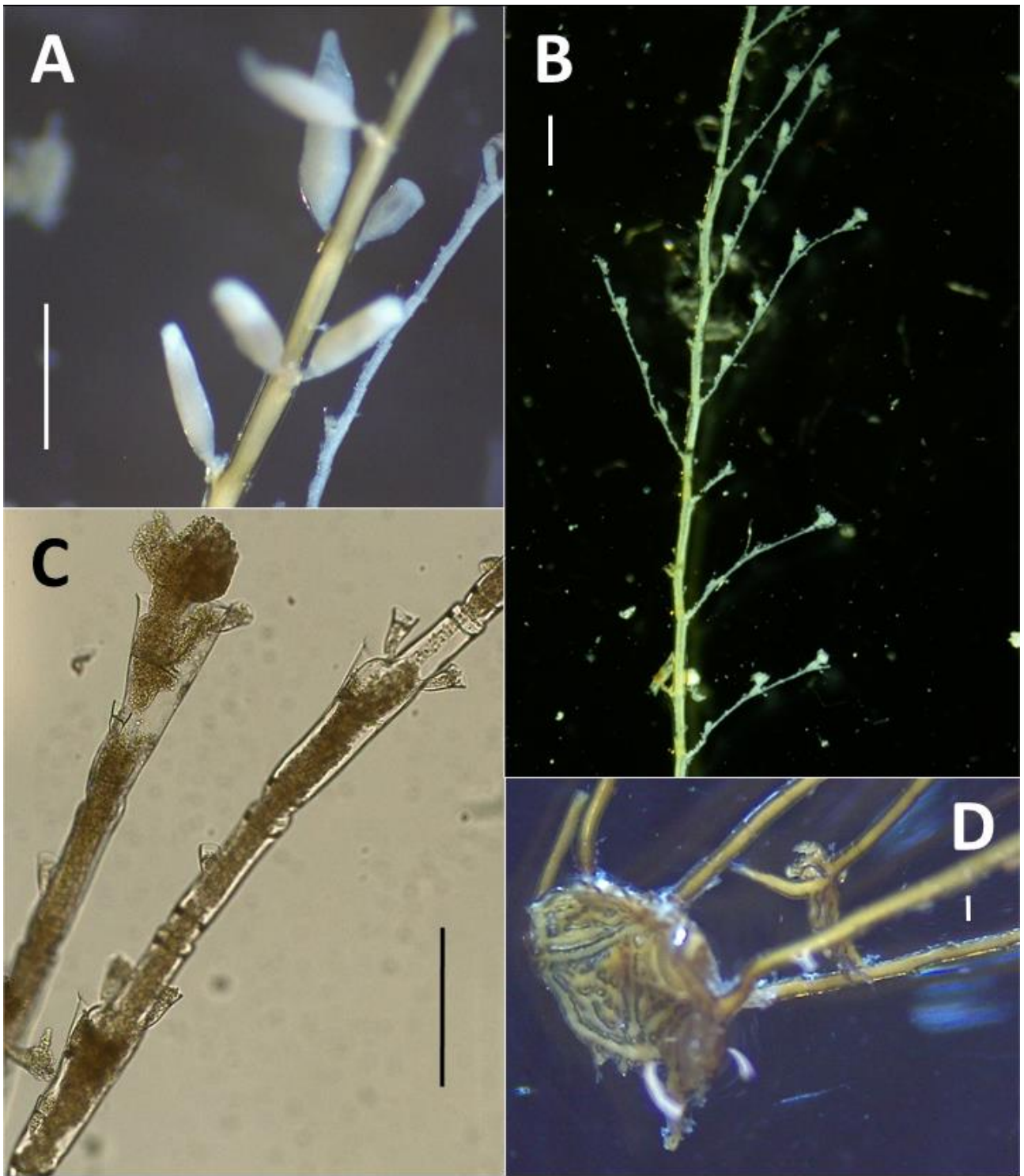
**Figure S9.** *Filellum serratum*: colony detail (A), hydrotheca (B), coppinia (C,E), lateral view of dissected coppinia (D). Scale bars: 7.5 mm (A); 700  $\mu$ m (B); 1 mm (C,D); 2 mm (E).



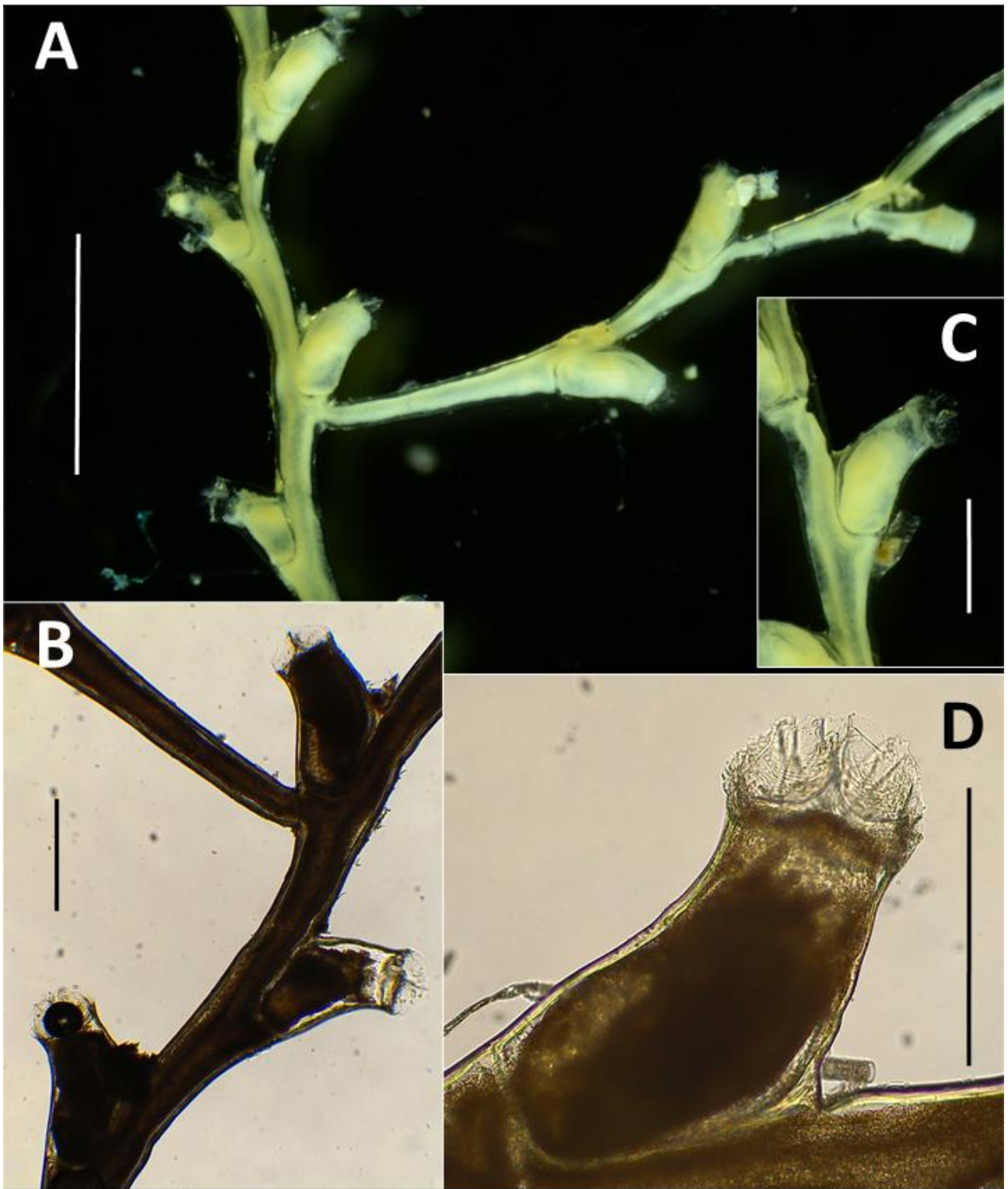
**Figure S10.** *Lafoea dumosa*: polysiphonic stem (A), colony detail (B), hydrotheca (C), coppinia (D). Scale bars: 600  $\mu\text{m}$  (A,B,C); 900  $\mu\text{m}$  (D).



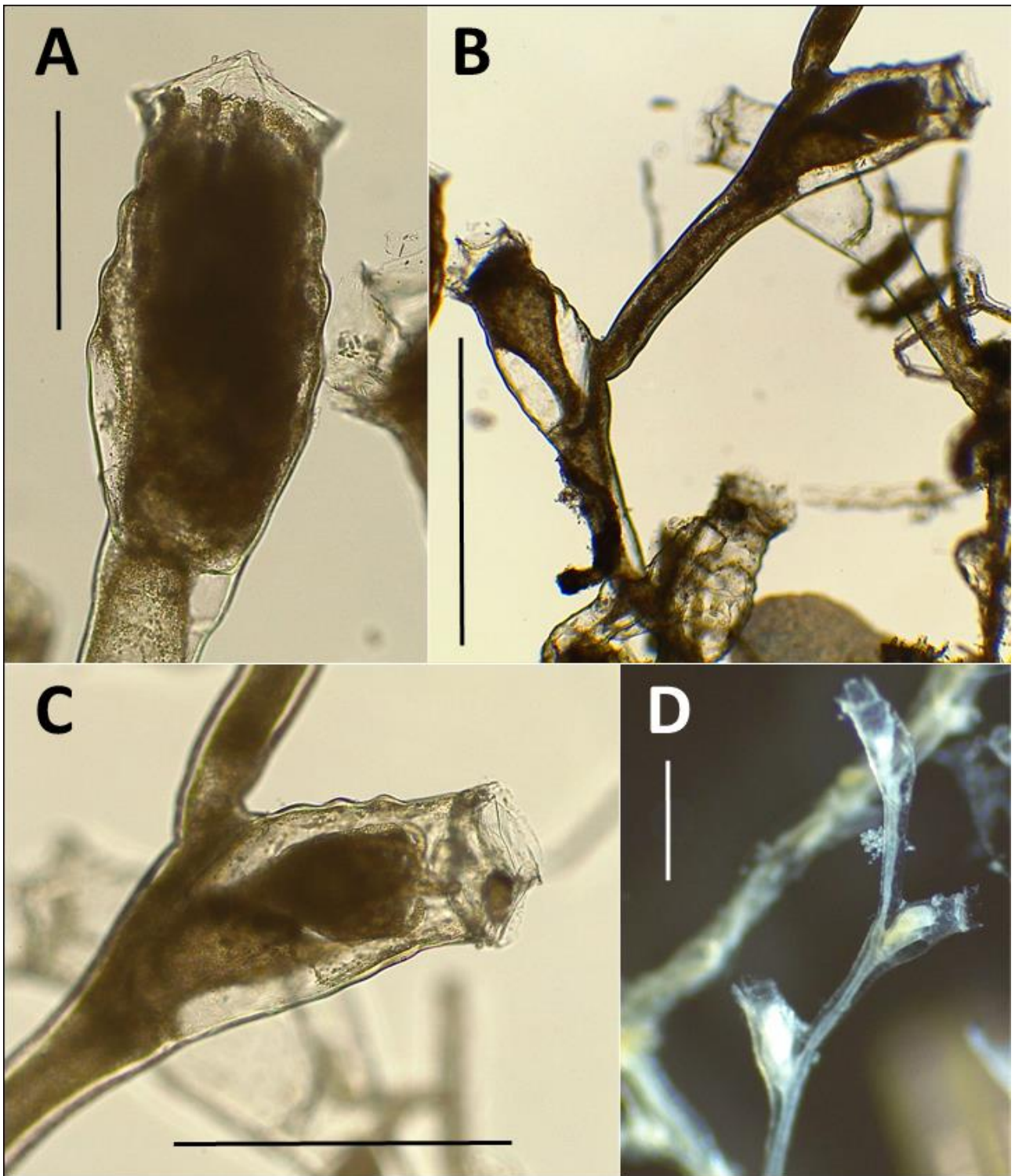
**Figure S11.** *Hebella striata*: hydrotheca (A,F), gonotheca (B,C), stolonial colony (D), parasitic form growing within *Symplectoscyphus filiformis* (E). Scale bars: 900  $\mu\text{m}$  (A,D,F), 1800  $\mu\text{m}$  (B,C); 800  $\mu\text{m}$  (E).



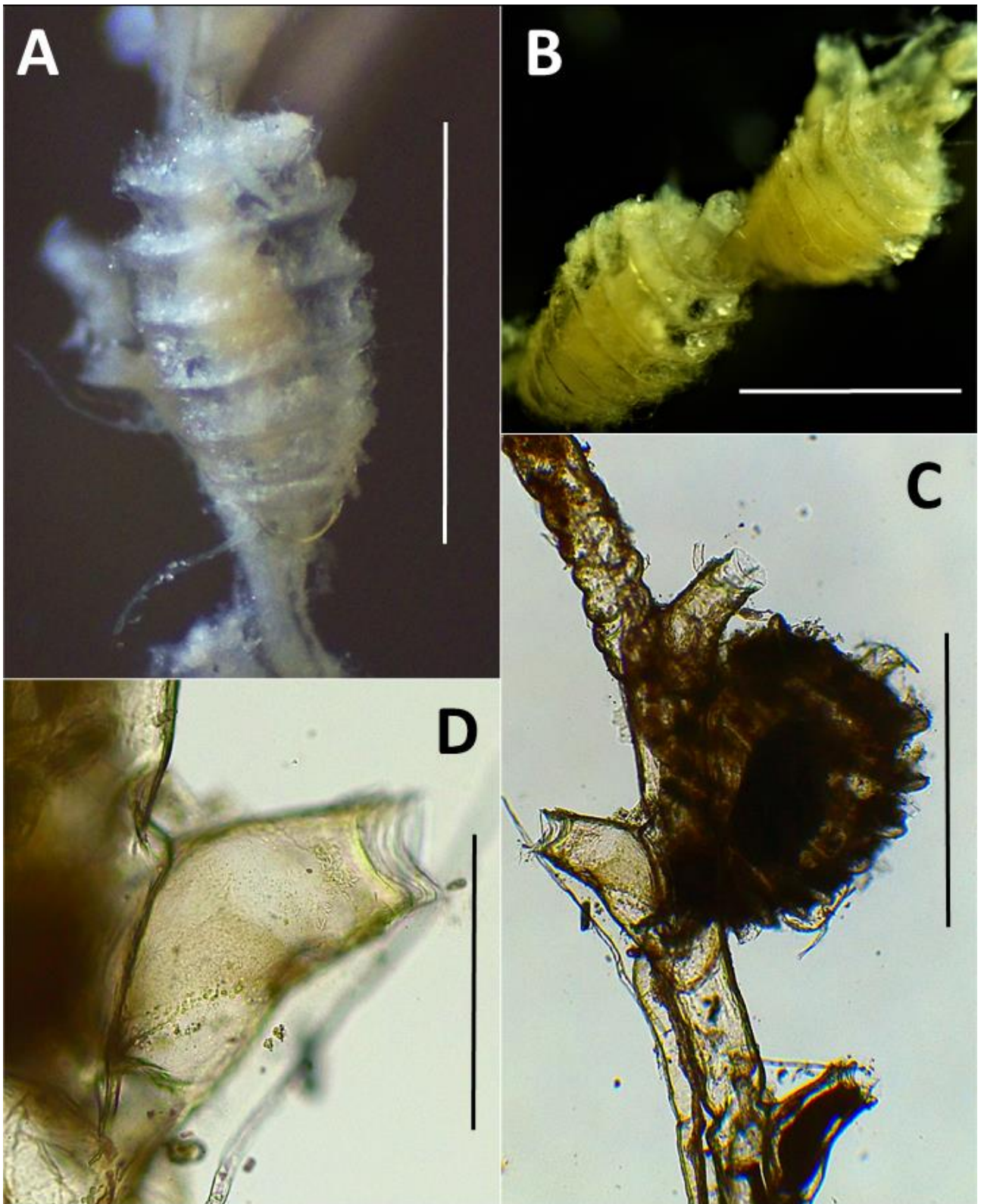
**Figure S12.** *Plumularia setacea*: gonotheca (A), colony detail (B), cladia bearing hydrothecae (C), rhizoids (D). Scale bars: 1000  $\mu\text{m}$  (A), 700  $\mu\text{m}$  (B); 300  $\mu\text{m}$  (C,D).



**Figure S13.** *Sertularella curvitheca*: colony detail (A,B), hydrotheca (C,D). Scale bars: 2000  $\mu\text{m}$  (A), 600  $\mu\text{m}$  (B,C); 500  $\mu\text{m}$  (D).

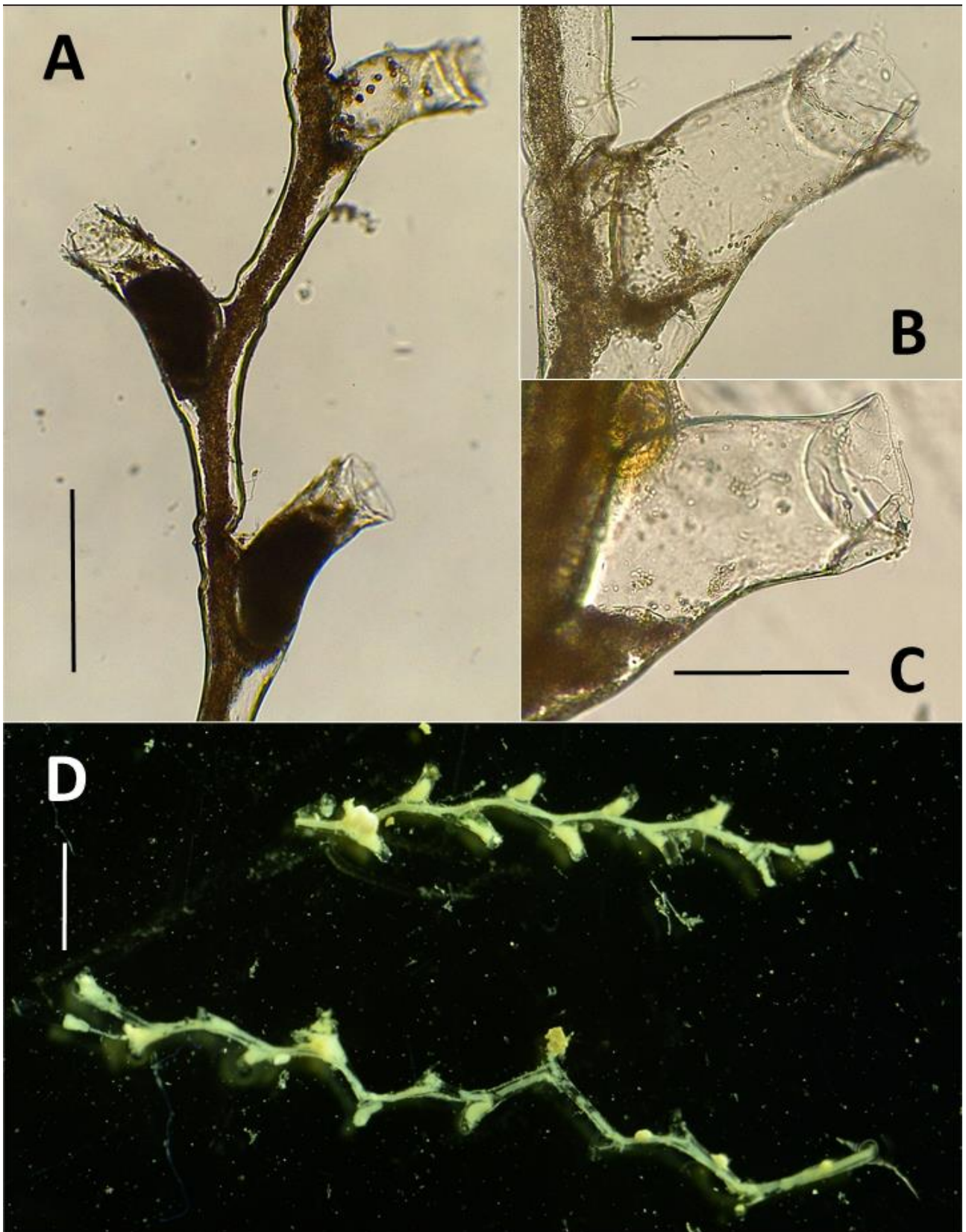


**Figure S14.** *Sertularella tenella*: hydrotheca (A,C), erect stem (B, D). Scale bars: 300  $\mu\text{m}$  (A), 600  $\mu\text{m}$  (C); 1100  $\mu\text{m}$  (B,D).



**Figure S15.** *Symplectoscyphus filiformis*: gonothecae showing sexual dimorphism (A,B), hydrotheca (C), detail of gonotheca (D). Scale bars: 1300  $\mu\text{m}$  (A), 1100  $\mu\text{m}$  (B,C); 370  $\mu\text{m}$  (D).

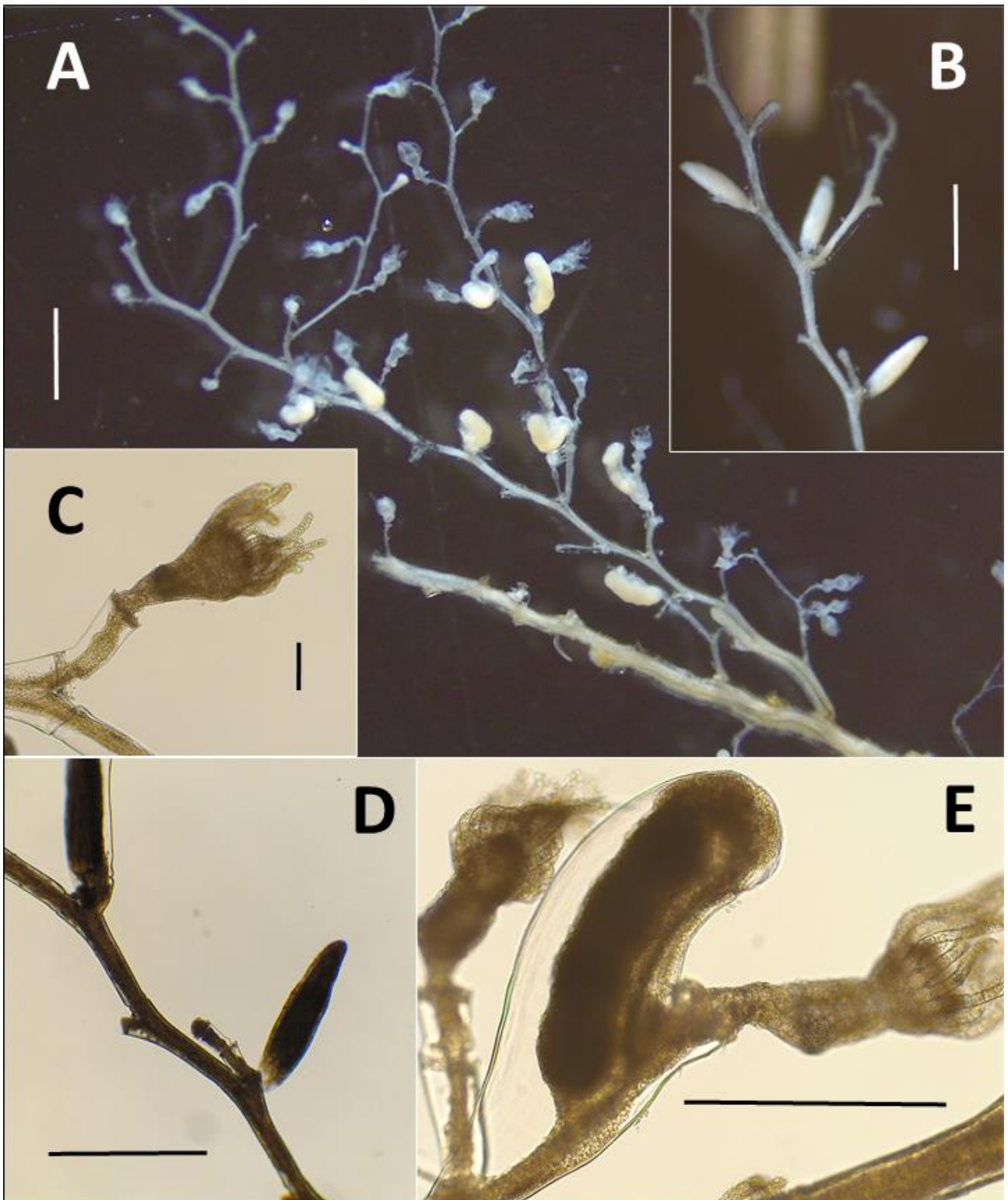




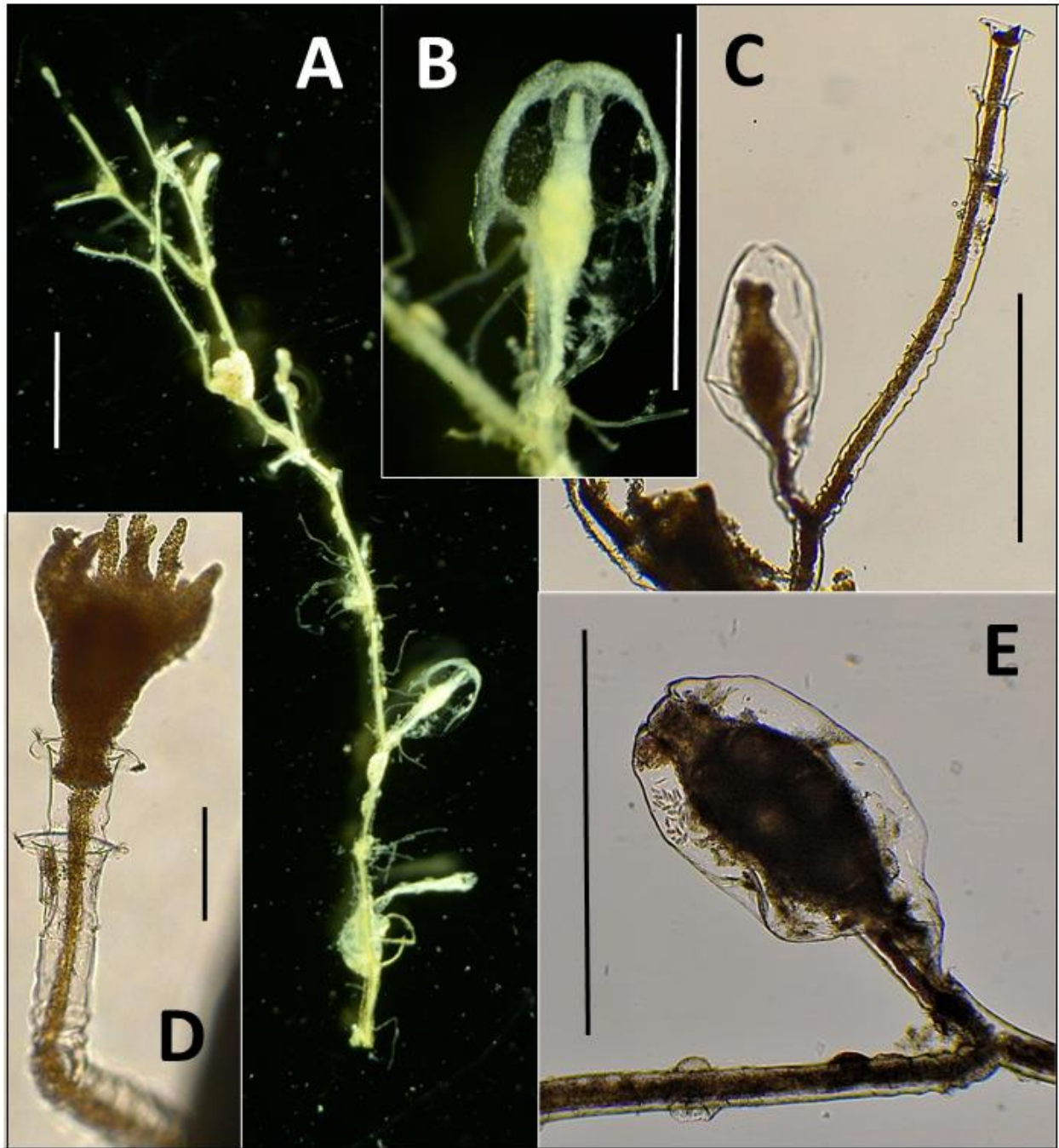
*Figure S16.* *Symplectoscyphus* sp.: erect stem (A), hydrotheca (B,C), colony detail (D). Scale bars: 500  $\mu\text{m}$  (A); 250  $\mu\text{m}$  (B,C); 200  $\mu\text{m}$  (D).



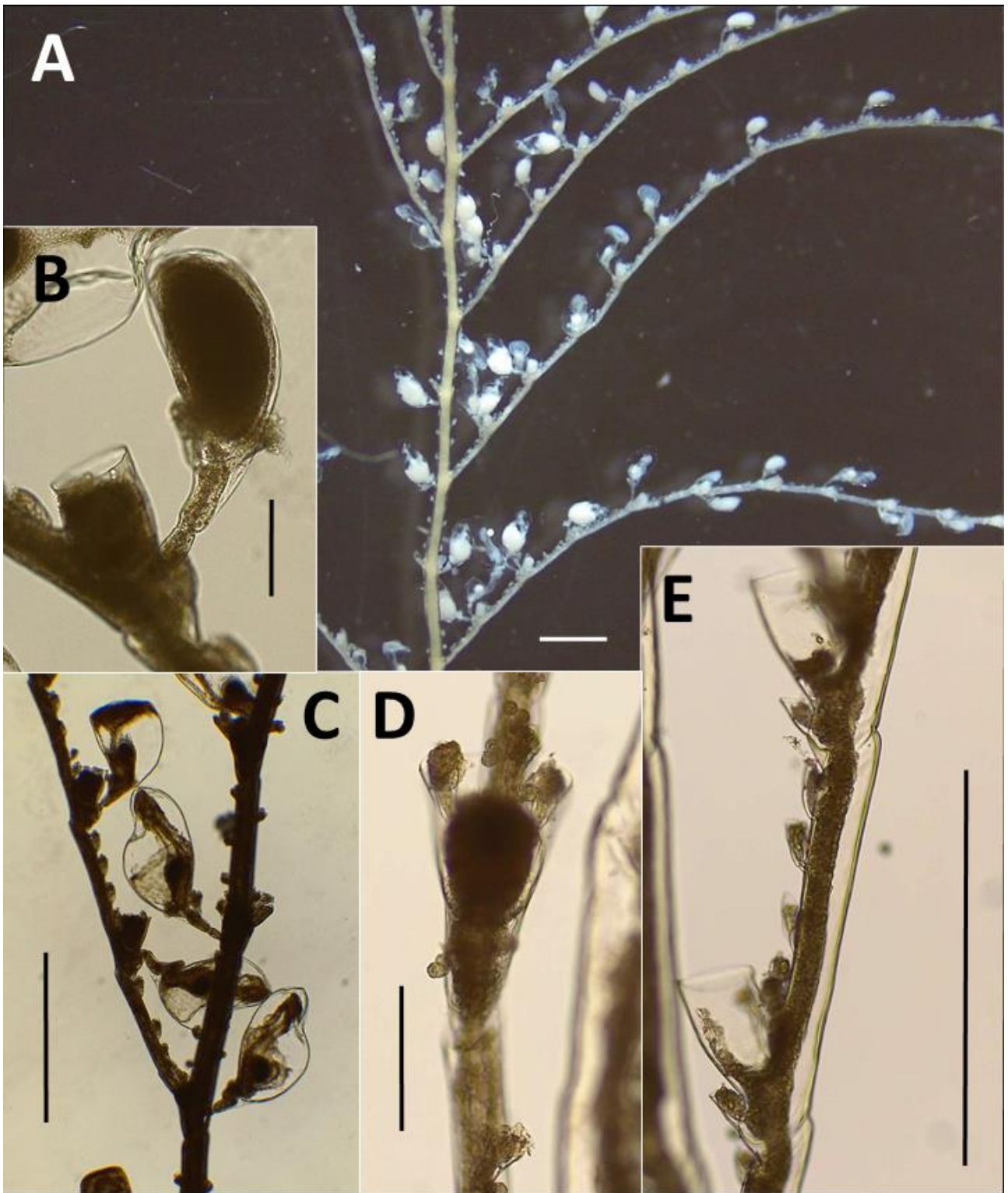
**Figure S17.** *Modeeria rotunda*: hydrotheca (A,B), stolonial colony (C). Scale bars: 300  $\mu\text{m}$  (A,B), 1000  $\mu\text{m}$  (C).



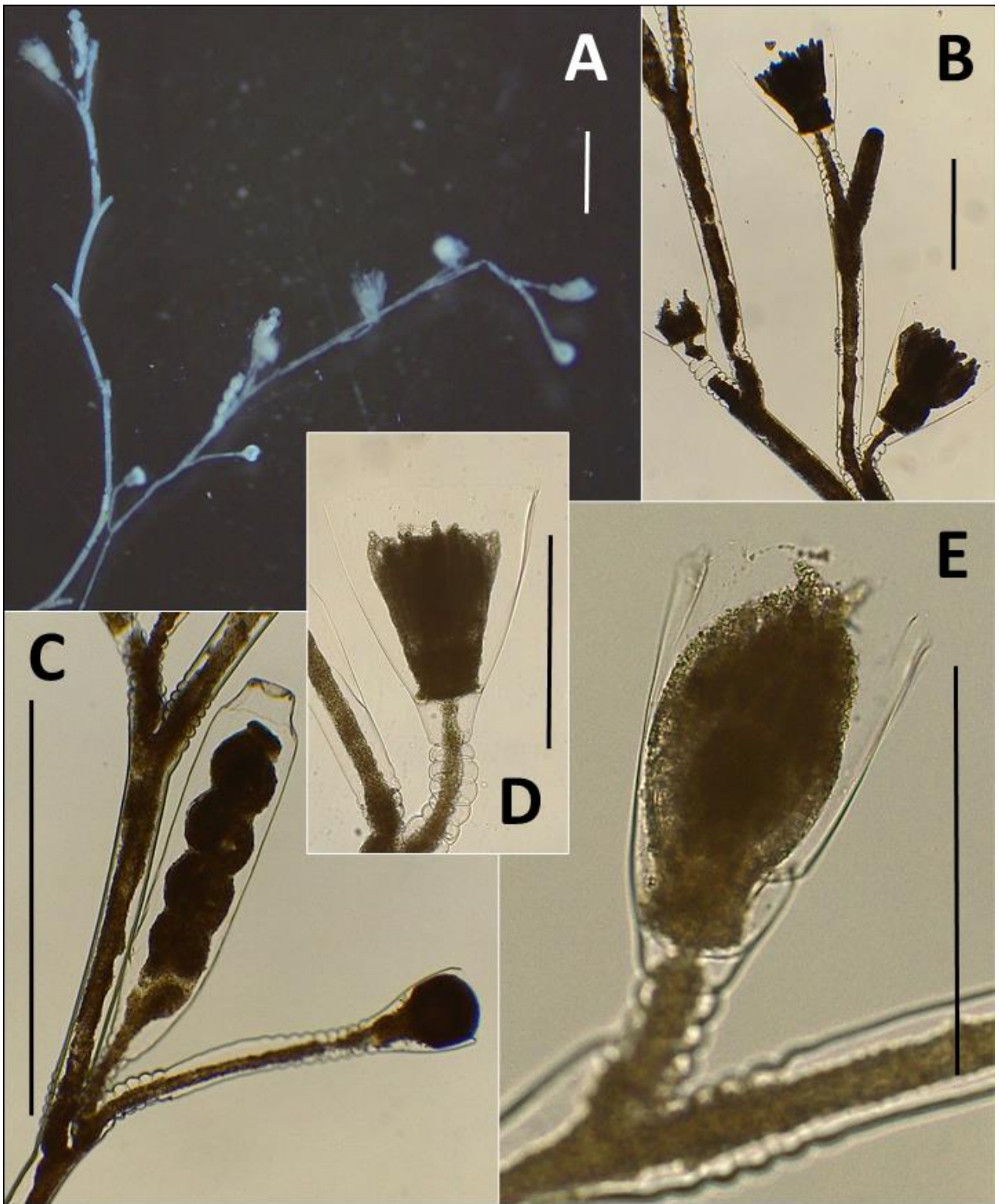
**Figure S18.** *Halecium fjordlandicum*: colony bearing female gonothecae (A), male gonothecae (B,D), hydranth (C), female gonotheca (E). Scale bars: 1200  $\mu\text{m}$  (A), 950  $\mu\text{m}$  (B,D); 140  $\mu\text{m}$  (C); 600  $\mu\text{m}$  (E).



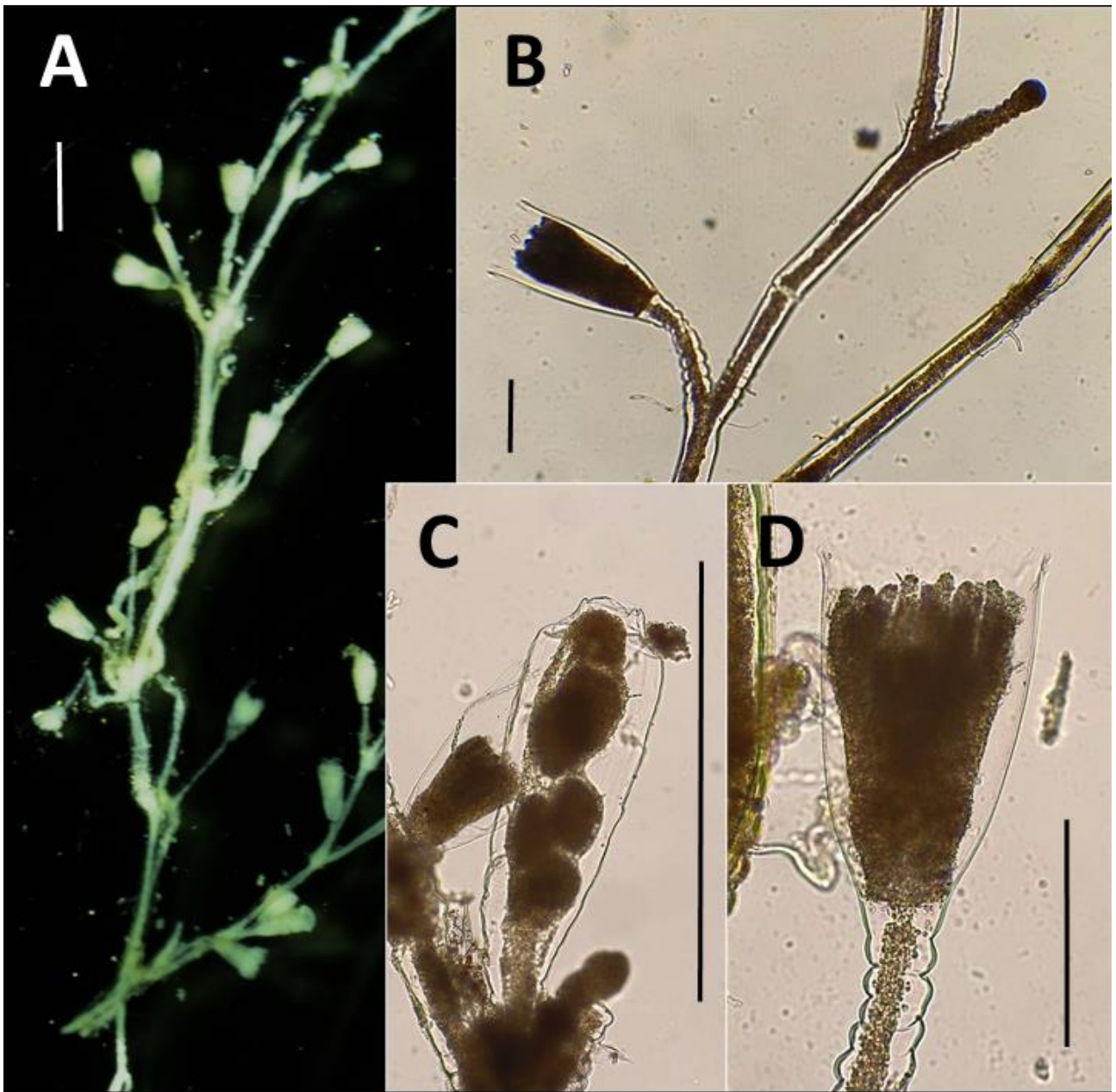
*Figure S19.* Halecium sp.: colony detail (A), gonotheca (B,E), stem detail (C), hydranth (D). Scale bars: 900  $\mu\text{m}$  (A, B, C, E), 160  $\mu\text{m}$  (D).



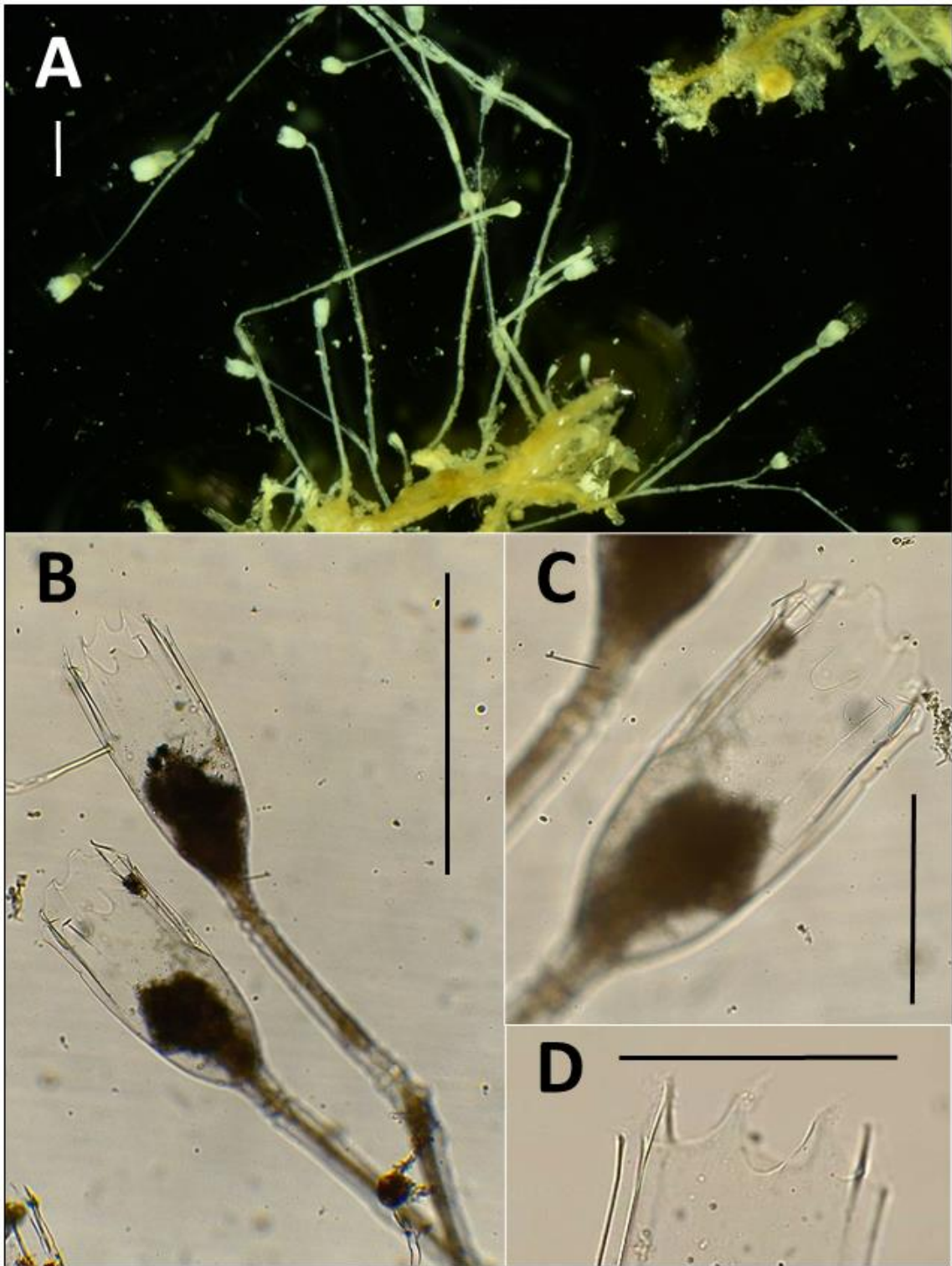
**Figure S20.** *Halopterus schucherti*: colony detail (A), male gonotheca (B), female gonothecae (C), cladial hydrotheca (D), nematothecae along a cladial internode (E). Scale bars: 830  $\mu\text{m}$  (A, C, E), 160  $\mu\text{m}$  (B, D).



**Figure S21.** *Obelia dichotoma*: colony detail (A,B), gonotheca (C), hydrotheca (D,E). Scale bars: 1100 µm (A,C); 500 µm (B,D,E).



**Figure S22.** *Obelia longissima*: colony detail (A,B), gonotheca (C), hydrotheca (D). Scale bars: 900  $\mu\text{m}$  (A, C), 270  $\mu\text{m}$  (B, D).



**Figure S23.** *Clytia linearis*: colony detail (A,B), hydrotheca (C) with a detail of the rim (D). Scale bars: 750  $\mu\text{m}$  (A, B), 350  $\mu\text{m}$  (C, D).

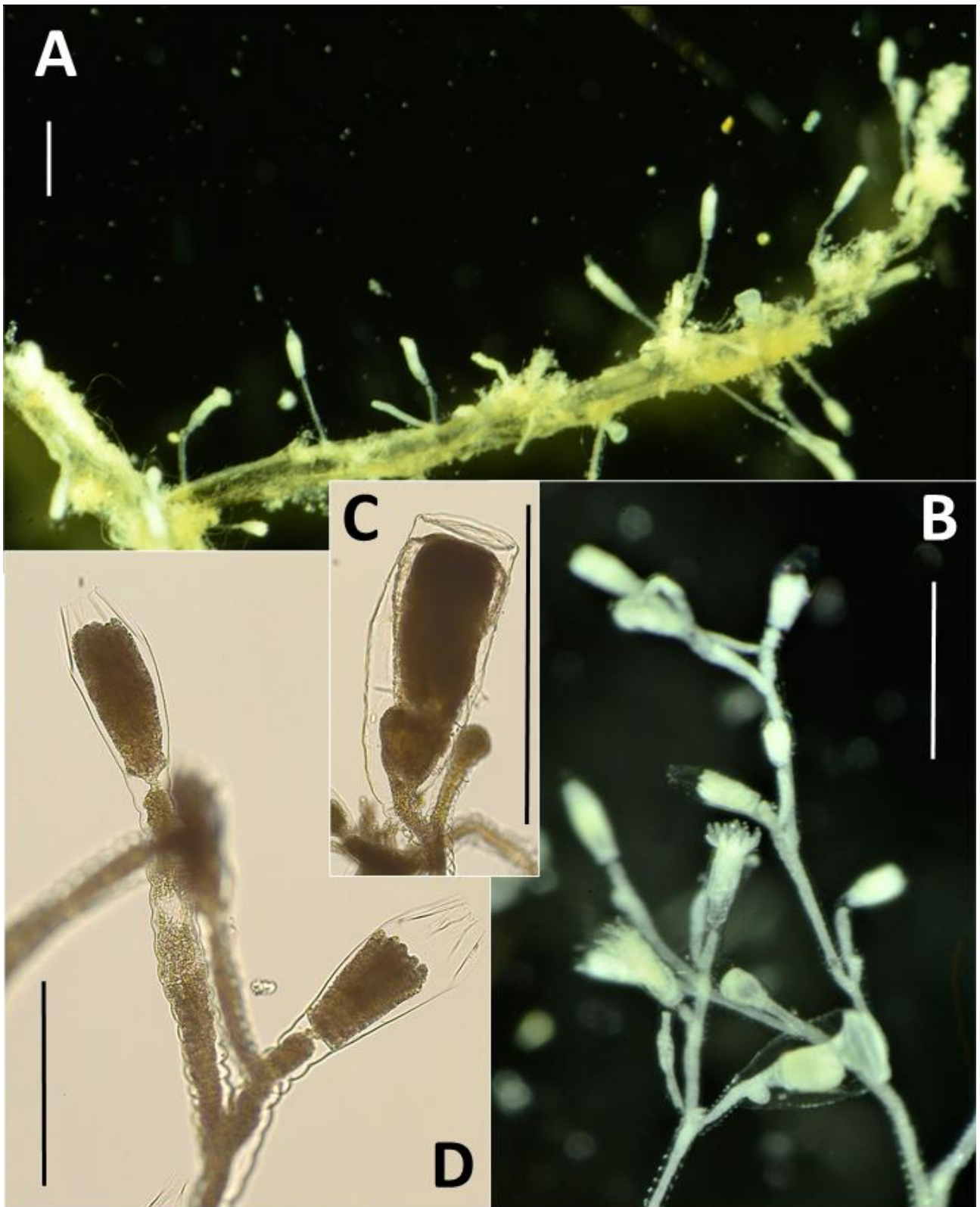




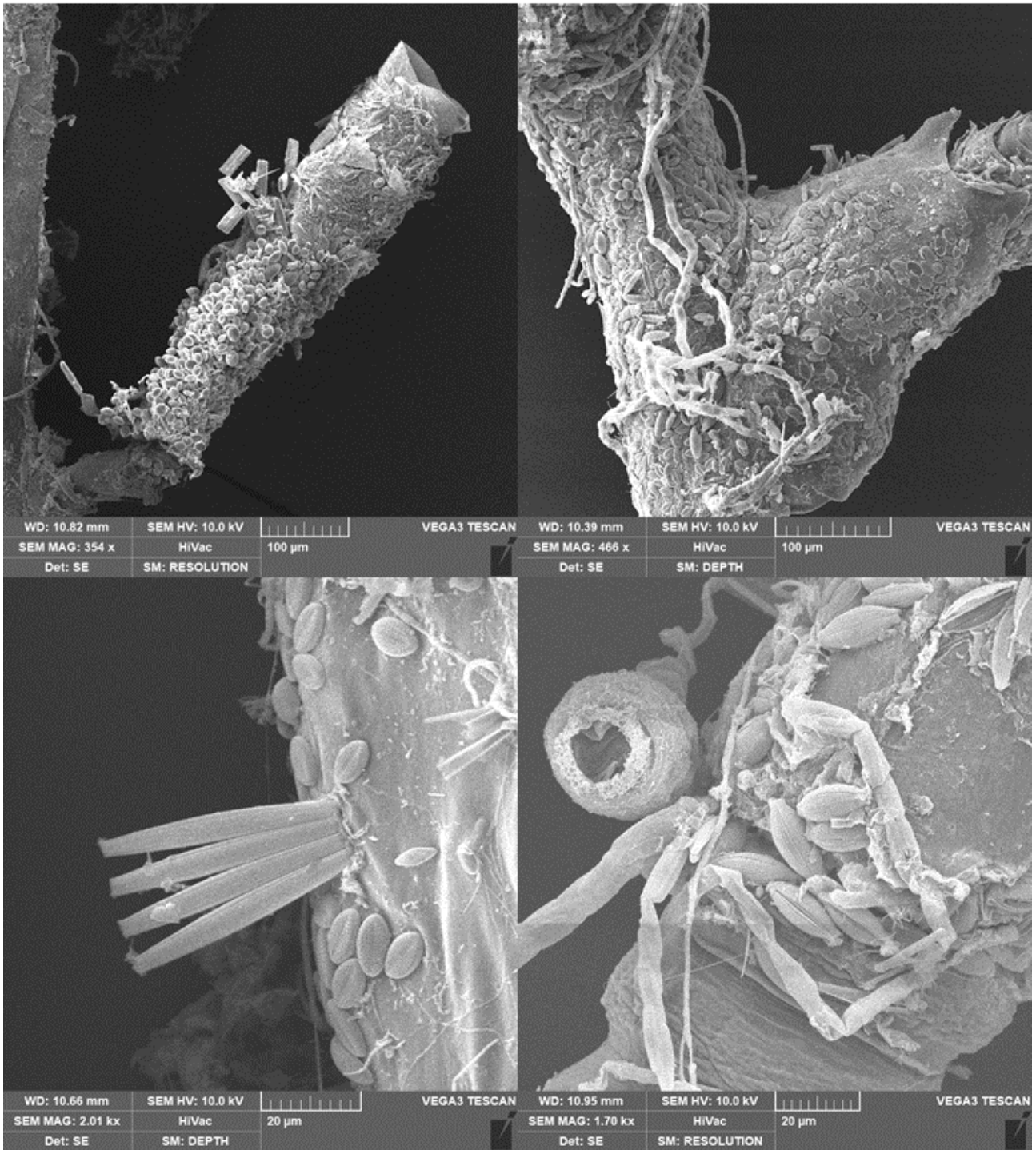
**Figure S24.** *Clytia reloncavia*: stem detail (A), hydrotheca with a detail of the rim (B,D), colony detail (C). Scale bars: 700  $\mu\text{m}$  (A, B); 1200  $\mu\text{m}$  (C, D).



*Figure S25.* *Clytia* spp.: colony detail (A), hydrotheca (B) with details of the rim (C). Scale bars: 500  $\mu$ m (A), 250  $\mu$ m (B).



**Figure S26.** *Phialella cf. quadrata*: stolonal (A) and erect (B) colony, gonotheca (C), hydrothecae (D). Scale bars: 600  $\mu\text{m}$  (A); 700  $\mu\text{m}$  (B, C); 400  $\mu\text{m}$  (D).



*Figure S27: Pictures taken through SEM showing epibionts (especially diatoms) colonising hydroids.*