

Mucus secretions in Cnidarian, an ecological, adaptive and evolutive tool

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ABSTRACT

Mucus secretion provides an interface with unique and multifunctional properties between the epithelial cells of many aquatic organisms and their surrounding environment. Indeed, mucus is involved in various essential biological processes including feeding, reproduction, osmoregulation, competition for space, defense against pathogens, xenobiotics, and a multitude of environmental stressors. The ability to produce a functional mucus layer is an important evolutionary step, arising first in Cnidaria that allowed for the development of the mucus-lined digestive cavity seen in higher metazoans. Mucus secretion by cnidarians has been moderately investigated in both corals and jellyfish, which among cnidarians are the ones that have shown the highest secretion rates to date. However, although in corals the production of mucus has received more attention, especially in view of the important ecological role played in coral reefs, in medusozoans the topic is little considered. Although the mucus secreted by corals has innumerable and important immunological, nutritional, and protective responsibilities, it should be remembered that jellyfish too represent a fundamental component of marine trophic web, playing numerous and important roles that are still unclear today. What is certain is that jellyfish are characterized (especially in the era of climate change) by large fluctuations in population density, the ecological implications of which are poorly understood. However, in both cases (Medusozoans and Anthozoans) to date some aspects relating to mucous secretions seem completely obscure, such as the microbiome and its variations as a function of environmental conditions or ontogenetic development, its implications in the field of immunological ecology, the consequent energy costs and finally the role played by the mucus in evolutionary terms. This review summarizes the properties, functions, ecological implications and evolutionary importance of mucus, in cnidarians, mainly focusing its roles in corals and jellyfish. Understanding these aspects relating to the ecological and evolutionary importance played by mucus is of fundamental importance for the ecosystems functioning.

INTRODUCTION

The study of mucus secretion by cnidarians has seduced scientists for nearly a century (Brown and Bythell, 2005). Mucus is produced to a greater or lesser extent by almost all cnidarians, in particular Anthozoans and Scyphozoans, and is essential for numerous life processes such as heterotrophic nutrition and sediment cleansing and as a defense against various environmental stressors and pathogens (Parisi *et al.*, 2020). Much of the literature has examined the functions and composition of mucus in a limited number of cnidarians, investigating the trophic significance of mucus production, especially in coral reef species, but neglecting fundamental aspects of its ecological, physiological, and evolutionary role in a multitude of organisms belonging to this Phylum (Bythell and Wild, 2011; Mydlarz *et al.*, 2016; Bakshani *et al.*, 2018; Palmer and Traylor-Knowles, 2018). Furthermore, the prevalence of issues related to climate change has redirected the research on implications related to this phenomenon, reducing the interest in the secretion of mucus in *sensu stricto* as a process underlying the adaptation and evolution of this ancient Phylum.

Indeed, mucus is involved in several biological processes essential for almost all aquatic metazoan acting as the first contact stratum with surrounding media from Cnidaria to Chordata (Stabili *et al.*, 2015; Alesci *et al.*,

2022). The mucus layers provide a multifunctional and protective hydrogel interface between the organisms' epithelial cells and the external environment (Cabillon and Lazado, 2019; Kramar *et al.*, 2019). Aquatic invertebrates and fish use a layer of mucus to protect body surfaces, gills, and intestines. It effectively acts as a dynamic physical and biochemical barrier, showing numerous biological and ecological roles such as protection against abrasion, toxins, environmental pollutants and pathogens, and osmoregulation, chemical communication, parental nutrition and many others (Hanaoka *et al.*, 2001; Ames *et al.*, 2020). Mucus has exceptional properties including elasticity, changing rheology and the ability to self-repair, thus representing an ideal means of trapping and immobilizing pathogens (Brown and Bythell, 2005). It is a key feature of the innate immune system in most aquatic and terrestrial metazoic phyla, playing a vital role in the prevention of microbial disease. In addition, while acting as a protective barrier, mucus allows the exchange of oxygen, carbon dioxide and nutrients and metabolites, lubricating the surfaces, reducing damage due to lesions, reducing dehydration of the epithelia and providing the polymer matrix which allows the transport of ciliary mucus particles (Reverter *et al.*, 2018; Alesci *et al.*, 2022). The properties of the secreted mucus generally depend on its composition consisting of exudates, such lipids, and mucins, polymeric glycoproteins that give the mucus its ability to gel, both released by mucocytes of

the epithelium (Brown and Bythell, 2005). Aging and some physical factors, such as depth and irradiance levels (Crossland, 1987; Zamzow, 2007), may influence the composition of the mucus, varying temporally within the same species and among different ones (Crossland *et al.*, 1980; Meikle *et al.* 1988; Ferrier-Pages *et al.*, 1998; Hadaidi, 2019). It would seem that the main biophysical characteristics of mucus, like the ability to form gels of different viscosity and elasticity that lubricate and protect the underlying epithelia, depend on the type of mucins expressed (Bythell and Wild 2011). Many hard and soft corals, for instance, continually release mucus, with a species-specific composition.

Mucus produced by cnidarians, similarly to other phyla, represents a fundamental aspect of the biology of these organisms and it is essential for several biological functions, including feeding, defending against pathogens, xenobiotics, and a multitude of environmental stressors, warding off aggression, and acting as an attacking weapon (Baier *et al.*, 1985; Rivera-Ortega and Thomè, 2018; Camacho-Pacheco *et al.*, 2022;). Although continuous mucus releasing is physiological, several studies demonstrated that some environmental stressors, such as high particle concentrations or high sediment loads, and exposition to air due to low tide conditions, can increase mucus production (Schuhmacher, 1977; Rublee *et al.*, 1980; Krupp, 1984; Wild *et al.*, 2004; Wild *et al.*, 2005; Liu *et al.*, 2018;).

Additionally, there is limited information in the literature on mucus release as a consequence of ocean acidification and global warming (Bythell and Wild, 2011); however, during coral bleaching, caused by rising temperatures, an increase in mucus production has been detected (Niggel *et al.*, 2009; Fransolet *et al.*, 2012), possibly resulting in a mucus composition changes (Wooldridge, 2009).

Anthozoan mucus has been studied for its biophysical characteristics, including rheology (activity under strain forces), and it has been discovered that it contains high molecular weight glycoproteins with characteristics that are similar to those of vertebrate mucins (Jatkar *et al.*, 2010), suggesting a similarity of mucus function between cnidarians and chordates (Bythell & Wild 2011). Effectively, the ability to produce a functional mucosa represents an important evolutionary step, which first evolved in Cnidaria and which was conserved into higher organisms, including terrestrial and human mammals. Although cnidarians are widely used as model systems for evolutionary and biological investigations in metazoans, the importance of the evolution of a functional mucus layer in invertebrates is often overlooked (Bakshani *et al.*, 2018).

Another fundamental but little explored aspect is represented by the ecological role of mucus in the life strategy of cnidarians, especially in jellyfish (*e.g.*, habitat for microbial colonization, involvement in biogeochemical cycles, dispersal of larvae, reproduction, and fertilization) (Pitt *et*

al., 2009; Liu *et al.*, 2018). Zooxanthellae have been found to contribute substantially to the high gross primary production in coral reefs; however, corals release nearly half of the carbon assimilated by their zooxanthellae in the form of mucus (Tarrant, 2007; Bythell and Wild, 2011;). The released mucus effectively traps organic matter from the water column and transports energy and nutrients to the sediment which acts as a biocatalytic mineralizing filter. In this way the mucus supplies energy to the heterotrophic reef community, thus establishing a recycling loop that supports benthic life, while reducing the loss of energy and nutrients from the reef ecosystem (Wagner *et al.*, 2012; Goldberg, 2018). In this perspective, there is very little information on the ecological role of mucus in jellyfish. For example, up to 7% of the carbon assimilated by jellyfish is released into the environment in the form of mucus (Hansson and Norrman, 1995), which appears to play an important role in the carbon cycle (Hansson and Norrman, 1995; Condon *et al.*, 2011; Tinta *et al.*, 2021). However, jellyfish mucus has received little attention, resulting in a poor understanding of mucus excretion rates, composition, and its fate in the ecosystem. In the context of the expected increase in the jellyfish population, it is desirable to include jellyfish in energy flow models and ecosystem studies (Ramondenc *et al.*, 2020). Lack of knowledge of the characteristics and functions of jellyfish mucus makes it more difficult to understand and model its role in the marine ecosystem.

Despite the multitude of ecological and physiological roles played by cnidarian mucus, and although some aspects of mucus secretion, function and composition have been widely investigated in some cnidarians, there are still many gaps in the knowledge of its composition variability, production rate, inter- and intraspecific variability, energetic significance, and ecological and evolutionary roles.

The purpose of this review is therefore to examine what is known about cnidarian mucus in *sensu stricto*, sites and mechanisms of secretion, composition, function and ecological role and fate, providing an “evolutionary key reading”.

Cnidarian ecology: general features and evolution

Cnidarians occupy a key evolutionary position as basal metazoans and are ecologically important as predators, prey, and structure builders (Goffredo and Dubinsky, 2016; Santos *et al.*, 2016). The cnidarians are collectively an extremely diverse group of highly successful ancient aquatic organisms, which represent animals with incredibly different morphologies and life-history traits, but united by the presence of a specialized cell type: the cnidocyte (Basso *et al.*, 2019). Molecular data suggest that the first cnidarians appeared about 740 million years ago (Park *et al.*, 2012). In 200 million years the phylum has undergone significant diversification (Park *et al.*, 2012) and today it consists of about 14,866 accepted species (WoRMS, 2022), taxonom-

ically divided into five classes Anthozoans, Cubozoa, Hydrozoans, Scyphozoa and Staurozoa, with an estimated number of species of ~11,000, including mainly marine invertebrates such as anemones, corals and jellyfish (Daly *et al.*, 2007). Together, cnidarians have a global distribution and can occupy a wide range of both marine and freshwater environments.

Cnidarians present two forms, the polyp and the jellyfish, sessile and planktonic respectively. These are formed by three layers: an internal gastrodermis derived from the endoderm, surrounding the gastrovascular cavity, an intermediate matrix called mesoglea, and an external epidermis derived from ectoderm (Lommel *et al.*, 2018; D'Ambra *et al.*, 2021; Zhao *et al.*, 2021). The oral opening of the polyp is surrounded by tentacles, suitable for capturing the prey since heterotrophy is required to adequately supply nutrients for some species when photosymbiotic partners do not sufficiently supply the nutritional requirement (Arai, 1997; Goldberg, 2018). Polyps can form colonies or live as solitary organisms. Apart from the polyp stage, Cubozoa, Hydrozoa, Scyphozoa, and Staurozoa have a free-swimming planktonic stage, the jellyfish, which coexists with the polyp stage, but not all Scyphozoa exhibit a polypoid phase, such as *Pelagia noctiluca*. Cubozoa, Hydrozoa, and Scyphozoa classes have a metagenic life cycle: this consists of a pelagic jellyfish that reproduces sexually and a benthic polyp that reproduces asexually (Lucas *et al.*, 2012). This suggests that they may have separated evolutionarily from Anthozoa since most of them have only the polyp stage. Cnidarians are phylogenetically basal aquatic animals belonging to Metazoa, with radial symmetry and simple tissue organization. Evolutionarily they represent the first Metazoa; some of them can live for several centuries despite continuous exposure to different pathogens during their lifetime (Petralia *et al.*, 2014). Since they possess only an innate immune system to protect themselves against pathogens, it is difficult to understand how cnidarians can achieve such high levels of longevity (Parisi *et al.*, 2020). Phylogenetic analyses have confirmed that Anthozoa appeared earlier than the other classes in the evolutionary history of the Metazoa as they have circular DNA, in contrast to Cubozoa, Hydrozoa, and Scyphozoa, which have linear DNA (Technau and Steele, 2011). Due to their key position in evolution, these organisms play an essential ecological role in marine ecosystems and trophic web (Tarrant, 2007).

Since Cnidarians represent the most primitive metazoans, their evolution is of fundamental importance to study the origin of animal. The phylogeny of Cnidaria has been debated for decades, and still remains unresolved for some taxa (Kayal *et al.* 2018; McFadden *et al.*, 2022). The origin and evolution of Cnidaria phylum posed the basis for their ecological success but the mechanisms lie at the origins and subsequent diversification of some characters, like symbiosis, colonial body plans, elaborate life histories,

and cnidocytes, remain source of debate. However, a today accepted version of Cnidaria phylogeny, based on morphology, life-history traits, and molecular data, is presented below. It is accepted that the common ancestor of all Cnidaria is represented by a single polyp that lacked a medusoid stage. From this ancestor, around 15,100 species sorted in the following clades: Anthozoa, Endocnidozoa, and Medusozoa. Anthozoa comprise most of the species (~10,130) of Cnidaria sorted in two accepted subclasses Octocorallia and Hexacorallia (see McFadden *et al.*, 2022 for a detailed phylogeny of Anthozoa). Endocnidozoa consist of around 798 species of endoparasites (Myxozoa) and the monospecific Polypodiozoa, *Polypodium hydriforme* Ussow, 1887 (a parasite of the oocytes of acipenseriform fishes (paddlefish and sturgeons). Medusozoa encompass Cubozoa (~48 species), Hydrozoa (~3,875 species), Scyphozoa (~241 species), and Staurozoa (~49 species) (Evans, *et al.* 2008; Chang *et al.*, 2015; Zapata *et al.*, 2015; Kayal *et al.*, 2017; McFadden *et al.*, 2022).

The phylogenetic relationships of Cnidaria are still discussed and in some cases far from being elucidated. Despite this, recent studies using morphological, transcriptome, genome (both mitochondrial and nuclear), single gene, data tried to disentangle the complicated question (Chang *et al.*, 2015; Zapata *et al.*, 2015; Kayal *et al.*, 2017). Despite the divergencies between the studies of Chang *et al.*, 2015 and Zapata *et al.*, 2015, large congruence resulted in the evolutionary reconstructions of the cnidarian lineages, highlighting the importance of using large genomic datasets and increased taxon sampling in dealing evolutive questions (Kayal *et al.*, 2018). In this latter study, the authors, providing the most comprehensive taxon sampling of Cnidaria for phylogenomic analysis, supported the monophyly of Anthozoan, considering Ceriantharia as the sister group of Hexacorallia; and Zoantharia as the sister group of all other Hexacorallia. This, due to the presence in all the cited taxa of a single siphonoglyph (a ciliated groove located in the actinopharynx) shading light on the possible bilateral character of the Anthozoa, and obviously of Cnidaria, ancestor already proposed by Finnerty *et al.*, 2004. Antipatharia were not included in the study by Kayal *et al.*, 2018, for the unavailability of genomic data for this group, that still represent a gap in evolutionary useful data for the Cnidaria. For Medusozoa the phylogenetic background is less entangled respect to Anthozoa. In fact, it is accepted that Scyphozoa, Staurozoa, Cubozoa, and Hydrozoa, composing Medusozoa, clade as two distinct monophyletic groups: i) the first, encompassing Scyphozoa, Staurozoa, and Cubozoa, of which the earlier name is Acraspeda in Haeckel, 1880, that used the name with its present sense; and ii) the Hydrozoa composed of monophyletic Hydroidolina and Trachylinae. Finally, the sister relationship between Endocnidozoa (Myxozoa and Polypodiozoa) and Medusozoa, is corroborate by genomic

analyses too (Siddall *et al.*, 1995; Jimenez-Guri *et al.*, 2007; Collins, 2009; Chang *et al.*, 2015; Okamura *et al.*, 2015; Kayal *et al.*, 2018; Novosolov *et al.*, 2022).

Depicting off an evolutionary processes conclusion it seems that all the Cnidaria evolved from an ancestral non-symbiotic, stinging, and medusa-lacking, solitary polyp with a planula larva (Kayal *et al.*, 2018; Khalturin *et al.*, 2019). Symbiosis, coloniality, medusa life-history stages (also comprising losses of medusa stage events) occurred independently during the evolution of Cnidaria.

In addition to their key evolutionary position, cnidarians are also important as both predators and prey in aquatic ecosystems, playing a key role in biogeochemical cycles as recently suggested by Tinta *et al.* (2021). Gelatinous cnidarians are prey to several taxa including other cnidarians, fish and turtles. Although gelatinous cnidarians are sometimes considered to be relatively unsightly or of low nutritional value (*e.g.*, Avent *et al.*, 2001), in reality they are often underestimated as a food source because they tend to be digested quickly (Arai *et al.*, 2003; Arai, 2005; Costa *et al.*, 2018). As predators, cnidarians can dramatically alter plankton composition and even compromise fishing yield through dietary overlap and direct predation (Arai, 1988; Purcell and Arai, 2001; Purcell and Sturdevant, 2001). Suspension-fed benthic cnidarians also impact planktonic composition and may play an important role in benthic-pelagic coupling. For example, a Mediterranean gorgonian has been found to consume a large number of invertebrate eggs and larvae, in particular larval bivalves, with unknown effects on bivalve recruitment and consequently on population dynamics (Rossi *et al.*, 2004). Particularly influential can be the aggregations or blooms of jellyfish (Hydrozoa, Scyphozoa or Cubozoa) which can have important ecological consequences.

Recognition of the importance of jellyfish in marine ecosystems is growing steadily (Tinta *et al.*, 2021). The clade Medusozoa includes four classes: Cubozoa (Carybdeida and Chirodropida), Hydrozoa (Hydroidolina and Trachylina), Scyphozoa (Coronatae and Discomedusae), and Staurozoa (Cleistocarpida and Eleutherocarpida).

Gelatinous cnidarians are found in all the world's oceans and can occur in very high densities in large blooms; however, trends in jellyfish abundance appear to act on a local rather than a global scale (Richardson *et al.*, 2009; Brotz *et al.*, 2012; Condon *et al.*, 2013; Schaub *et al.*, 2018). For example, distinct coastal jellyfish hotspots that can span tens of square kilometres can occur in coastal waters (Houghton *et al.*, 2006). Global jellyfish outbreaks appear to have become increasingly frequent and abundant in several coastal areas around the world and to last longer in recent years (Heaslip *et al.*, 2012). It is not yet clear whether this is just an upward phase of a natural pattern of decadal oscillations or a real increase in gelatinous zooplankton blooms (McCanch and McCanch,

1996; Arai, 2005; Purcell, 2005). It has been hypothesized that jellyfish have benefited from human-caused environmental changes, such as: climate change, overfishing, eutrophication, habitat modification (Cardona *et al.*, 2012; Hamilton, 2016). Outbreaks of jellyfish have caused concern about their potential harm to human welfare, tourism, and fisheries (Graham *et al.*, 2014). Indeed, it would appear that due to their high abundance and spatial overlap, jellyfish could have a negative impact on fish of commercial interest through direct predation or through competition for plankton prey (Decker *et al.*, 2018). Considering the extremely negative perception of jellyfish by the general public, it is not surprising that these organisms are often considered as stressors affecting the viability of ecosystem services (as in the case of competition with commercial fish stocks or reduction of the quality of bathing). In this regard, the role of jellyfish as “providers” of ecosystem services in terms of regulation, support, and provisioning should be redefined and highlighted.

Jellyfish have characteristics that place them in an influential position to structure the flow of energy through pelagic food webs, such as high growth and reproduction rates, large planktivorous diets, and few apparent predators (Richardson *et al.*, 2009). A wide range of taxa including other jellyfish, some molluscs, arthropods, fish, and birds regularly or opportunistically include jellyfish in their diet. Even though jellyfish can have a low nutritional value compared to other prey items (Doyle *et al.*, 2007), consumption of sufficient quantities can sustain large predators.

Jellyfish are also extremely important predators in pelagic marine systems (Pauly *et al.*, 2009). The diversity in their feeding mechanisms and body size allows jellyfish to feed on a wide range of prey types and sizes (micro-heterotrophs, zooplankton, other jellyfish, fish, fish eggs and larvae). Furthermore, most jellyfish are characterized by some sort of selectivity. When jellyfish blooms occur their rate of collective prey consumption can be so high as to directly or indirectly control the population size of other zooplanktonic organisms, including fish larvae (Purcell, 1989). In particular, intense jellyfish predation on some prey items can cause a shift in the trophic structure of marine communities as a result of trophic cascades. Thus, large jellyfish populations that can influence pelagic food webs, exerting top-down control over zooplankton communities (Purcell, 2005; Sommer and Lengfellner, 2008; Canepa *et al.*, 2014; Milisenda *et al.*, 2018;). Jellyfish can therefore significantly redirect the flow of energy through food webs and nutrient recycling (Deason and Smayda, 1982; Suchman *et al.*, 2008; Condon *et al.*, 2012; Ruzicka *et al.*, 2020). One of the most important services jellyfishes provide is climate regulation through the process of sequestering and transporting carbon through the water column. The sinking or accumulation of jellyfish carcasses on the seabed may also play an important role in the transfer of carbon from surface

waters to the seabed (Lebrato *et al.*, 2012) through a complex pelagic-benthic coupling process. Through the process of carbon sequestration, jellyfish provide regulating services (Doyle *et al.*, 2014), nutrients that support primary production (West *et al.*, 2009), and organic matter that stimulates microbes. Indeed, jellyfish can also provide small but significant amounts of nutrients to support primary production (Pitt *et al.*, 2009). Inorganic nutrients such as carbon, nitrogen and phosphorus are “regenerated” by jellyfish excretion or also through mucus production. Similarly, regenerated jellyfish products released into water are available to heterotrophic bacteria, and thus for respiration rather than primary production, creating a “jelly loop” involving the carbon cycle between jellyfish, bacteria, nanoflagellates heterotrophs, and ciliates (Condon *et al.*, 2011).

Numerous studies have investigated the role of bacteria during jellyfish bloom highlighting that variations in bacterial community structure associated with living or decaying jellyfish can have important consequences in trophic interactions and implications for carbon, nitrogen and phosphorus recycling (Titelman *et al.*, 2006; Pitt *et al.*, 2009; Tinta *et al.*, 2010; Tinta *et al.*, 2012; Blanchet *et al.*, 2015; Tinta *et al.*, 2016; Aprill, 2017). Bacteria associated with the outer surfaces of cnidarian epithelia may play a number of crucial roles, such as nitrogen fixation (Lesser *et al.*, 2004), antibiotic synthesis (Ritchie and Smith, 2004; Kelman *et al.*, 2006) decomposition of organic compounds (Di Salvo, 1969), primary defense against pathogens (Ritchie, 2006).

The surfaces of cnidarians, as well as other marine organisms, are a unique and favorable habitat for colonization by microorganisms and microbial communities often showing a marked variability (Aprill, 2017). In fact, jellyfish can also provide important habitats for various species of marine organisms. The relationships and uses of jellyfish are so varied and complex that they resemble those typically described for tropical rainforests. Jellyfish can provide (1) pelagic refuges or shelters, (2) pelagic substrate, and (3) a host for algal symbiotic associations. One of the best-documented biological interactions between jellyfish and marine organisms is the interaction between jellyfish and juvenile fish, generally considered a facultative symbiotic relationship (Kramar *et al.*, 2019).

Gelatinous cnidarians can provide a pelagic substrate (habitat) for a range of taxa from microbes to invertebrates, including crustaceans (Perissinotto and Pakhomov, 1998; Pagès, 2000), pycnogonids (Pagès *et al.*, 2007), digeneans (Martorelli, 2001) and protists (Moss *et al.*, 2001). Studies on cnidarian jellyfish show the presence of endobiotic bacteria in tentacle jellyfish (Kramar *et al.*, 2019), as in the case of the upside-down jellyfish *Cassiopea sp.* This spends most of the time upside down resting on the seabed in order to maximize the photosynthetic activity of the zooxanthellae present in their oral arms; their

activity can increase benthic oxygen production nearly 100-fold (Welsh *et al.*, 2009). Another algal host is the pleustonic jellyfish *Velella velella* (Purcell *et al.*, 2012), in which its symbiotic zooxanthellae are able to photosynthesize and provide energy to the host.

Cnidarian-microorganisms interactions are well documented due to the extraordinary ecological importance of the mutualistic symbiosis between coralline anthozoans and cellular photosynthetic dinoflagellates (Davy *et al.*, 2012).

Cnidarians, mainly Anthozoans, provide a three-dimensional structure to benthic ecosystems, particularly tropical coral reefs. Coral reef ecosystems provide habitat for several taxa, protect coasts, and provide commercial and recreational resources for humans.

Indeed, several species of anthozoans play a vital role as bio-constructors, creating habitats that serve as shelter for many other organisms and are home to great biodiversity. Anthozoans make up a class within this phylum and comprise a relatively well-known group consisting of hard and soft corals, gorgonians, sea feathers, black corals, and anemones (Palmer and Traylor-Knowles, 2018).

Anthozoans are widely distributed throughout the seas of the world from the intertidal to the deep sea. Unlike other classes of cnidarians, anthozoans never produce jellyfish during their life cycle (Goffredo and Dubinsky, 2016).

Within the anthozoans, the subclass Octocorallia refers to the colonial species with eight tentacles arranged in a single cycle and has three orders: Alcyonacea, Heliopora and Pennatulacea. The other subclass, Hexacorallia, includes species of anthozoans that can be solitary, colonial or aggregated, and consists of 6 orders: Actiniaria, Antipatharia, Ceriantharia, Corallimorpharia, Zoanthinaria and Scleractinia (Otero *et al.*, 2017). The latter are mainly responsible for the construction of coral reef structures, especially in tropical and subtropical seas, as well as Cold-Water Corals (CWCs) that are among the main ecosystem engineering species in the deep sea worldwide and particularly in the Mediterranean Sea (Soetaert *et al.*, 2016; Angiolillo *et al.*, 2021).

Anthozoans are the most speciose class of the phylum Cnidaria, with an estimated 10,130 extant species (Daly *et al.*, 2007). Anthozoans are phylogenetically basal, both within the Metazoans as a whole and probably within Cnidaria (Kayal *et al.* 2013), with Scleractinia already appearing in the Middle Triassic (about 250 million years ago (Romano and Palumbi, 1996). Most existing anthozoans live in obligate endosymbiosis with dinoflagellates members of the genus *Symbiodinium* (Aranda *et al.*, 2016), a relationship that underlies the ecological success of the class. In this association, *Symbiodinium* provides over 90% of the energy needs of the anthozoan (Muscatine and Porter, 1977) and, for hard corals, facilitates the calcification of the exoskeleton, allowing the formation of coral reef ecosystems. In return, the anthozoan host protects its algal

partner useful for the purpose of recycling waste carbon and nitrogen (Jeong *et al.*, 2012). This coral-scleractinian algae association is among the most investigated of the relationships that anthozoans have with the microbiota.

This interaction could be closely related to the secretion of mucus in corals, with a preponderant role also in the ecology of the anthozoan immune system. Cnidarians, particularly corals, possess a microbiota that is not only distinct from that of their surroundings, but also from other coral species (Cooney *et al.*, 2002; Frias-Lopez, 2002; Ritchie and Smith, 2004; Brown and Bythell, 2005). It is therefore plausible to hypothesize that the evolution of the superficial mucosa as a barrier may be associated with the ability to exclude certain bacterial species from body tissues, with the exception of a selected central microbiome. With a layer of mucus, as in Cnidaria, non-commensal bacteria are essentially excluded from the tissues of the cnidarians. The activity of mucus in the exclusion of non-commensal bacteria may have initiated the evolution of the alimentary canal and therefore the evolution of higher organisms, as well as representing an essential feature of the innate immune system. It is therefore increasingly evident that the microbiome associated with anthozoans is crucial for their health and is possibly partially modulated by the immune mechanisms of corals (Bourne *et al.*, 2016). Deciphering the immunological complexities of coral-microbe symbiosis is an ecologically key research field that could provide important insights into the establishment and functioning of symbiosis throughout the animal kingdom.

This is particularly true when one considers that, despite their phylogenetic position and apparent morphological simplicity, anthozoans are immunologically complex (Miller *et al.*, 2007; Shinzato *et al.*, 2011), with large genomes and gene families that are comparable to those of Bilateria (Augustin and Bosch, 2010), which is why they represent a very interesting group for the study of the evolution of immunity and mutualism. Like all organisms, anthozoans possess innate immune mechanisms (Palmer and Traylor-Knowles, 2012), but as invertebrates they lack the more complex adaptive component of immunity. Innate immunity allows a non-specific and immediate response to both endogenous and exogenous threats with the aim of restoring homeostasis (Beutler, 2004; Medzhitov, 2008). However, at the same time, anthozoans utilize a large, complex, and diverse repertoire of immune receptors (Miller *et al.*, 2007), signaling pathways (Wolenski *et al.*, 2011) and “stress” responses (Palmer *et al.*, 2008), which allow to eliminate pathogens, heal wounds, and defend oneself (Palmer and Traylor-Knowles, 2012; Mydlarz *et al.*, 2016). Ecological immunology theory hypothesizes that variations between and within constituent immunity and immune responses are due to energy trade-offs between costly functional traits such as reproduction, growth, and maintenance / immunity (Sheldon and Verhulst, 1996; Sadd and Schmid-

Hempel, 2009). In this regard, one of the first signs of suffering of corals is the increase in mucus secretion (Brown and Bythell 2005), a function that requires huge energy investments and that leads to the exhaustion of reserves, compromising the organism’s immunity (Sheridan *et al.*, 2014). Similarly, thermal bleaching events result in the loss of *Symbiodinium* which supplies energy to the coral causing it to die (Brandt and McManus, 2009). The interruption of this interaction results in a state of energy deficit and malnutrition, which causes a lowering of the defenses and an increase in energy expenditure in order to resist or tolerate the disease (Mayack and Naug, 2009).

Site, mechanism of mucus secretion and composition

In cnidarians mucus secretion is mainly attributed to specific cells, the mucocytes (Goldberg, 2002; Clarke *et al.*, 2020), the only cells currently identified with mucus production in these organisms (Brown and Bythell 2005). However, other glandular cells have been identified in coral tissues (Kinchington, 1981, Le Tissier, 1987; Parker and Krumlauf, 2017).

Mucocytes can occupy up to 90% of the ectoderm in some tissue areas: this has been confirmed by observation of histological sections in selected coral species (Brown and Bythell 2005). Several studies highlighted the presence of mucocytes in three coral species: *Galaxea fascicularis* (Linnaeus, 1767), *Tubastrea faulkneri* (Wells, 1982), *Acropora muricata* (Linnaeus, 1758) (Marshall and Wright, 1993). These three species belonging to class Anthozoa, seem to be evolutionarily separate from the other classes of Cnidarians, but they represent a good model for the description and mode of mucous secretion. In *G. fascicularis*, large mucocytes from 10 to 20 μm in size, were found on the external oral ectoderm, and in the oral gastrodermis. These cells were characteristically club-shaped, with basal nuclei and large granular inclusions. In the oral gastrodermis, they surrounded the zooxanthellae and presented granular inclusions larger than ectoderm mucocytes. In contrast, the aboral gastrodermis (opposite to the oral gastrodermis) was characterized by fewer and smaller mucocytes, 5 to 10 μm in length, although structurally comparable. Few small mucocytes were also found in the calcicoblastic layer, the portion of epidermis responsible for the formation of the skeletal structure. In *T. faulkneri*, mucocytes were very abundant in the calcicoblastic layer and seem to be closely related to the skeletal structure. In *A. muricata*, no mucocytes were found in the apical portion of the oral ectoderm, although a thick layer of mucus covering the ectoderm was observed; in contrast, numerous mucocytes were found in the basal portion oral ectoderm (Marshall & Wright, 1993). This demonstrates that there is no single pattern of mucocytes distribution and abundance valid for all Cnidarians, although such differences may depend on the physiological development/exchange

of mucocytes (Brown & Bythell, 2005).

It has been noted that due to induced stress the number of mucocytes increases. In a study by Fransolet *et al.* (2013), the sea anemone *Exaiptasia diaphana* (Rapp, 1829) was subjected to a transient increase in temperature combined with high illumination for 30 hours; this resulted in bleaching, as endosymbiont microalgae belonging to the genus *Symbiodinium* disappeared. During the first day after the stress, a significant increase in cell proliferation was recorded at the gastrodermis and ectoderm levels, the ratio of ectodermal mucocytes increased significantly three weeks after the induced stress. The increase in mucocytes numbers may help restore symbiosis with endosymbiont dinoflagellates of the genus *Symbiodinium* (Fransolet *et al.*, 2013).

In general, the main mucus functions are to lubricate the epithelium and keep it hydrated and provide protection from pathogens (Mall, 2008). Mucus prevents the passage of bacteria due to its particularly high viscosity while maintaining its impermeability to water and gases (Cone, 2009). The ability of mucus to trap particles is closely related to its unique physicochemical properties as well as its phospholipid and glycolipid content (Murty *et al.*, 1984). An important characteristic of mucus is its layered structure: the layers are cyclically removed and regenerated, which allows contaminants to be efficiently eliminated, thus not reaching the underlying tissues (Ducklow and Mitchell, 1979), in a process known as sloughing, that further than playing an essential role in defense against pathogens, it determines the thickness of the mucus layer (Cone, 2009). Furthermore, mucus has elasticity, provided by the mucin fibres, which are composed of alternating glycosylated (hydrophilic) and bare (hydrophobic) protein regions; this conformation allows them to trap particles using a large number of low-affinity bonds that form and break very easily (Cone, 2009). The mucus of the anemone *Actinia equina* (Linnaeus, 1758) contains biomolecules that exhibit lysozyme-like antibacterial activity, and it has been shown that the efficiency of these compounds is influenced by some environmental parameters, such as temperature, pH and ionic strength (Stabili *et al.*, 2015). However, these bioactive molecules have shown relevant antimicrobial effects under controlled conditions (temperature of 37 °C) that rarely occur in the natural environment of *A. equina*; this highlights the limitations of these compounds in performing their antibacterial activity at lower temperatures and more basic pH (Stabili *et al.*, 2015). Similarly happens in hard and soft corals (class Anthozoa) (Kelman *et al.*, 2006). However, the efficacy of antimicrobial compounds in the absence of mucus and the efficacy of mucus in the absence of antimicrobial compounds have not been tested (Bakshani *et al.*, 2018).

In general, mucus in the Animalia kingdom is predominantly composed of water (approximately 95% of its total

wet mass), while the remaining 5% is composed of mucins, phospholipids, cholesterol, salt, lipids, fatty acids and proteins with defensive purpose, such as lysozyme, immunoglobulins and defensins (Marshall and Wright, 1991; Celli *et al.*, 2005; Bansil & Turner 2006; Pearson *et al.*, 2011; Hubot *et al.*, 2022).

Mucus of Cnidaria is composed principally, as for other Metazoa, of water at a percentage around 95%, with the remaining part composed by glycoproteins (□3%) and a mixture of other molecules (□2%), mostly represented by both inorganic salts (NaCl) and organic compounds like peptides, nucleic acids, lipids, and antibodies (Stabili *et al.*, 2015; Bakshani *et al.*, 2018; Hubot *et al.*, 2022). These components, mainly glycoproteins, manage the mucus elasticity and viscosity (Bansil and Turner, 2018) useful in the defense (through antibiotics and antimicrobial peptides), lubrication of underlying epithelia and act as a trap for food particles and transport to digestive system (Bakshani *et al.*, 2018; Hubot *et al.*, 2022). It has been reported the presence of nematocysts and toxins in the mucus of *scyphomedusae* (Shanks and Graham, 1988). Mucus, when released, is inevitably contaminated by several elements, such as sediment, and a wide range of microorganisms: therefore, attempts have been made, in a controlled environment, to exploit artificial stresses such as dehydration and physical stimulation in order to achieve the release of mucus free of other components. However, any functional differences between mucus released under natural conditions and mucus released under artificial stress have not been investigated (Brown and Bythell, 2005). In this regard, previous work suggests that mucus obtained through artificial stress induction had a higher organic content than mucus taken in the natural environment (Gottfried and Roman, 1983).

To our best knowledge, mucus macromolecular composition (proteins, lipids, and carbohydrates) and the C/N ratio in cnidarian has been described for few species including mainly belonging to Anthozoa and Scyphozoa (Ducklow and Mitchell, 1979; Ducklow and Mitchell, 1991; Vacelet and Thomassin, 1991; Stabili *et al.*, 2015; Hubot *et al.*, 2022). Ducklow and Mitchell (1991), studied the composition variability of the mucus of different Anthozoa species, highlighting its utilization by microbial communities and the protective role of mucus especially related to water insolubility, chemical resistance to degradation, and inhibiting properties allowing a long degradation time by bacteria. In Scyphozoa, Hubot *et al.*, 2022, evaluated the mucus macromolecules in the species *Aurelia aurita*, *Chrysaora fulgida*, *Chrysaora pacifica*, *Eupilema inexpectata*, and *Rhizostoma pulmo* concluding a non-species-specific composition, highlighting the absence of data that demonstrate the variation in mucus biochemical features, related to different conditions and situations as feeding, reproduction and stress proposed by

Tinta *et al.*, 2021).

Biological and ecological function of cnidarian mucus

As stated above, most cnidarian species secrete mucus more or less constantly, which seems to be involved in both physiological and non-physiological functions. Moreover, under certain stressful conditions, a considerable increase in mucus secretion rate can be observed (Camacho-Pacheco, 2022). From the literature is clear that the functions of mucus have been documented for some groups, especially in corals, where this seems to be closely related to their role as ecosystem engineers (Bythell and Wild, 2011). Instead, the information about the role and the ecological and evolutionary implications of the mucus secreted by medusozoans is less substantial. Basically, the secretion of mucus in invertebrates performs three essential functions, identified in defense, feeding and locomotion activities (Brown and Bythell, 2005). However, particularly in cnidarians, this assumes much more important roles and closely connected to the well-being of the cnidarians themselves and to the provision of ecosystem services. These include for example resistance to desiccation, sediment shedding, abrasion protection, defense against predators and pathogens, feeding, reproduction, settlement behaviour, spatial competition (Stabili *et al.*, 2015; Camacho-Pacheco, 2022). Recently, some authors (Liu *et al.*, 2018; Ames *et al.*, 2020; Hubot *et al.*, 2022) have reported for some jellyfish species the mucus composition, excretion, and possible fate in marine ecosystems, which, considering the scarce information available in the literature, could represent an important piece in the understanding the biological and ecological function network claimed by mucosal products.

Several authors have eviscerated, demonstrated, or hypothesized all the possible biological functions of the mucus secreted by cnidarians, with particular attention paid to corals. However, our feeling is that few studies or reviews, currently present in the literature, have paid attention to the implications and ecological effects of the mucus produced by cnidarian (Tinta *et al.*, 2021).

Coral tissue is often heavily covered with cells that produce copious amounts of mucus (*e.g.*, Marshall and Wright, 1993). Although less well known, the epidermis and gastrodermis of jellyfish, including *A. aurita*, also contain numerous types of single-celled, mucus-producing glandular cells, leading to the formation of thin mucus layers that are constantly renewed on the outer surface of the jellyfish. Under certain conditions such as stress, during reproduction, feeding and digestion, and even during death, the amount of mucus released is even more pronounced (Rotini Sandrini and Avian, 1991; Doyle *et al.*, 2014).

Secretion of mucus sheets is known to be an important means of trapping and ingestion of small nutrient particles (*e.g.*, Yonge, 1930) by scleractinian corals and gorgonians (Bessell-Browne *et al.*, 2017). Lewis and Price (1975) showed that increased mucus secretion by corals within dif-

ferent groups was a common response to the presence of food, which produced a dense net of filaments of various thicknesses, depending either on the species or water conditions. Several jellyfish taxa have been listed as mucus net filter feeders (salps) (Doyle *et al.*, 2014). The production of mucus greatly facilitates the capture of prey by jellyfish due to the formation of lumps or conglomerates. Studies of other jellyfish have reported that the mucus aids in the transport of food through the oesophagus to the gastric pouches, even when prey items were small (Ames *et al.*, 2020; Daly *et al.*, 2007). Others can produce toxic mucus, such as *Cassiopea* spp, which release large amounts of toxic mucus into the water column (Ohdera *et al.*, 2018; Ames *et al.*, 2020). *Cassiopeia* mucus kills some fish species on contact (Ames *et al.*, 2020). Motile cellular structures that trap and paralyze prey have been identified in the mucus of the jellyfish *Cassiopea xamachana* (Ames *et al.*, 2020). In the order *Rhizostomae*, mucus can facilitate feeding (Arai, 1997), although its precise role and function are not yet fully understood (Camacho-Pacheco, 2022).

The mucus is also involved in some reproductive processes, effectively becoming part of the reproductive or larval settlement strategy of some cnidarian species. A study conducted on the genus *Eudendrium* (class Hydrozoa) reported that polyps release planulae which remain attached to a thread of mucus which detaches once it reaches the bottom. This strategy allows the species to occupy well-defined sites, maintaining a gregarious behavior (Wasserthal and Wasserthal, 1973). A similar strategy has been found in *Nemertesia antennina* (Linnaeus, 1758, class Hydrozoa), where the mucous filament reaches considerable lengths (up to 50 m) and allows the planulae to reach areas further away from the mother colony (Hughes, 1975). In *Pelagia noctiluca*, mucus increases the probability of fertility (Lilley *et al.*, 2014). First, each mature female medusa lays the oocytes in a mucus tape, holding the eggs together for several minutes before its dissolution. This peculiarity can favor the fertilization of the entire set of oocytes by the spermatozoa released by one or a few male partners (Aglieri *et al.*, 2014). Only about 50% of the carbon and nitrogen invested during reproduction goes into the eggs, while the rest it produces a thread of mucus that binds all the eggs together. The mucus presumably increases the chances of fertilization and may increase the buoyancy of the egg series in *Pelagia* (Lilley *et al.*, 2014).

In a study performed on *S. meleagris* the greatest number of oocytes were found in the mucus, suggesting that it is also important in sexual reproduction, as previously reported for *P. noctiluca* (Nagata and Morandini, 2018)

Mucocyte secretions have distinct functions including cleansing sediment, healing wounds, and protecting against invasive microbes, as well as shielding from desiccation and UV damage (reviewed by Brown and Bythell 2005). Increased mucus production is observed in

colonies that are in direct contact with sunlight (remaining fully exposed during low tides) as a strategy to avoid desiccation (Santos *et al.*, 2016; Sebens, 1982), as reported in the coral *Orbicella annularis* (Ellis & Solander, 1786) (Piggot *et al.*, 2009).

Briefly, in sessile cnidarians the mucus represents a strong protection against desiccation (Krupp, 1984), as its hygroscopic characteristics allow to keep the coral surface moist during exposure to air due to low tide conditions; however, the mechanisms that control these processes are still unclear. Although the mucous layer is not waterproof, it can greatly reduce the airflow and water exchange rate. In anemones, Shick (1991) observed that the mucus presents few barriers to the diffusion of water, but can produce a boundary layer which, when dried, separates from the external tissues (Griffiths, 1977). Another factor that may influence mucus secretion rates in corals is sedimentation (Bak and Elghershuizen, 1976; Schumacher, 1977; Rogers, 1990; Stafford-Smith and Ormond 1992; Stafford-Smith, 1993). In some cases, repeated influxes of sediment can lead to depletion of mucus secretion causing the rejection of sediment to slow and cease (Schumacher, 1977). In other species, such as *Gardinoseris planulata*, on the other hand, mucus secretion continues long after the sediment rejection activity has ceased, suggesting that in this coral exhaustion of the ciliary mechanism rather than mucus secretion occurs (Stafford-Smith, 1993). Stabili and collaborators (2015) demonstrated that some properties of the mucus secreted by *A. equina*, such as osmolarity and viscosity, as well as the chemical composition, play a key role in the defense against sedimentation and desiccation, however it is still evident that the hydrodynamism has a relevant influence on these phenomena. During an experimental manipulation, Coffroth (1985) points out that the reduction of water movement also led to the formation of mucous sheets, thus the formation of the mucous sheet may be a secondary mechanism to cope with sediment stress, especially when currents are not strong enough to relieve environmental conditions. Several studies demonstrated an increase in mucus secretion in corals due to sedimentation (Bak and Elghershuizen 1976; Schumacher 1977; Rogers, 1990; Stafford-Smith and Ormond 1992; Stafford-Smith 1993; Bongaerts *et al.* 2012; Weber *et al.*, 2012). This strategy turns out to be energetically quite expensive since (the carbon requirement for mucus secretion is more than doubled) (Edmunds and Davies, 1989; Riegl and Branch, 1995). A study conducted on several species belonging to the orders Scleractinia and Malacalcyonacea showed that, in absence of sediment, mucus production was around 35% of daily respiration; in the presence of sediment, production increased up to 65%. Therefore, sediments affect coral metabolism decreasing photosynthetic production, with greater carbon losses due to the greater amount of mucus produced (Riegl and Branch, 1995; Weber *et al.*, 2012).

As a barrier defense, mucus on jellyfish surfaces has also been found to play a role in surface cleaning and predator defense (Patwa *et al.*, 2015). For scyphozoans, including *S. meleagris*, the mucus was found to contain nematocysts and toxins that serve defensive purposes (Shanks and Graham, 1988).

Shanks and Graham (1988) identified mucus secretion as an important chemical defence mechanism against predators. In previous studies with *Aurelia coerulea*, mucus was shown to function as a “cleaner”, preventing the accumulation of bacteria and debris on their surfaces (Patwa *et al.*, 2015). In addition to mechanical protection, the mucus of many cnidarians contains specific compounds to make the animal venomous, unpleasant, irritating or a combination of these characteristics. It is not surprising that these invertebrates have developed an innate immune system that produces a considerable number of defense molecules, such as lytic compounds (Mayer *et al.*, 2013), bioactive antimicrobials (Aneiros and Garateix, 2004; Otero Gonzalez *et al.*, 2010; Smith *et al.*, 2010), toxins, and carbohydrate-based anti-adhesives (Bavington *et al.*, 2004).

Effectively the mucus acts as a physical barrier and the presence of cilia on the ectodermal cells favours the muco-ciliary transport of particles, including foreign cells, towards the mouth of the polyp where they can be digested or removed by the secretion of mucus. The first line of defense against invading pathogens in cnidarians is the superficial mucous layer. In reality, the superficial mucous layer represents the natural microbiota of the cnidarian surface, which may also include pathogens. The secreted mucus is an attractive niche for bacteria. Since jellyfish mucus is composed primarily of proteins, lipids, and a lower proportion of carbohydrates (Ducklow and Mitchell, 1979), it is a high-quality energy source that is readily utilized by bacteria. Cnidarians indeed host a variety of microbial species (Rohwer *et al.*, 2001; Webster and Bourne, 2007). A large number of evidence (reviewed by Ainsworth *et al.*, 2010) shows for example that “healthy” corals in their natural environment are associated with microbial groups and that when they are stressed or the environment changes, the associated microbes change in their turn. The cnidarian’s ability to control the production and composition of the superficial mucus layer and its associated bacteria may represent an important portion of their immunity. Antibacterial compounds produced by the cnidarian host, as well as its associated microbial consortium, are released into the mucus and play an important role in the control of the mucus-associated microbial community (Brown and Bythell, 2005; Reshef *et al.* 2006; Ritchie 2006; Rosenberg *et al.*, 2007; Shnit-Orland and Kushmaro, 2009; Rypien *et al.*, 2010; Krediet *et al.*, 2013). The identification of the role of the microbiota in the development of the eukaryotic host and their response to environmental variations and/or stress, has led

to the definition of a “holobiont”. There is now strong evidence indicating that the innate immune system of cnidarians is not only involved in the destruction of harmful microorganisms but is also crucial in the structuring of the microbial communities associated with the tissues that are essential components of the holobiont and with the health of the organism (Rivera *et al.*, 2015). Cnidarians have many microorganisms associated with their tissues (Rivera *et al.*, 2015; Tinta *et al.*, 2019). Actually, it is not entirely clear whether the bacteria adhere directly to the outer cell layers of the cnidarians or are associated only in the thin mucus layer, however, the association between bacteria and cnidarians is highly dynamic and complex. Recent studies have focused on the relationships between microbes and their host organisms, investigating the composition and ecological role of microbial communities associated with cnidarians (Basso *et al.*, 2019; Kramar *et al.*, 2019; Stabili *et al.*, 2020). These studies addressed questions relating to the ecological role and composition of cnidarian-associated microbial communities, the mechanisms underlying these interactions, and the nature of the relationships that arise between cnidarians and their associated microbiome. Further investigations involved bacteria associated with the outer surfaces epithelia in several cnidarian species and at different life stages, documenting their involvement in a multitude of important potential roles including antibiotic synthesis, nitrogen fixation, decomposition of organic compounds, the primary defence against pathogens or the modulation of contractile activities (Weiland-Bräuer *et al.*, 2015; Kramar *et al.*, 2019; Tinta *et al.*, 2019). The microbial communities associated with the jellyfish species *Aurelia aurita*, *Mastigias papua*, *Cotylorhiza tuberculata* and *Rhizostoma pulmo* and *Tripedalia cystophora* analyzed in several studies, showed extremely variable bacterial associations. The microbiome associated with different life stages of *A. aurita* (polyp, strobila, ephyra, juvenile and adult medusa) and with different compartments of adult specimens (exumbrella, mucus and gastric cavity), from different geographical areas was examined by Weiland-Bräuer *et al.* (2015). The results of this study showed that the *A. aurita* microbial community appears to be highly host-specific and distinct from bacterioplankton suspended in the surrounding water column. In adults, the microbiota showed significant differences between the various compartments, showing a more variable bacterial composition associated with the mucus than that present in the gastric cavity. Furthermore, Kramar *et al.* (2019) monitored the bacterial community associated with the moon jellyfish *Aurelia solida*. In particular, different parts of the body (umbrella surface, oral arms and gastric cavity) were analysed for bacterial community diversity. The authors reported that the microbiota associated with this species was different from the microbial assemblages in

the surrounding seawater and differed significantly between different body compartments. Furthermore, during the senescent phase, the bacterial community was found to mutate in structure with increased *Gammaproteobacteria* (entirely *Vibrio*). Based on these results, it was hypothesized that the bacterial community associated with jellyfish may play an important role for the host. The compositional analysis of the microbiome associated with jellyfish mucus was conducted by Tinta *et al.* (2019) to conclude that the *Gammaproteobacteria* (mainly *Pseudoalteromonas* and *Vibrio*) are the most abundant, followed, to some extent also by the *Alphaproteobacteria* (*Phaeobacter*, *Rugeria* and *Roseovarius*). These bacteria are known for their ability to synthesize antimicrobial compounds when attached to live or inert surfaces, and therefore involved in defense of the host against pathogens and encrusting organisms from the surrounding environment.

The microorganisms associated with the mucus of cnidarians appear to be characterized by a great diversity and the mucus represents the compartment richest in bacterial associates compared to the oral arms and the umbrella. In anthozoans, microbial agents perform key functions, including regulation of metabolism, immune defense, development, and behavior. Bacteria associated with anthozoan tissues can fix nitrogen, digest complex polysaccharides, and produce antibiotics to prevent infection by pathogens. In turn, *Symbiodinium* produces dimethylsulfo-niopropionate (DMSP) as an osmolyte, an antioxidant agent (Lawson *et al.*, 2018) and a nutrient source for associated bacteria (Rosenberg *et al.*, 2009).

A certain specificity has also been found in the Anthozoa-bacteria association; Porporato *et al.* (2013), for example, described the bacterial communities associated with *Pennatula phosphorea* and *Pteroeides spinosum*, showing a high species-specificity. Moreover, since within the same species only a few phylotypes were shared between mucus and tissues, the authors also hypothesized that a partition of the microhabitat could exist between the associated microbial communities. In the case of *P. phosphorea*, both tissue and mucus associated communities were characterized by the predominance of *Alphaproteobacteria*. Conversely, *Alphaproteobacteria* prevailed in the mucus layer of *P. spinosum* and the tissues were dominated by *Gammaproteobacteria*. The isolates of strains belonging to *Vibrio* spp., mainly obtained from coral mucus, showed an antibacterial activity against some indicator organisms, indicating a protective function of the bacterial communities associated with the coral as in the case of jellyfish.

Based on this evidence, the ability of cnidarians to control the production and composition of a mucous matrix and its associated bacteria may represent an important part of immunity (Ocampo and Cadavid, 2015). The ability of some bacteria to produce antimicrobial compounds is likely

to contribute to competition for space and resources with potential pathogenic host bacteria. Due to these characteristics, mucus and its components have interesting implications in molecular ecology and biotechnology.

The specific interactions of microbial colonization of mucosal surfaces are still unknown.

Calow (1979) highlighted that any differences in the biochemical composition of the mucus can influence the attack of microbial agents that use exoenzymes to degrade the mucoid polymers. The microbes themselves can transform dissolved and particulate matter into living matter, attracting other predatory organisms.

It also appears that changes in the composition and abundance of bacterial communities may affect the health of the host, making it more vulnerable to disease (Reshef *et al.*, 2006).

Recent documentation on the succession of microbial communities associated with the developmental stages of *Porites astreoides* (Sharp *et al.*, 2012) and the discovery of beneficial functions in favor of *Alphaproteobacteria* and *Marinobacter* strains (Lubbock, 1980) provide fundamental support to the hypothesis of “hologenome evolution”, *i.e.* the idea that in symbiotic organisms that were colonial, the hologenome, and thus sprung from all members of the holobiont, actually may act as a single unit of evolution, with rapidly evolving microorganisms providing the plasticity to adapt to the changing environment (Rosenberg and Zilber-Rosenberg, 2011).

The highly diverse mucosal microbiome is therefore generally believed to perform vital services and to be involved in the flow of energy within marine ecosystems.

In this prospective, after detachment from the surface of cnidarians, mucus can play several important roles in the functioning of the ecosystem services it provides. First of all, the mucus acts as an energy vector (Bythell and Wild, 2011).

Some authors (Haas *et al.*, 2010; Naumann *et al.*, 2010; Wild *et al.*, 2010) confirm and demonstrate that all examined scleractinian corals release organic matter in the form of mucus, which includes both a particulate fraction and a dissolved fraction (mainly organic carbon, DOC (Crossland, 1987; Naumann *et al.* 2010) and that mucus release by corals is largely independent of the carbon acquisition mechanism (autotrophy versus heterotrophy). Studies conducted by Naumann *et al.*, 2010 suggest that photosynthates translocated by the endosymbiotic zooxanthellae of cnidarians represent the basis of mucus production (Naumann *et al.* 2010). Although the energy cost is quite high, (approximately 20-45% of the daily net photosynthate produced (Brown and Bythell, 2005), coral mucus is continuously released into the water column, accounting for half of the total mucus released by all benthic organisms (animals and plants) on coral reefs (Crossland, 1987; Naumann *et al.* 2010). Suffice it to say that *Acropora*

spp., the dominant scleractinian genus on the Great Barrier Reef, releases up to 4.8 L of mucus per square meter of coral reef surface per day (Wild *et al.*, 2004).

Zooxanthellae, endosymbiotic algae of reef-building corals, contribute substantially to the high gross primary production of coral reefs, supplying a substantial portion of their hosts' energy needs by transferring photosynthetically fixed carbon to the coral. The high arabinose contents found in the carbohydrate fraction of coral mucus suggest that much of the fixed carbon is released in the form of mucus, since arabinose is not usually a constituent of animal cells (Wild *et al.*, 2004). Between 56% and 80% of the released adhesive mucus dissolves in the reef water and effectively traps organic matter from the water column, increasing its initial organic carbon and nitrogen content by three orders of magnitude in short time and rapidly transporting energy and nutrients to the sediment, which acts as a biocatalytic mineralizing filter. Coral mucus provides light energy transformed by zooxanthellae and trapped particles to the heterotrophic reef community, thus establishing a recycling cycle that supports benthic life, reducing energy and nutrient loss from the reef ecosystem (Wild *et al.*, 2004).

However, mucus release can vary between species and depending on conditions. Tanaka *et al.* (2009) found that only about 5% of the net daily photosynthetic production was released by *Acropora pulchra*. Muscatine *et al.* (1984) observed that in *Stylophora pistillata*, depending on the irradiance levels, the loss of the newly fixed carbon varied from 6 to 50%. Tremblay *et al.* (2012) found that in *S. pistillata*, the availability of heterotrophic foods and high light levels were required for the accumulation of autotrophic carbon, subsequently released as dissolved organic carbon.

Mucus release appears to constitute a dominant form of organic matter generated in coral reef ecosystems (*e.g.*, Ferrier-Pagès *et al.*, 1998; Hatcher, 1988; Bythell and Wild, 2011) and represents the major route by which primary production of coral enters the food web (Hatcher, 1988).

Freshly released coral mucus differs between species due to variations in lipid, sugar, and amino acid composition (Ducklow and Mitchell, 1979; Crossland, 1987; Meikle *et al.*, 1988; Wild *et al.* 2010). Particulate mucus may also contain varying levels of phosphate or nitrogen, which may for example be influenced by planktonic food availability, colonization by picoplanktonic organisms and nitrogen-fixing bacteria (Hubot *et al.*, 2022). An old view held that coral mucus was a negligible source of nutrients (*e.g.*, Krupp, 1984; Coffroth, 1990). Today, however, it is known that mucus represents an energy substrate, rich in glucose (Wild *et al.*, 2010), degradable by microbes and higher organisms (Benson and Muscatine, 1974; Grange, 1991; Rinkevich *et al.*, 1991; Patton, 1994; Naumann *et al.*, 2010). Several experimental studies (Ducklow and

Mitchell, 1979; Ferrier-Pagès *et al.*, 2000; Wild *et al.*, 2004; 2005; 2009; 2010) have shown a stimulation of planktonic or benthic microbial activity after the addition of coral mucus. Additional studies (Allers *et al.*, 2008; Schöttner *et al.*, 2009) have also shown that not only microbial activity, but also its diversity can be influenced by the presence of coral mucus. The cycles of production, aging and elimination of mucus are accompanied by variations in total microbial abundance, confirming that this colonization increases the nutritional value, in terms of carbon and nitrogen, of the released mucus (Ferrier-Pagès *et al.* 1998a; Nakajima *et al.* 2009; Grover *et al.* 2014; Bednarz *et al.*, 2017 and therein references). This enriched exudate becomes a downstream pelagic food source for fish (Benson and Muscatine, 1974) and zooplankton (Gottfried and Roman, 1983), and after sinking into the sediment, it is recycled back to members of the benthic community (Wild *et al.*, 2005; Huettel *et al.*, 2006; Mayer and Wild, 2010; Tanaka *et al.* 2011; Naumann *et al.*, 2012). This results in a mechanism by which the pelagic food supply is coupled to the benthos (Naumann *et al.*, 2009; Bythell and Wild, 2011). In addition to its energy carrier function, the released adhesive mucus also functions, for obvious reasons, as a particle trap, which by forming aggregates of various inorganic and organic particles caught in the water column, greatly increases its sedimentation speed (Wild *et al.*, 2004; Huettel *et al.*, 2006). It is easy to hypothesize that such a mucus-induced and accumulated material cycle could support the recycling of essential nutrients within marine ecosystems, contributing to its functioning. A study done in the Red Sea documented that particle entrapment by coral mucus occurs while the mucus is still attached to the surface, due to the weaker velocities of tidal currents causing the mucus to remain longer at the surface of the coral (Mayer and Wild, 2010) than reported for Great Barrier Reef, in which the mucus is rapidly detached (Wild *et al.*, 2004; Huettel *et al.*, 2006). This could result in a faster cycling of matter within the reef. Thus, organic compounds can be rapidly recycled (Wild *et al.*, 2004; 2006), so that regenerated nutrients are released (Wild *et al.*, 2005) and feed new primary production by autotrophic coral reef organisms, including zooxanthellae. Coral mucus can also trap picoplankton particles (Davy and Patten, 2007; Futch *et al.*, 2010) from the water column and transform them into larger mucus aggregates (Naumann *et al.*, 2009) allowing benthic filter of using picoplankton as a food source and once again facilitating the coupling between the water column and the benthic environment.

Even the mucus secreted by jellyfish can have important ecological implications, although less explored than corals. Jellyfish can provide small but significant amounts of nutrients that support primary production (Pitt *et al.*, 2009). This is particularly important given the fact that

jellyfish populations are characterized by large and rapid fluctuations in abundance. It is conceivable that the adaptive characteristics of jellyfish will allow them to thrive in anticipation of future catastrophic events directed by climate change, namely warming, acidification, oxygen loss and increasing human exploitation of ocean services; therefore, understanding the response of marine ecosystems to this natural and/or anthropic perturbation is of fundamental importance (Richardson *et al.*, 2009; Purcell, 2012; Steinberg and Landry, 2017).

Regardless of the divergent scientific opinions on the causes of these fluctuations in jellyfish populations, the combined effect of natural oscillations and anthropogenic factors can lead to an increase in their populations, with consequent ecological and socio-economic impacts (Richardson *et al.*, 2009; Purcell, 2012; Condon *et al.* 2012, 2013; Sanz-Martín *et al.*, 2016).

Precisely because of their demographic dynamics of boom and bust, jellyfish are likely to influence the cycles of matter in the ecosystems they inhabit. Jellyfish blooms represent a significant and largely overlooked source of organic matter, especially at local and regional scales. Recently, jellyfish have been recognized as key carbon export agents to the interior ocean, demonstrating the need to include jellyfish in oceanic biogeochemical models as a key component of the biological soft tissue pump (Lebrato *et al.*, 2012; Steinberg and Landry, 2017) so far not considered. Jellyfish acquire C, N, and P by assimilating organic compounds from ingested prey, by absorbing small amounts of dissolved organic material, and some species instead actively assume dissolved inorganic forms. A portion of the ingested elements is incorporated into their biomass and the undigested material is eliminated in the faeces or released via “sloppy food”. The organic forms of C and N are recycled into the environment as mucus together with both organic and inorganic metabolic products. During bloom formation, populations increase in size acting as a net sink for C, N and P. During decomposition processes the elements bound to their biomass are “recycled” into the water column as dissolved inorganic and organic compounds, finally available for pelagic and benthic microbial communities. Regenerated organic C by mucus production and decomposition supports microbial production, while regenerated inorganic N and P support algae production. Additionally, few species, such as *Linuche unguiculata* Schwartz and many *Rhizostome* species (genera *Cassiopea*, *Mastigias* and *Phyllorhiza*) form a symbiosis with zooxanthellae. In zooxanthellate jellyfish, translocation of photosynthetic products from zooxanthellae is likely to be the major source of C for the host (Cates, 1975). Furthermore, inorganic excretory products can be translocated from the host to the zooxanthellae instead of being released into the external environment. Once released into the environment,

jellyfish mucus is metabolized by bacteria, creating important variations in microbial assemblages and diverting carbon to bacterial respiration (Condon *et al.*, 2011).

Mucus release therefore not only initiate biogeochemical cycles, but also control a range of processes including the microbial activity. So, again microbes are the main actor. As stated above, jellyfish host and interact with taxonomically and metabolically diverse microorganisms throughout their entire lives. The limited research available highlights the importance of the environmental microbial community for the recruitment of members of the jellyfish microbiome and a certain degree of microbiome specialization with some preferences for specific jellyfish taxa, life stages and body parts (Basso *et al.*, 2019; Kramar *et al.*, 2019; Tinta *et al.*, 2019). The role of the microbiota associated with jellyfish (or their mucus) is generally related to digestion, defense mechanisms against pathogenic microorganisms and possible predators (Basso *et al.* 2019 and references therein), and reproduction (Weiland-Bräuer *et al.*, 2020)

Collectively, the review of the current state of knowledge on the jellyfish microbiome reveals that this topic is grossly underestimated and should be studied in more detail in the future.

Mucociliary transport not only aids feeding by serving as a trap for nutrient particles, but also acts to remove non-nutritive particles from the surface of cnidarians. This is actually a common mechanism in several invertebrates, wherein the secreted mucus traps particulate debris which is then directed through the ciliated surface to a disposal site (Sleigh, 1989). Duerden (1906) was among the first to demonstrate the movement of mucus-bound non-nutritive particles up the edge of the disc of fungiid corals to the underlying substrate.

It has been suggested that mucus have structural properties to efficiently accumulate, absorb or maybe bind pollutants, such as aromatic hydrocarbons (Neff and Anderson, 1981) or heavy metals (Brown and Howard, 1984; 1985), thus giving some protection to the underlying coral tissues by physically protecting them and acting as a pathway for pollutant release (Neff and Anderson, 1981). It seems likely that one of the primary detoxification mechanisms employed is increased mucus production.

Increased mucus secretion has been described in response to exposure to a wide range of pollutants: crude oil (Mitchell and Chet, 1975; Neff & Anderson, 1981), drilling mud (Thompson *et al.*, 1980), mercury (Bastidas and Garcia, 2004), copper sulphate (Mitchell and Chet, 1975), peat (Dallmeyer *et al.*, 1982). In histological studies, an increase in the number and size of mucosal secretory cells has been observed after exposure of *Manicina areolata* (Linnaeus, 1758) coral to chronic oil pollution (Peters *et al.*, 1981). In experiments using drilling mud, colonies of *Acropora cervicornis* (Lamarck, 1816) produced mucous filaments after

30 minutes of exposure, while mucus production by other species (*Porites astreoides* Lamarck, 1816, *Porites divaricata* Le Sueur, 1820, *Porites furcata* Lamarck, 1816 and *M. annularis*) was observed only after 24 hours (Thompson *et al.*, 1980). An ecotoxicological study conducted by Howe *et al.* (2012), tested copper toxicity on *Exaiptasia diaphana* (Rapp, 1829), a tropical symbiotic anemone; specifically, acute tests were conducted on juveniles (1-2 mm). The organisms responded to copper with severe (and often complete) retraction of tentacles, the collapse of the column, overproduction of mucus, the expulsion of grouped and individual zooxanthellae, and necrosis within 96 hours. These effects were rapid, with obvious changes in morphology occurring at concentrations ≥ 27 $\mu\text{g/L}$ within the first hour. However, most anemones that survived acute copper exposure also survived continuous exposure, likely because they have successfully reduced their copper exposure and uptake through significant tissue retraction and employed detoxification mechanisms by increased mucus production, which allows the expulsion of metal-rich zooxanthellae.

Mucus produced by cnidarians can act as a trap for particles because of its adhesive properties. This can justify the presence of microplastic fibres found in Cnidaria and Ctenophora, as reported by a recent study conducted in Orkney, Shetland, and the North Sea (Devereux *et al.*, 2021). This aspect deserves the attention of the scientific community, as the entry of microplastics through the cnidarians along the trophic chain can represent a potential risk both for ecosystems functioning and implications for human food safety and health due to the trophic transfer (Barboza *et al.*, 2018; de Oliveira Soares *et al.*, 2020; Albano *et al.*, 2021; Devereux *et al.*, 2021; Bruno *et al.*, 2022). Microplastic effects on freshwater cnidarians, particularly *Hydra thomseni* (Cordero, 1941) belonging to the class Hydrozoa and on jellyfish of the genus *Aurelia* were evaluated. These studies show that these organisms are capable of ingesting microplastics with associated impacts on feeding, causing significant morphological changes in *H. thomseni*. In *Aurelia sp.*, however, short-term exposure to microplastics compromises behavior as well as survival (Murphy and Quinn, 2018; Costa *et al.* 2020). Riegl and Branch (1995) attempted to measure energy expenditure during coral cleaning processes, concluding that mucus secretion in sediment cleansing was energetically very costly. In fact, under stress, the carbon requirement for mucus secretion doubled. Similar data were obtained by Edmunds and Davies (1989), who suggested that mucus secretion by *Porites porites* stressed by the presence of non-food particles constituted an important pathway for energy loss.

Moreover, mucus overproduction has been also seen in cases of increased water temperature (Neudecker, 1983) and decreased salinity (Coffroth, 1985), associated with high energetic costs. Climate change and anthropogenic stressors are threatening the long-term survival of many

marine species, and coral reefs are among the most threatened ecosystems (Hughes *et al.*, 2017). Long-lived organisms, such as scleractinian corals, are particularly vulnerable to environmental stresses and climate change, the rate of which occurs exceeds the time it takes for a population to adapt through natural selection (van Oppen *et al.*, 2017). One of the first signs of anthozoic suffering is represented precisely by the increased production of mucus (Brown and Bythell, 2005), which in turn requires huge energy investments, which can lead to the depletion of metabolic reserves, compromising the body's immune system (Riegl and Branch, 1995; Sheridan *et al.*, 2014;). In *Acropora acuminata*, energy expenditure through mucus exudation following environmental stress can account for up to 40% of the net carbon fixed by photosynthesis (Crossland *et al.*, 1980). An energy investment of this magnitude could therefore increase the risk of secondary adverse effects deriving from subsequent exposure to environmental stressors (Anthony *et al.*, 2009). Subsequently, environmental stress could further deplete energy resources by inducing immune upregulation, known to be very expensive in terms of energy (Armitage *et al.*, 2003). Unfavourable environmental conditions are compromising the health of many anthozoan species; global warming and therefore warmer and eutrophic waters, seem to promote the seizure of nutrient resources by symbiotic algae at the expense of their hosts (Wooldridge, 2017; Baker *et al.* 2018) and this shift from symbiosis to parasitism may presage the well-known expulsion of symbiotic coral partners and a change in the nature of their microbial communities (*e.g.*, Bourne *et al.*, 2009; Sokolow, 2009; Work and Meteyer, 2014; Hughes *et al.* 2017). Symbiotic relationships are highly sensitive to environmental change. Regardless of their narrow temperature range, zooxanthellae become photosynthetically impaired, undergoing an expulsion process and varying degrees of bleaching. Hosts in these conditions vary in their ability to obtain heterotrophic nutrition (Grottoli *et al.*, 2006; Rodrigues and Grottoli, 2007; Palardy *et al.*, 2008; Ferrier-Pagès *et al.* 2011), and if bleaching is severe, heterotrophy it must supply 100% of the metabolic needs of the coral (impossible for some species). Thus, disruption of this mutualism results in a state of starvation and energy deficit, leaving the host vulnerable to infection, (*e.g.*, Siva-Jothy and Thompson, 2002). Similarly, infection is energetically very costly as resources are concentrated and invested in resisting or tolerating any disease (Mayack and Naug, 2009).

According to ecological immunology theory, variations between and within constituent immunity and immune responses are due to energetic trade-offs between costly functional traits, such as reproduction, growth, and maintenance/immunity (Sheldon and Verhulst, 1996; Sudd and Schmid-Hempel, 2009). Therefore, studies of molecular ecology and immunity could offer a better understand-

ing of the drivers that underlie the health status of both corals and other marine organisms in order to more effectively conserve and restore ecosystems of high ecological and socio-economic value such as the coral reefs.

Evolution of the mucus layer

The development of the mucus layer is a key event in the evolutionary history of the kingdom Animalia (Bakshani *et al.*, 2018). Secretion of a functional mucus layer first appeared in the Phyla Cnidaria and Ctenophora (Lang *et al.*, 2016). In a study published in 1984, the luxury carbon hypothesis was introduced, where the only function of mucus was to remove excess photosynthetic carbon from the coral-zooxanthellae symbiosis (Davies, 1984). This hypothesis originated because mucus contains very high percentages of carbon. However, mucus did not evolve exclusively for this purpose, because this hypothesis is only applicable to Cnidaria (Bakshani *et al.*, 2018). Later, other important functions to the evolution of mucus were attributed, including capturing particles for feeding, preventing suffocation due to sediment, and providing a physical barrier that can keep pathogens out (Edmunds and Davies, 1989; Riegl & Branch, 1995; Wild *et al.*, 2004).

Sponges, belonging to the Phylum *Porifera* (which evolutionarily predates *Cnidaria*), have genes that could be precursors of mucins (Iwai *et al.*, 2002; Lang *et al.*, 2007; 2016), so some sponges are even capable of producing mucus (Biggerstaff *et al.*, 2017; McGrath *et al.*, 2017). Sponges are constantly in contact with environmental bacteria (found in abundance) (Kennedy *et al.*, 2008), and as Cnidaria, have a distinct microbiota from the environmental one (Cooney *et al.*, 2002; Frias-Lopez *et al.*, 2002; Brown and Bythell, 2005; Savoca *et al.*, 2019), with numerically fewer bacterial populations than *Porifera* (Ainsworth *et al.*, 2010).

The occurrence of microbes in mucus samples was confirmed by Scanning Electron Microscopy (SEM) And Transmission Electron Microscopy (TEM) microscopy analysis; however, they have not been found on the epithelial surfaces of polyps or on the exumbrella of jellyfish (the external part of the umbrella) (Turk *et al.*, 2021).

Cnidaria is often exploited as model organisms in developmental biology, yet the evolution of a functional mucus layer from invertebrates is rarely examined (Bakshani *et al.*, 2018), even though similarities are evident by comparing the cnidarians and vertebrates (including human) mucus composition (Lai *et al.*, 2009).

Bakshani *et al.* (2018), established the evolutionary conservation of the antimicrobial function of mucus by focusing on mucin genes and structure of mucus secreting cells among invertebrates and vertebrate. In the review, the authors resumed how secreted mucins evolved in early metazoans as Cnidaria and the mechanisms lying at its bases is functional conserved from the first metazoans to

mammals.

CONCLUSIONS AND FUTURE RESEARCH NEEDS

The importance of mucus in invertebrates, especially in Cnidarians, is evident, as it is a fundamental secretion for the biology of these organisms and the marine ecosystems they inhabit. Scleractinian corals have long been studied for their importance as ecosystem engineers and often used as model organisms for the study of symbiosis and reciprocal nutrient exchange. However, in examining the current state of knowledge on cnidarian mucus secretion, we found several gaps to be filled in the future.

- i) Further efforts are required to determine and deepen the role played by the microbiome, its composition in species and the ecological implications of its species-specific variability, dependent on the life stage, or due to environmental stresses. Similarly, it is not clear whether there is a substantial difference between organisms adhered to the surface and those present in the mucus and whether they act differently in the recycling of matter and/or in the flow of energy in coral ecosystems.
- ii) Mucus production by scleractinian corals is prolific, but the amount of dissolved or particulate forms of this secretory material and their fate in the environment are still unresolved.
- iii) Although the involvement of mucus in the innate immune system of cnidarians is clear, there are still discrepancies that prevent a complete evolutionary understanding of mucus. In this, and for many other aspects relating to the biological and ecological sphere of the cnidarians, studies on the hologenome could be particularly useful, involving all members of the holobiont and accepting the fact that this acts as a single unit of evolution, where the microorganisms, by adapting more rapidly, provide the plasticity necessary for the host to adapt to the rapidly changing, and probably for the worse, environment.
- iv) Mucus secretion by jellyfish is a poorly explored field, although it has important ecological functions in antimicrobial defense, chemical defense and protection from environmental stress. The few existing studies on the jellyfish-microorganism association demonstrate the importance of these associations in various fundamental aspects for the life cycle, well-being and the ecological role played by these organisms. However, further studies on the interannual and seasonal dynamics of the associated jellyfish microbial community and possible variations under the pressure exerted by anthropogenic factors are needed. Furthermore, new investigations are needed to produce potential common models of impacts of jellyfish biomass and their mucus production on both marine microbial communities and ecosystems worldwide. In particular, the link between jellyfish, mucus and microorganisms as final recipients and recyclers of the oceanic dissolved organic matter should be ad-

dressed more thoroughly. Overall, an increased focus on this topic will contribute to understanding the dynamics of marine biodiversity and related ecological processes, as well as addressing the implications arising from climate change.

- v) It is somewhat demonstrated that the increase in mucous secretion in cnidarians has a high energy cost, which very often translates into an increased vulnerability of the organism. However, although described for a few coral species, it is largely misunderstood for cnidarians what the energy trade-off between costly functional traits (growth and reproduction) and maintenance/immunity is and how much energy investment is required for increasing mucus secretion in the Anthropocene era.

In conclusion, it is strongly suggested for these future studies that the combined use of ECO-EVO-DEVO approaches and ecological genomics would allow the individual disciplines and fields of investigation to enrich each other and would allow to improve not only the understanding of this topic in an evolutionary key, but also of the ecological, biological, and genetic mechanisms underlying the responses of organisms to their natural environments.

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