

Possible beneficial interactions of ciliated protozoans with coral health and resilience

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Abstract

Microbial interactions contribute significantly to coral health in the marine environment. Most beneficial associations have been described with their bacterial communities, but knowledge of beneficial associations between protozoan ciliates and corals is still lacking. Ciliates are important bacterial predators and provide nutrition to higher trophic level organisms. The mucus secreted by corals and the microenvironment of the coral surface layer attract ciliates based on their food preferences. The mixotrophic and heterotrophic ciliates play a major role in nutrient cycling by increasing nitrogen, phosphorus, and extractable sulphur, which can enhance the proliferation of coral beneficial microbe. Besides, bacterial predator ciliates reduce the pathogenic bacterial population that infects the coral, and also act as bioindicators for assessing the toxicity of the reef ecosystem. Thus, these ciliates can be used as a beneficial partner in influencing coral health and resilience under various stress conditions. Herein, we explore the urgent need to understand the complex beneficial interactions of ciliates that may occur in the coral reef ecosystem.

Keywords: ciliates; corals; beneficial; symbiosis; health

Introduction

Corals are invertebrate animals of the Anthozoa class of the phylum Cnidaria with gastrointestinal cavities and tentacles. Coral reefs are formed by compact groups of genetically identical individual polyps held together by calcium carbonate. Coral reefs are microbe-driven ecosystems as they rely on host-related microorganisms for food, nutrients, and trace elements to survive in oligotrophic seas [1]. As a result, while corals get their organic nutrients from the photosynthetic dinoflagellate Symbiodiniaceae, they also get their nutrition and defense-enhancing qualities from other helpful microorganisms like viruses, bacteria, fungus, archaea, and protists that are present in their environment [2-8]. Thus, an assemblage of a host and the many other species living in or around it, which together form a discrete ecological unit is called holobiont [9]. Nutrients derived from the associated organisms are used by corals for reef formation using calcium carbonate and carbon-rich mucus secretion [10]. Of all the microorganisms associated with corals, ciliate species distribution and interactions with host coral are not clearly described, though they occur in almost all environments [11,12]. For example, many ciliated species have been described for their close association with marine ecosystems as symbiotic interactions with invertebrates, fishes, and even prokaryotes [13]. Also, the benthic ciliates of coral reefs are known to acquire photosymbiosis phototrophy hosting *Symbiodinium* endosymbionts [14,15]. Thus, the protozoan ciliates have attracted increased attention over the last few decades to understand their role and function in the coral ecosystem. Nevertheless, these protozoa are widely discussed as secondary invaders of immunosuppressed coral fragments, foraging voraciously on the microbial community including the *Symbiodinium* with coral tissues [16]. However, other diverse ecological interactions of the ciliates benefitting the coral host are the least targeted.

Ciliates are a group of alveolates, single-celled eukaryotic organisms whose cells measure about 10 μm to a few millimeters [13]. These ciliates have short-hair like structures called cilia that beat in an integrated way to form water current for locomotion and feeding bacteria. Ciliates also act as essential regenerators and contribute significantly to maintaining new and high production in the water column [17]. Free-living ciliates obtain nutrients by eating microbes, such as bacteria, algae, fungi, or other protozoa. Therefore, the primary role of ciliates feeding on bacteria, or organic matter such as dead tissue or living cells (histophagy or “tissue eating”) by phagotrophy on diseased corals described them as secondary invaders [18]. Some ciliates also utilize dissolved organic compounds (osmotrophy). Thus, both phagotrophy and osmotrophy are found in both symbiotic and free-living ciliates [19]. However, the phagotrophic and osmotrophic processes for a particular species that are associated with coral health have not been studied. Ciliates of different life stages associated with

corals may interact or develop opportunistic, mutualistic, commensal, or parasitic relationships with respect to ambient environmental conditions (Fig.1). A ciliate may also be an ectocommensal that feeds on detritus from diseased or dead corals. Some ciliate–coral interactions can be food specific and influenced by the size, shape, and biochemical composition of prey cells [16]. For instance, ciliates have been described for their direct or indirect transmission in diseased corals and for devouring the damaged tissues [20-27]. We can therefore define four potential types of ciliate interactions with corals. First, ectocommensal or free-living ciliate feed on dead, dying remains and detritus from living corals. The second relationship of mutualism with corals is the exchange of nutrients. A third group would be free-living or symbiotic ciliates that either inhibit or inactivate the microbial pathogens of corals. A fourth group would be free-living ciliates that can serve as food for the early life stages of corals. However, the distinct role of ciliates in all the above possible interactions is not well understood. Although the ciliates have been related to coral associated diseases, their pathophysiology in immunocompromised tissues is not well understood [28]. Besides, Koch's postulates have not yet been satisfied for any of the described ciliates that are associated with coral diseases [29]. This complication is because mixed ciliate communities have been notified of blooming over the infected coral tissues [29] along with the other microbes and macroalgae. Consequently, there is no clear experimental demonstration of their possible role as primary or secondary causal agents, although some ciliates are described for the direct consumption of symbiotic algae [25,30-32]. Besides, the ciliates biodiversity and ecological roles in the coral reef ecosystem are unclear. Thus, the ciliate diversity and other biological and nutrient parameters in the coral ecosystem are reviewed comprehensively to understand their possible beneficial influence on coral health.

Diversity of ciliates - on different types of ciliates (heterotrophic, autotrophic, free-living, host-associated) associated with different coral species

Ciliates are classified into three types: free-swimming ciliates, crawling ciliates, and stalked ciliates. Free-swimming ciliates possess cilia on all surfaces of the body (e.g., *Litonotus* and *Paramecium*). Crawling ciliates have cilia only on the ventral or belly surface near the mouth (e.g., *Aspidisca* and *Euplotes*). Stalked ciliates have cilia around the mouth and have a head and stalk (e.g., *Carchesium* and *Vorticella*). All of these ciliate forms were characterized using various ecological strategies ranging from heterotrophy to mixotrophy, and from free-living to symbionts [13] (Table 1). The diversity of benthic ciliates in Arctic sea sediments and China's coastal areas were found to be influenced by habitat type, salinity, and granulometric composition of sediments, which promoted changes in the ciliate community [33,34]. Thus, seawater temperature, dissolved oxygen, water depth, pH, salinity, and grain size are described as the important factors that drive ciliate diversity [33,34].

Symbiotic ciliates depend on an external source for organic compounds in mutual, commensal, or parasitic relationships with different types of species of corals (Table 1). All major types of symbiotic ciliates are known to control microbial community composition and biomass [35,36] leading to a strong control over pelagic and benthic food webs [37-41]. Thus, ciliates act as major predators by consuming more food than mesozooplankton during all seasons [17].

Functional roles of ciliates - on ciliates and nutrient cycling

The role of a protozoan in nutrient cycling is frequently influenced by its natural habitat and adaptations to its environment. Their nutrient dynamics are greatly affected by the nutrient transformation, whether it is energy-demanding or yielding, and most transformation involves a prey-predator relationship, which increases mineralization and leads to nutrient cycling [42]. Thus, bacterial grazing improves nutrient mineralization of carbon, nitrogen, and phosphorus and excretes surplus nutrients [43]. Furthermore, amoebal grazing has been discovered to aid in the biochemical and biological mineralization of bacterial sulfur to extractable sulphur [43]. Bacterial grazing by ciliates also occasionally releases partially decomposed cells and other bacterium components, whose mineralization raises nitrogen and phosphorus levels in the ecosystem [44,45] (Fig. 2). Protozoans, as another carbon flux, assimilate carbon dioxide in glucose fermentation to succinic acid and serve as a carbon sink and source [46,47]. It has also been described that phytoplankton grazing ciliates emit algal dimethyl sulfoniopropionate (DMSP), also known as prey particulate DMSP, into the seawater [48] (Fig. 2). Thus, released DMSP, an organic carbon, and the sulfur source may increase the prevalence of coral beneficial microbes (phytoplankton, heterotrophic bacteria, and bacterivore and herbivore microzooplankton) [49] (Fig. 2). For example, coral-associated bacterium, *Pseudovibrio* sp. can use DMSP as a sole sulfur or carbon source and potentially as a precursor in the biosynthesis of (tropodithietic acid) TDA, which inhibits the growth of coral disease causing pathogens, *Vibrio coralliilyticus* and *V. owensii* [4]. The nutrients produced by these interactions, such as C, N, and P, may help to revive Symbiodiniaceae growth and increase the resilience of the afflicted corals (Fig. 2). Similarly, coral-associated stramenopile protists of *Fungia granulosa* have been reported as delivering food and nutrients to coral hosts while they recover from stress such as bleaching events and tissue loss [50]. Henceforth, the nutrient cycling of ciliates in the coral reef ecosystem may aid in coral recovery with possible beneficial microbiomes including the invasion of endosymbiont *Symbiodinium* in the coral tissues.

Role of ciliates in coral disease- on causation/secondary infection or amelioration of disease

Halofolliculina corallasia was known to cause the first ciliate disease Skeleton-eroding band (SEB) in Caribbean and Indopacific corals [11,32,51]. *H. corallasia* influenced tissue loss in black band disease (BBD) affected corals was also described [16]. However, no other species of the genus *Halofolliculina*, and none of the other 31 genera in the family Folliculinidae, are known to cause diseases in corals or any other animal [51]. *Philaster guamense* (formerly termed *Porpostoma guamense*) was found dominantly associated with the lesions of brown band disease (BrB) [21,26,30]. The ubiquitous disease, White syndrome (WS) also described for varied ciliate community associations on the disease lesions [11,26,32]. Thus, varied diseases such as Brown Jelly Syndrome (BJS), White Plague (WP), and White Band Disease (WBD) with different ciliate community associations were discussed in detail [32] (Table 2). About 28 ciliate species were described for their association with varied coral diseases and among which 12 ciliate species have been described for engulfing the symbiotic algae (Table 1) [32]. Although the previous investigations related different ciliate species associations with various coral diseases, only a few were associated with disease progression [11,32]. Thus, no extensive research on the specific involvement of ciliates in coral pathobiology and their pathogenesis on immune-compromised tissues has been described [26,32]. For example, even though the association of ciliates with Porites white patch syndrome (PWPS) was reported, the bacterial pathogen *Vibrio tubiashii* has been confirmed as a causative agent of PWPS [20] Therefore, the difficulty in confirming the roles of mixed ciliate communities in coral disease remains unclear [21,26,29]. Besides, no distinct ciliates infection experimental demonstration for their possible role as primary or secondary causal agents based on Koch's postulates was made, even though the fact that some ciliates are known to consume symbiotic algae directly [22,26,29,30-32].

Ciliate's ingestion of symbiotic algae

Ciliates are known for predation of different prey categories (bacteria, pico-, and nanoplanktons, diatoms, and dinoflagellates) through mixotrophy and heterotrophy [52]. Their mixotrophic forms (e.g. *Mesodinium rubrum*) exhibit both phototrophy and heterotrophy. Protozoan ciliates such as *Paraeuplotes tortugensis*, *Euplotes uncinatus*, and *Maristentor dinoferus* are described to be associated with Symbiodiniaceae members. Also, dinoflagellates (around 50– 800 dinoflagellates) of genus *Symbiodinium* clade C are noticed internally inside a single *Maristentor dinoferus* performing symbiotic exchange of nutrients from ciliate to dinoflagellate and photosynthates from dinoflagellate to its ciliate host [14,15,53]. In this act, the host ciliates are benefitted from algal photosynthate and the photosynthetic oxygen generations, which are utilized to increase their oxic respiration diffusion limits under closely populated diseased lesion conditions [30,54]. Besides, the

ingested Symbiodiniaceae remains undamaged within the cytostome and maintained actively within the ciliates host for 2-3 days, until digested [21,30,55,56,57] (Fig. 2 and Fig. 3; Table 3). Also, the chloroplasts of the ingested dinoflagellates are demonstrated to remain functional by fixing carbon which is metabolized by the ciliate [57,58]. Furthermore, beyond 50 Symbiodiniaceae members are ingested by a brown band (BrB) disease associated ciliate of class Scuticociliata, foraging voraciously upon the diseased polyps *Acropora hyacinthus* and *A. muricata* and remain photosynthetically competent [30,31,54,59]. Thus, BrB and White syndrome (WS) disease are associated with nine ciliate ribotypes, among which four ciliates ingested the endosymbiotic algae, an indicative of ciliate histophagy over the coral tissues [26]. Similarly, different ciliates (*Propostoma guamense*, *Philaster lucinda*, *Varistrombidium* sp., *Trachelotractus* sp., *Condylostoma* sp., *Holosticha* sp. and *Cohnilembus verminus*) associated to *Acropora* spp. and *Porites* sp. are described for engulfing the endosymbiont through histophagy from the immune-compromised corals [16,21,56,60] (Table 3; Fig.3; Supplementary video1 and 2). Symbiodiniaceae of the decaying octocorals are also devoured by ciliate histophagy (*Propostoma*, and *Philaster*) [61]. Thus, about 16 ciliate species have been reported for ingestion of coral-associated endosymbiotic algae [32] (Table 3). The ciliate heterotrophy or mixotrophy nature of feeding in coral reefs described above were the only known examples of marine ciliates that host real endosymbionts. However, the ciliate ingestion of coral associated endosymbiont is not well understood for a specific function in the coral–ciliate interactions or their prevalence in coral reef ecosystems [32,52,56,62]. Also, it is unclear whether ingestion of Symbiodiniaceae by the ciliate occurred during feeding live or dead tissues of coral (carnivorous/histophagous) or attains from elsewhere (algivorous) [54].

Ciliates as bioindicators

The short generation time and delicate membrane of ciliates are most reactive to environmental changes. Thus, ciliated protozoans are used as a biological indicator in assessing the pollution and toxicity of an aquatic ecosystem [63]. Ciliates perform an important role in balancing the biological ecosystem by grazing the majority of dispersed bacteria to reduce the biological oxygen demand (BOD) and suspended matter content of the wastewater [64,65,66,]. Any change in these protozoan communities affects the entire food web and thereby the biological performance of the waste treatment. Thus, the protozoan community structure is an important indicator of the working conditions of artificial waste treatment plants [67]. It was also observed that increasing eutrophication brought ciliate assemblage shift from oligotrich algivorous to omnivorous-nonselective gymnostomatids to detritivorous-bacterivorous scuticociliatids [68]. Thus, the nutrient content of the seawater plays a major role in the occurrence of varied ciliate communities. Besides, it has been demonstrated that the

algivorous ciliate *Tintinnopsis baltica* and *Favella ehrenbergii* as indicators of low levels of nutrients and bacterivorous/detritivorous, while, *Uronema marinum* as an indicator of eutrophication/organic-rich and oxygen-poor environments [68]. Ciliates are also observed frequently in industrial waste containing toxic matters such as heavy metals, detergents, antibiotics, etc, serving as an indicator of the toxicant presence in the affected ecosystem [69]. In this process, around 230 protozoan species (160 ciliates) such as *Uronema nigricans*, *Pseudocohnilembus pusillus*, *Euplotes aediculatus*, *E. affinis*, *E. patella*, etc. are identified [70, 71]. Further, they have a wide ecological significance and perform major functions in elementary cycling and energy flow in aquatic food webs [72]. Henceforth, ciliates can be assumed to be bioindicators of wastewater intrusions into the coral ecosystem. In this context, the corals affected by anthropogenic wastewater inflow can be controlled by their associated ciliates through predation or grazing, reducing the BOD, and suspended matter. This might reduce the pathogenic bacterial intrusion into the coral ecosystem and reduce the chances of a bacterial infection or disease severity in the corals.

Bacterivorous ciliates against coral pathogens

The protozoan has been recognized as a potential biological control for pathogen removal within ecological systems such as aquaculture [73]. They are also used as bacterivorous organisms to prey on pathogens in order to avoid bacterial infection in an environmentally friendly manner [73]. Thus, as bacterial predators, protozoans play a vital role in maintaining the ecology of the aquatic environment [74]. The marine ciliate *Strombidium* sp. was studied for its ability to feed on pathogenic species such as *Vibrio campbellii*, *V. harveyi*, and *E. coli* [73]. Apart from bacteriophages, ciliates are important bacterial predators of the microbial ecosystem [75,76]. Other bacterivorous ciliates like *Paramecium caudatum*, *Halteria grandinella*, *Tetrahymena vorax*, and *Tetrahymena pyriformis* are reported to prey on microbes un-restricted to any bacteria type by non-selective phagocytosis [77]. Also, the feeding response of estuarine ciliate *Uronema nigricans* is larger when fed *Vibrio* sp. than when fed *Bacillus* sp. [74]. *Vibrio cholerae* is a common saltwater bacterium that often serves as a food source for planktonic bacterivorous ciliates, and so *Cyclidium glaucoma*, a ciliate isolated from a wastewater treatment plant, is reviewed to consume bacterial assemblages such as *V. cholerae*, *Shigella* sp., and *Salmonella typhi*. [78]. Similarly, numerous bacterivorous ciliates that feed on pathogenic bacterial species have been studied extensively. Two heterotrophic protists, for example, Thraustochytrids, and labyrinthulids associated with corals are hypothesized for their bacterial predation, production of polyunsaturated fatty acids, and provision of carbon that helps in host coral recovery [79]. Thus, the ciliate's ecological role can be adapted to the coral ecosystem. That is, the invaded ciliates can hunt infectious organisms (bacterial pathogens) that cause coral disease

(Supplementary video 3, 4, and 5). As a result, the microbial pathogenic effect that contributes to the progression of coral disease lesions would be reduced, benefiting coral health and the coral reef ecosystem (Fig. 2 and 3; Table 2).

Potential roles of ciliates in ecosystem health and the possibilities that can be used in coral reef assessments

Although many studies had posed ciliates as pathogenic survivors, they have also demonstrated beneficial functions in numerous aspects such as in waste treatment, bacterivorous of pathogenic bacteria, and symbiosis between the ciliate and ingested microbes [71, 80, 81, 82], which may be beneficial to coral health as well. Recent research has revealed a synergy of coral-associated microbial communities that play a vital part in the health of the coral colony [83], in which ciliate symbiosis is frequently mutualistic, parasitic, and commensal (Table 1) [80]. Symbiosis in the form of mutual interaction benefits both the organism's fitness and their ability to exist in new ecological niches [80]. It assists both parties in the delivery of energy and nutrition, as well as protection from environmental stressors like pollutants or free radicals, and predator defense [84]. Ciliates function as hosts for symbionts such as eukaryotes, bacteria, and archaea [80]. These ciliate symbiotic action benefits symbionts by providing nutrition, CO₂, protection from grazing, inorganic and organic material disposal, and genetic exchange. [80]. Where genetic alterations are accelerated through genome evolution as a result of the close physical proximity of both symbiotic partners [85]. Similarly, in cases of phosphate limitation in a freshwater system, some ciliate algal symbiosis can store phosphate under favourable conditions. [80]. A few associations also aid in sulfur oxidation and sequester algal plastids by keeping their chloroplast intact, which the host maintains and employs in photosynthesis. [80, 86] (Table 2). As a result, these ciliates and their symbiotic relationship with matter cycling are involved in nitrogen fixation, sulfur transformation, high photosynthesis, phosphate storage [80], and UV protection due to the release of Mycosproine-like amino acids (MAA) [87] (Fig. 2), which may aid corals in recovering from diseased or stressed conditions (Table 2). For example, the functional ecology of the coral-associated ciliate *Chromera velia* revealed their potential to infect and develop an endosymbiotic interaction with coral larvae [88]. They also function similarly to *Symbiodinium* sp. as coral photosymbionts [89]. Thompson et al. [79] also hypothesized that ciliates benefit corals through the production of carbon sources, polyunsaturated fatty acids, and predation of bacteria, Hence, these poorly studied ciliate interactions with corals are likely to play an important role in coral health with the influence of changes in nutrient availability and associated microorganisms [12].

Research gaps and future perspectives

Corals connect with a variety of complex microbial communities, the most well-studied of which are Symbiodiniaceae and bacteria for their symbiotic relationship. Other microorganisms, such as protistan ciliates, fungi, and bacteriophages, are little understood in terms of their symbiotic benefits to the host. Ciliates are an important component of aquatic ecosystems because of their role as predators of bacteria, algae and providing nutrients for organisms at higher trophic levels. Thus, coral-associated microeukaryotic ciliates must be useful to the host in a variety of ways, such as nutrient suppliers, pathogenic bacterial and algal removers, which must be explored in order to understand their potential beneficial influence on coral health. Besides, various coral-associated heterotrophic and mixotrophic ciliates must now be isolated, identified, cultivated, and maintained in the lab and used as a model to investigate ciliate life-cycle stages and diverse forms of nutrition. In lab aquaculture conditions, such analysis of feeding patterns and the nature of interaction with the coral holobiont may show their nutrition exchange, material disposal (organic and inorganic), UV protection capability, and genetic exchange. Furthermore, the presence of plastids and other unique photosynthetic pigments in ciliates can be used to study their interaction and distinguish between photosynthetic and heterotrophic forms in order to find mixotrophic ciliates connected with corals. Besides, characterization of the photosynthetic pigments of ciliates and endosymbiotic algae can provide insights into the exchange of ciliate photosynthetic derivatives with host corals. Ciliates in elemental cycling may also be studied to evaluate their impact on nitrogen and phosphorus cycling, as well as other symbiotic benefits that may lead coral reef resilience. Furthermore, multiple investigations have shown ciliates grazing on bacteria, suggesting that coral-associated ciliates can prevent bacterial infection. Therefore, focusing on identifying and characterising more non-pathogenic protozoan symbionts that actively graze bacteria for growth and proliferation can be used as biological control agents. Performing co-infection experiments of compatible protozoan and coral bacterial pathogens also gives the protozoan with the potential to graze on the bacteria that infect the corals. This will allow us to gain the knowledge we need about ciliate specificity, as well as broaden the application of such an approach in pathogen-infected corals. As a result, the next step would be to identify, isolate, and culture more potential protozoan ciliates, screen infecting ciliates with various diseased, immunocompromised, and bleached corals, and characterize the mechanisms involved in bacterial inhibition, nutrition exchange, and other beneficial activities that support coral health using more realistic microcosm environments. Finally, DNA-based molecular approaches such as PCR (polymerase chain reaction) amplification and sequencing of ITS (internal transcriber spacer), 5.8S and 28S rRNA (ribosomal RNA) regions of ciliates may provide identity [32], and studying the

metagenome and transcriptome of coral holobiont may reveal the extent of ciliate diversity and functions [90].

Conclusion

Various protozoan ciliate species have been described for their relationships with corals all around the world. However, the nature of their relationship and potential ecological importance of ciliate-coral interaction is not well understood. The current study highlights some of the essential topics that need to be addressed regarding the significance of ciliates and their host coral connections, as well as the involvement of ciliate communities in nutrient cycling and the colonization of immunocompromised and bleached coral tissue. Furthermore, ciliate cultures could be utilized to better understand the feed specificity of ciliates linked with corals, which could aid in better understanding the host specificity, if any, in the biochemical interactions that enhance coral health.

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Authors contribution

Conceptualization: CR; writing—draft preparation: CR, LI; writing— editing and review: CR, LI, HPR; processed figures: CR, LI, HPR. All authors read and approved the final manuscript.

Declaration

The authors declare that they have no conflict of interest or competing interests.

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Figure legend

Fig. 1 Ciliates and their different life stages identified and isolated from coral species. (a) *Cohnilembus verminus* adult (b) *C. verminus* larvae (c) *C. verminus* division (d) *Holosticha diademata* adult (e) *H. diademata* larvae (f) *H. diademata* division (g) *Euplotes* sp. adult (h) *Euplotes* sp. larvae (i) *Euplotes* sp. division (j) *Uronema marinum* adult (k) *U. marinum* larvae (l) *U. marinum* division were observed and isolated from *Acropora* sp. and *Porites* sp. *C. verminus* was observed for its occurrence only in *Porites* sp. (from coral reefs of Gulf of Mannar reserve regions, Tamil Nadu, India).

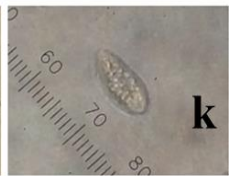
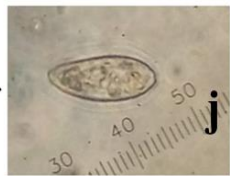
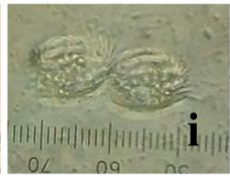
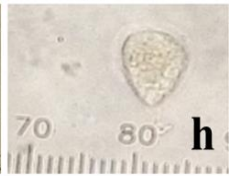
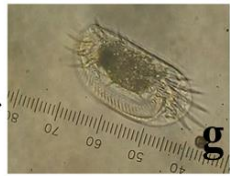
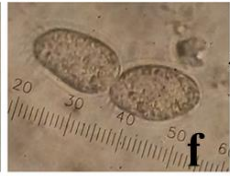
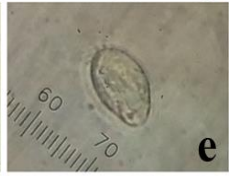
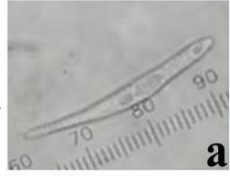
Fig. 2 Ciliates nutrient cycles in the coral reef food web and their possible role in coral resilience. (A) Ciliates heterotrophic nutrition on the microbes (intruded by wastewater) excretes C, N and P., (B) At high temperatures, the pathogenic microbes of waste intrusions or coral reef associates gain virulence and cause coral disease leading to coral Symbiodiniaceae expulsion., (C) The expelled or elsewhere symbionts consumed by mixotrophic ciliates, excrete C, N, P and DMSP., (D) This DMSP is further utilized as a precursor by the coral beneficial microbes (CBM) in the production of tropodithietic acid (TDA) (antimicrobial compound) and thereby exhibits biological control over pathogens. CBM also fixes the carbon, phosphorus, and nitrogen of the excreta to bring about the organic compound distribution., (E) Beneficial ciliates interaction with corals might possibly bring coral resilience due to nitrogen fixation, sulfur transformation, bacterivorous activity against coral pathogens, phosphate storage, and high photosynthesis. These activities of mutual interactions between ciliate and corals may aid coral health by structuring bacterial communities and attracting the Symbiodiniaceae.

Fig. 3 *Cohnilembus verminus* feeding on coral detritus and zooxanthellae.

(a). *C. verminus* adults from *Porites* sp., (b) and (c). *C. verminus* feeding the zooxanthellae with white arrows denoting their bulged portions due to engulfed feed, (d). *C. verminus* feeding on coral dead tissues and bacteria denoted with red arrows, (e). *C. verminus* with engulfed zooxanthellae, white arrows denoting the presence of zooxanthellae inside and outside the cell of ciliate.

Figure 1

Porites sp.



Acropora sp.

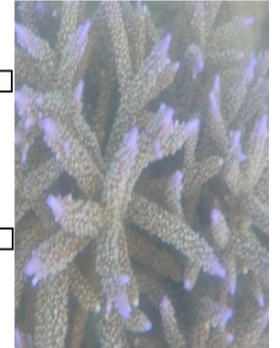


Figure 2

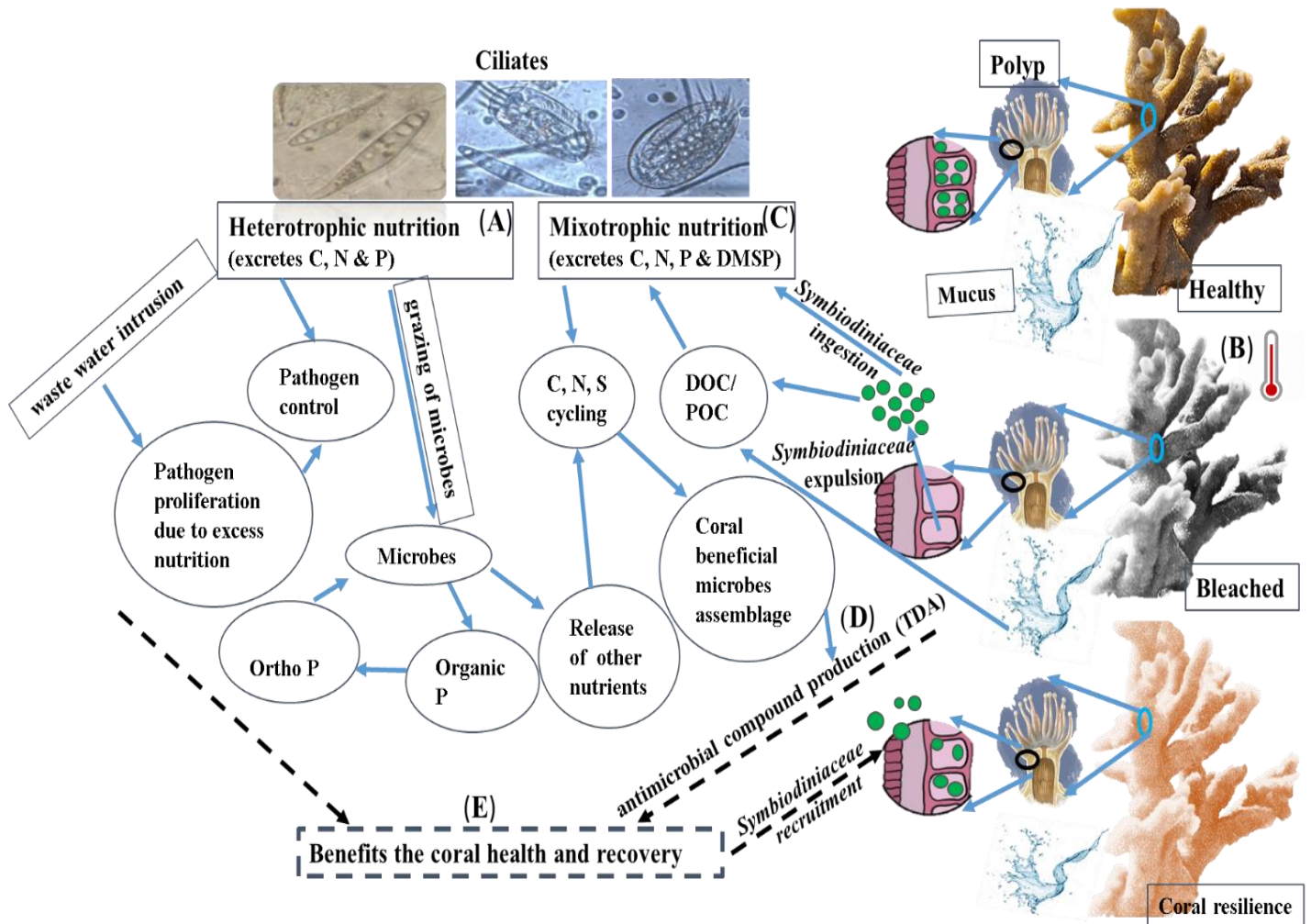


Figure 3

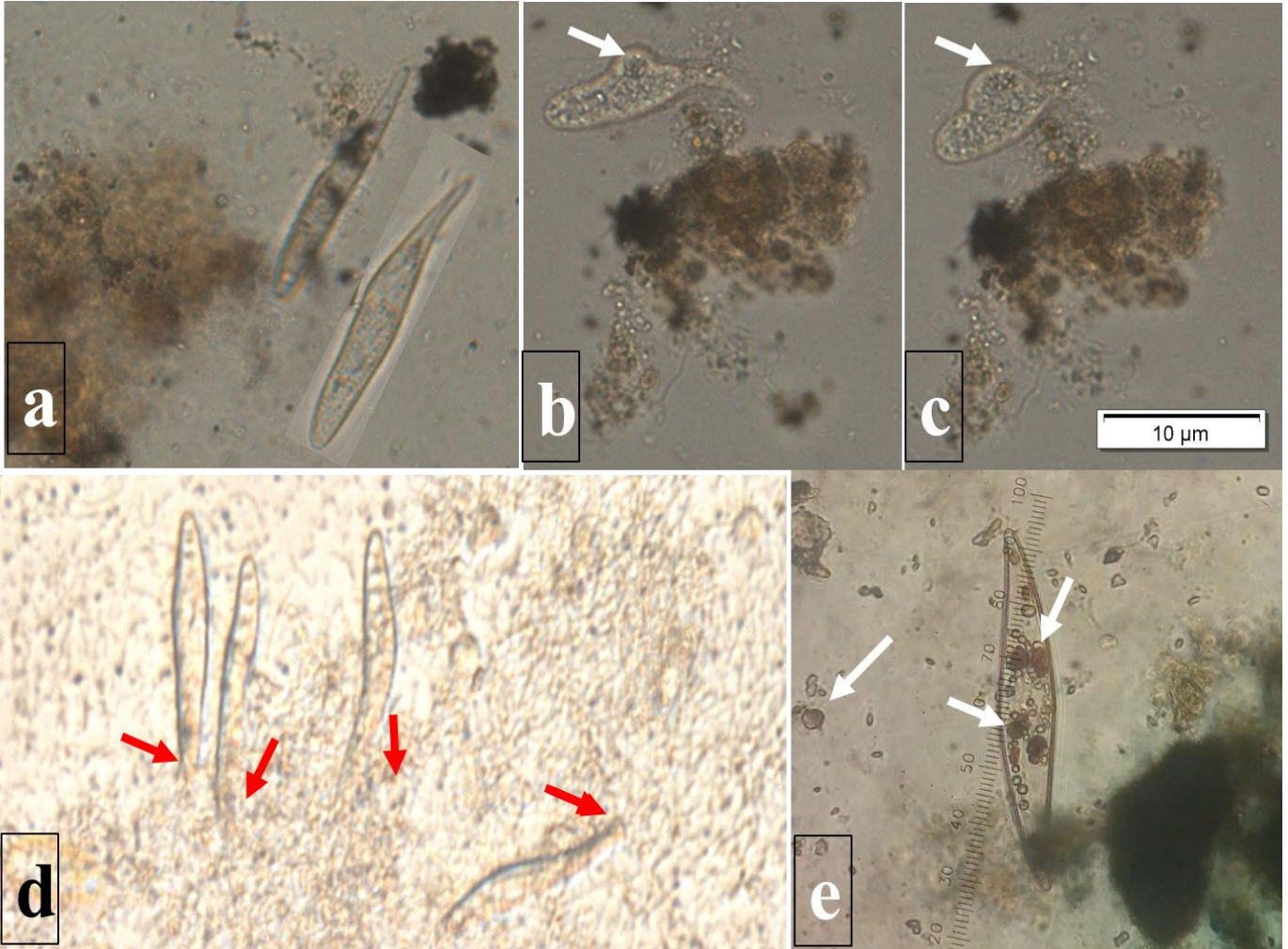


Table 1: Types of ciliates and their associated corals

Ciliate Types	Ciliate Sub types	Examples	Associated with corals
Heterotrophs	Bacterivores	Scuticociliates - <i>Cohnilembus verminus</i> , <i>Homalogastra setosa</i> , <i>Helicostoma nonatum</i> (=Porpostoma notatum), <i>Uronema</i> sp., <i>Paranophrys magna</i> .	<i>Acropora</i> sp. <i>Porites</i> sp., <i>Montastraea</i> sp., [11],[32]
	Herbivores	Oligotrichs - <i>Varistrombidium</i> sp., <i>Varistrombidium kielum</i> , choreotrichs, peritrichs, and prostomatids	<i>Acropora</i> sp. <i>Porites</i> sp., [11],[32]
	Carnivores	Haptotrichs, Hymenostomes, class-Litostomatea (subclass-Haptoria) - <i>Litonotus pictus</i> , <i>Trachelotractus</i> sp., <i>Chaenea vorax</i>)	<i>Pocillopora</i> sp., <i>Acropora</i> sp., <i>Dipolaria</i> sp., <i>Goniopora</i> sp., <i>Orbicella</i> sp., <i>Porites</i> sp. [11],[32]
	Histophages	scuticociliates - <i>Helicostoma nonatum</i> (=Porpostoma notatum), <i>Uronema</i> sp., <i>Paranophrys magna</i> , <i>Cohnilembus verminus</i> , <i>Homalogastra setosa</i>	<i>Porites astreoides</i> , <i>Montastraea faveolata</i>); <i>Acropora</i> [11],[32],[91],[92]
Symbionts	commensals	<u>Phyllopharyngia</u> - <i>Trochilia petrani</i> , <i>Trochilioides recta</i> , <i>Hartmannula derouxi</i> , <i>Dysteria derouxi</i> ; Suctoria- (<i>Paracineta limbata</i> , <i>Acineta</i> sp., <i>Suctoria</i> sp.); Many scuticociliates (<i>Uronema heteromarinum</i> ; <i>Philaster guamense</i> , <i>P. lucinda</i> , <i>Glaucanema trihymene</i>)	<i>Acropora</i> sp., <i>Porites</i> sp., <i>Pocillopora</i> sp., <i>Orbicella</i> sp., <i>Colpophyllia</i> sp., <i>Dipolaria</i> sp., <i>Goniopora</i> sp., <i>Montastraea annularis</i> . [11],[32],[93]
	Parasites	scuticociliates - <i>Uronema heteromarinum</i> ; <i>Philaster guamense</i> , <i>P. lucinda</i> , <i>Glaucanema trihymene</i> .	<i>Pocillopora</i> sp., <i>Acropora</i> sp. <i>Porites</i> sp., <i>Orbicella</i> sp., [11],[32]

	Facultative mixotrophs	Heterotrichia - <i>Protocrusia adherens</i> , <i>Licnophora macfarlandi</i> , <i>Halofolliculina coralliasia</i> , <i>Condylostoma</i> sp.); Hypotrichia -(<i>Diophrys</i> sp., <i>Euplotes</i> sp., <i>Aspidisca</i> sp.) Oligotrichia -(<i>Varistrombidium kielum</i>); Strichotrichia -(<i>Holosticha diademata</i> , <i>Pseudokeronopsis</i> sp., <i>Anteholosticha</i> sp., <i>Hemigastrostyla enigmatica</i>); Litostomatea -(subclass- Haptoria) (<i>Litonotus pictus</i>), Prostomatea (<i>Cryptocaryon</i> sp.).	<i>Pocillopora</i> sp., <i>Acropora</i> sp. <i>Porites</i> sp., <i>Orbicella</i> sp. <i>A. muricata</i> , <i>Diophrys</i> sp.- <i>Montastraea annularis</i> , <i>Colpophyllia</i> sp., [11],[32]
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Table 2. Protozoan ciliates and their possible mode of association in the coral ecosystem.				
Ciliates	Type	Regions	Reported occurrence in dead and diseased tissues of corals and the associated diseases	Possible functions
<i>Protocruzia adherens, Trochilioides recta, Trochilia petrani, Litonotus pictus, Hartmannula derouxi, Licnophora macfarlandi, Chaenea vorax, Dysteria derouxi, Hemigastrostyla enigmatica, Uronema heteromarinum, Acineta sp. Halofolliculina sp., Halofolliculina corallasia, Porpostoma guamense. Hartmannula derouxi, Diophrys sp., Aspidisca sp., Philaster sp., Varistrombis sp., Helicostoma nonatum, Diophrys sp., Varistrombidium kielum, Philaster lucinda, Philaster guamense, Glauconema trihymene, Euplotes sp., Pseudokeronopsis sp., Holosticha diademata</i>	Free-living	Great Barrier Reef Solomon and the Heron Islands, Fiji, Maldives, UK Aquaria	<i>Acropora muricata, A. aspera, Pocillopora damicornis, Acropora spp., Acropora muricata, Pocillopora damicornis and Porites cylindrica , Acropora muricata A. aspera , Acropora sp., A. acuminata, A. surculosa, Porites astreoides, Montastraea faveolata, Acropora muricata</i> [11], [16], [22], [26], [54], [60], [94], [95], [96]. skeleton eroding band disease (SEB), black band disease (BBD), white syndrome (WS), brown jelly syndrome (BJS), brown band disease (BrB),	Majority of the identified and reported ciliates here are described earlier as bacterivores [11]. Thus, might feed upon bacterial pathogens, dead coral tissues, or excess mucosal nutrients [11] that may reduce the disease progression/severity caused by bacterial pathogens.
<i>Halofolliculina sp., Holosticha diademata, Protocruzia adherens, Uronema heteromarinum, Anteholosticha sp., Cryptocaryon sp., Dysteria derouxi, Chaenea vorax, Trochilioides recta, Philaster lucinda, Acineta sp., Varistrombidium kielum, and Suctorina sp. Alveolate sp. Varistrombidium kielum, Trochilia petrani, Glauconema trihymene,</i>	Free-living	Caribbean sea, Venezuela and, Columbia	<i>Acropora cervicornis, Orbicella annularis, O. faveolata, Colpophyllia natans, Montastraea annularis, Acropora palmata, A. prolifera</i> [11], [16], [56], [97]. white band disease (WBD), SEB,	It is possible that these ciliates may help their coral hosts in acquiring essential nutrients or act as an additional food source during stress such as tissue loss and bleaching events [50].

<i>Pseudocarnopsis</i> sp., <i>Licnophora macfarlandi</i> , <i>Paracineta limbata</i> , <i>Trachelotractus</i> sp.				These coral surface microorganisms may provide protection against coral pathogens by secretion of antibiotic substances [98].
<i>Philaster</i> sp. <i>Paraphilaster</i> sp. and a ciliate belong to the order – Prostomatida, <i>Helicostoma nonatum</i>	Free-living	Florida Keys	<i>Orbicella faveolata</i> , <i>Siderastrea sidereal</i> [16], [28]. White plague (WP), BrB-like, and BJS-like signs	Ciliate species are known to recycle organic substances that may aid in the production of the number of essential nutrients required for corals [50].
<i>Philaster lucinda</i> , <i>Uronema heteromarinum</i> , <i>Dysteria derouxi</i> , <i>Varistrombidium kielum</i> , <i>Paracineta limbata</i> , <i>Holosticha diademata</i> , <i>Chaenea vorax</i> , <i>Philaster lucinda</i> , <i>Trochilioides recta</i> , <i>Licnophora macfarlandi</i> , <i>Halofolliculina corallasia</i> , <i>Paracineta limbata</i> , and <i>Condylostoma</i> sp.	Free-living	Moyonette, Reunion and South Africa reefs	<i>Acropora muricata</i> , <i>Porites lutea</i> [11], [16].	These ciliates and their symbiotic association with matter cycling are involved in nitrogen fixation, sulfur transformation, high photosynthesis, phosphate storage [63], and UV protection of the ciliate host with Mycosproine like amino acids (MAA) [71] which may aid corals to revive
<i>Porpostoma</i> sp., <i>Philaster</i> sp.	Free-living	Barrier reefs of Bermuda and Belize	<i>Montastrea annularis</i> and <i>Diploria strigma</i> [16], [62]; BBD	
<i>Philaster lucinda</i> , <i>Suctorina</i> sp., <i>Protocruzia adherens</i> , <i>Chaenea vorax</i> and <i>Holosticha diademata</i>	Free-living	South Africa, Venezuela Reunion, Maldives, and Moyonette	<i>Porites lutea</i> , <i>Acropora muricata</i> , <i>Goniopora djiboutiensis</i> , <i>Colpophyllia natans</i> , <i>Orbicella annularis</i> and <i>Diplora</i> sp. [11], [16].	

<i>Halofolliculina corallasia</i>	Free-living	Gulf of Aqaba, the Red Sea	<i>Stylophora</i> sp, <i>Acropora muricata</i> , <i>Seriatopora</i> sp., <i>Hydnophora</i> sp., <i>Galaxea</i> sp. <i>Pocillopora</i> sp., <i>Mycedium</i> sp., <i>Montipora</i> sp., <i>Echinopora</i> sp., <i>Lobophyllia</i> sp., <i>Goniastrea</i> sp., <i>Millepora</i> sp., <i>Platygyra</i> sp., <i>Fungia</i> sp., <i>Favia</i> sp., <i>Porites</i> sp., <i>Goniopora</i> sp., <i>Favites</i> sp., and <i>Pavona</i> sp. [16], [22]; [99]; [100]; SEB	from their diseased or stressed conditions.
<i>Condylostoma</i> sp., <i>Porpostoma</i> sp., <i>Philaster</i> sp., <i>Porpostoma guamense</i> , <i>Philaster lucinda</i> , <i>Varistrombidium</i> sp. <i>Trachelotractus</i> sp., <i>Holosticha diademata</i> , <i>Homalogastra setosa</i> , <i>Euplotes</i> sp., <i>Cohnilembus verminus</i> , <i>Halofolliculina</i> sp.	Free-living with ingested <i>Symbiodinium</i> sp.	Moyonette, Reunion and South Africa reefs, Caribbean sea, Venezuela and, Columbia, Great Barrier Reef Solomon and the Heron Islands	<i>Acropora muricata</i> , <i>A. surculosa</i> , <i>A. hyacinthus</i> , <i>A. cervicornis</i> , <i>A. palmate</i> , <i>A. prolifera</i> , <i>Diploria</i> sp., <i>Colpophyllia natans</i> , <i>Montastraea annularis</i> , <i>M. faveolata</i> , <i>M. franksi</i> , <i>Madracis mirabilis</i> , <i>M. decactis</i> , <i>Diploria labyrinthiformis</i> , <i>Porites furcata</i> , <i>P. astreoides</i> , <i>Agaricia agaricites</i> , <i>A. tenuifolia</i> , <i>A. fragilis</i> , <i>A. lamarcki</i> , <i>Siderastrea siderea</i> , <i>Scolimia cubensis</i> , <i>Leptoseris cuculata</i> , <i>Stephanochoenia intersepta</i> and <i>Millepora alcicornis</i> [11], [16], [21], [30], [60], [61], [97]; BrB, BBD, SEB	Mixotrophic ciliates containing endosymbiotic algae, or by sequestering chloroplasts may infect and establish an endosymbiotic relationship with corals, similar to <i>Symbiodinium</i> sp. until they recover from stress such as bleaching.
<i>Chromera velia</i>	Symbiotic;	Australia	<i>Montipora digitata</i> , <i>Acropora digitifera</i> (larvae) and <i>A. tenuis</i> (larvae) [72].	

Table 3. Marine ciliates containing Chloroplasts, Cleptochloroplasts, and Dinoflagellates	
Marine ciliates	Reference
<p>Marine ciliates containing chloroplast/cleptochloroplasts</p> <p><i>Myrionecta rubra</i> (Photoautotrophs) <i>Tontonia</i> sp. <i>Laboea strobila</i> (obligate mixotrophs)</p> <p><i>Strombidium conicum</i> (obligate mixotrophs) <i>S. rassoulzadegani</i> (obligate mixotrophs)</p> <p>Marine benthic ciliates (Photoautotrophs) <i>Mesodinium coatsi</i> - green plastid <i>M. pulex</i> <i>M. chamaeleon</i> - green plastid <i>M. rubrum</i> <i>M. major</i></p> <p>Marine ciliates containing dinoflagellates</p> <p>Many species of oligotrichs in the genera <i>Tontonia</i>, <i>Laboea</i>, and <i>Strombidium</i> sequester or enslave chloroplasts from ingested flagellates.</p> <p>Coral associated ciliates containing dinoflagellates</p> <p>Many reports described on ciliates containing the coral associated dinoflagellate species such as <i>Condylostoma</i> sp., <i>Porpostoma</i> sp., <i>Philaster</i> sp., <i>Varistrombidium kielum</i>, <i>Trachelotractus</i> sp., <i>Holosticha diademata</i>., <i>Homalogastra setosa</i>., <i>Euplotes</i> sp., <i>Cohnilembus verminus</i>, <i>Halofolliculina</i> sp., <i>Maristentor dinoferus</i>, and <i>Paraeuplotes tortugensis</i>.</p>	<p>[101]</p> <p>[102]</p> <p>[103,104]</p> <p>[105]</p> <p>[32]</p>