

DISTRIBUTION, HABITAT PREFERENCE, COMPETITIVE INTERACTIONS AND PREDATION OF FRENCH POLYNESIAN BRYOZOA

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Abstract. Sessile invertebrates are important for their contributions to community assemblages in terms of their competitive and trophic interactions. Colonial invertebrates make excellent model organisms for the study of ecological processes. Bryozoans, modular colonial filter feeders, are important competitors in a range of habitats and represent a potentially significant source of diversity. Little work has been done to catalog the Bryozoa of Mo'orea, French Polynesia. By examining coral rubble, artificial substrates and *Turbinaria* spp. algal fronds, I quantified the distribution of bryozoans in a shallow lagoon and simultaneously recorded their competitive interactions. I also quantified patterns of bryozoan richness and abundance with respect to depth and location. Finally, I conducted an experiment to determine the degree to which predation effects an abundant genus, *Rhynchozoon* spp. I found more bryozoans further from the barrier reef and in deeper water. There were vastly more cheilostomates than either cyclostomates or ctenostomates, though it remains unclear whether they are competitively dominant. A few genera dominated the epibiotic algal habitat, showing abundance patterns opposite those seen on coral rubble. I did not find any successional patterns on algae. I did not find a significant effect of predation on uncaged *Rhynchozoon* spp. colonies in the field. This study suggests that abiotic factors may be more important than trophic and competitive interactions in determining bryozoan abundance, but their relative influences remain unclear. This work lays the foundation for future ecological work on factors limiting bryozoans in French Polynesia and provides a guide to the genera found in this study.

Key words: bryozoan; competition; predation; Mo'orea, French Polynesia; distribution

INTRODUCTION

Fouling communities have long been studied for the potential and realized economic effects they produce through increasing drag on ships' hulls. However, they also provide an interesting context for the study of recruitment, succession and competition in a space-limited environment, where natural patterns are often spatially compressed (Cole et al. 2005, Paine and Levine 1981). These and other ecological processes are important in determining community composition. For instance, predation is a major source of disturbance among fouling organisms, many of which are sessile and therefore particularly vulnerable (Cole et al. 2005, Dick et al. 2006). It is important to understand how these ecological processes function to limit fouling organisms before attempting to explain their distributions.

Given the number of processes at work involving both biotic and abiotic factors, the ability to explain spatial variation in community composition is vital to

understanding diversity and distributions of fouling organisms (Barnes and Dick 2000a,b, Dick et al. 2006). Both spatial distribution and ecological processes can be examined in concert for the purpose of understanding species densities and competitive ability, which are key components of succession in a habitat characterized by the short-lived availability of free space (Buss 1979, Grischenko et al. 2008, Paine and Levine 1981). The resulting understanding of distributions and interactions among adults is a critical basis upon which to ask further ecological questions.

This is especially true for modular organisms, whose distributions may be affected by other ecological factors (Buss 1979). For example, for many sessile modular invertebrates, colony size can affect the probability of being overgrown or eaten and can also affect the ability of a colony to recover from such damage (Keough 1989). However, the effects of competition and recruitment on distributions are precluded to an unknown degree by the removal of colonies through

predation and other disturbances (Menge et al. 1999). It is difficult to understand these types of processes without a base knowledge of species distributions and interspecific interactions. Thus it is important to examine the distributions and competitive interactions of fouling taxa in different habitats in order to better understand the ecological processes that are most important in the formation of these communities and to build a base upon which such processes can be investigated in more depth. The present study provides such a platform for the study of bryozoans.

Bryozoans are modular, colonial filter feeders that are often a component of fouling community assemblages (Grunbaum 1987). They encrust a number of artificial substrata, as well as algal fronds, sea grass blades, coral rubble and other natural substrata (Keough 1989, Tilbrook et al. 2001). Bryozoans make a particularly good model organism for ecological studies because they have a relatively short-lived dispersal stage in the form of lecithotropic larvae (Humphries 1977) and are remarkably well adapted in terms of settlement and growth rates for the rapid utilization of space (Barnes and Dick 2000a, Harvell and Grosberg 1988). Additionally, as adult colonies grow, experimental evidence indicates that separate colonies as well as individual zooids within colonies can vastly affect local flow environments (Grunbaum 1987). This in turn affects the availability of food, oxygen and hydrodynamic waste removal. Although they are generally considered to have lower overgrowth ability than ascidians and sponges (Barnes and Dick 2000a), bryozoans serve an important role in the structure of fouling communities and contribute to the framework of coral reef ecosystems as well (Pachut et al. 2009). As such, it is important to understand bryozoan communities for their potential as model organisms, roles in marine environments and contributions to biodiversity.

In Mo'orea, French Polynesia, as with much of the tropical South Pacific, few studies have focused on bryozoan ecology or distributions, especially in shallow water habitats (Tilbrook et al. 2001). Although the Mo'orea Biocode Project now seeks to inventory species of Bryozoa, descriptions of distributions and habitat differences within this group are beyond the scope of their work. The facilitation of future ecological work on Bryozoa mandates an understanding of species distributions. As such, this study sought to contribute to the knowledge of

bryozoan distributions by testing the following hypotheses: 1) Abundance and richness of Bryozoa decreases from the mouth to the base of Cook's Bay, Mo'orea. 2) Bryozoa are found in greater abundance on coral rubble than artificial substrata, sea grass or algal fronds. 3) Bryozoa are more abundant in shallower waters at all sites. I also examined overgrowth interactions among bryozoans in Cook's Bay to test the hypothesis that order Cheilostomata is competitively dominant. Past work in other geographical regions has found that cheilostomatids are the most rich and abundant group in Bryozoa and dominate competitive interactions, although some evidence suggests that both ctenostomatids and cyclostomatids outcompete the former (Barnes and Dick 2000a). Finally, I conducted an experiment examining predation rates on *Rhynchozoon* spp. I tested the hypothesis that predation is density dependant for adults of this species. I sought to elucidate the effects of predation on a single species in the hopes of determining the magnitude to which the damage incurred limits the ecological effects of intra- and interspecific competition. If predation is positively correlated with density, it is less likely that competition will limit growth. This work provides an early catalog of distributions of Bryozoa in French Polynesia, which is a critical basis for further ecological work on this group and serves as a baseline for future biodiversity studies (Rowden et al. 2004, Tilbrook 2001). I have also begun to examine both trophic and competitive interactions as potential explanations of distributional patterns.

METHODS

Study Site

The island of Mo'orea (S 17° 30' W 149° 50') is located in the Society Archipelago in French Polynesia. It is basaltic high island surrounded by a fringing reef and an outer barrier reef, separated by a sandy-bottom lagoon.

Distributional Survey and Overgrowth Interactions

I completed a survey of coral rubble at four sites in Cook's Bay and one site at Temae beach in Mo'orea (Figure 1). At each site, I collected 10 pieces of rubble at 1 meter intervals along 10 m transects at both 1 m and 3 m depths (except at Temae, where depth

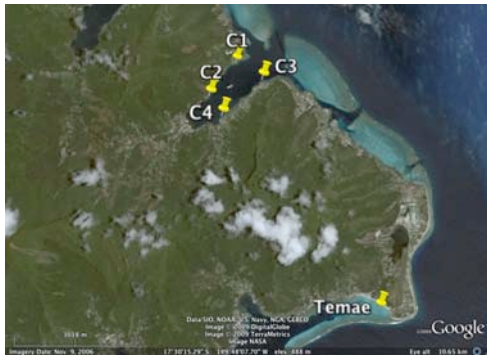


FIG. 1. Sampling locations for coral rubble, artificial substrate and *Turbinaria* spp. fronds (C1 and C2 only) in the lagoon of Mo'orea, French Polynesia. © 2009 Google, Image © 2009 DigitalGlobe, Image © 2009 TerraMetrics, Image NASA

does not reach 3 m, so I only collected along a 1 m transect). For each piece of rubble, I noted dimensions, displacement volume and topographical characteristics. I then examined each piece for any Bryozoa, breaking them apart when necessary. For all colonies, I identified to genus when possible and quantified overgrowth interactions by noting organisms overgrowing or being overgrown by each bryozoan. In general, a species was considered overgrown if its competitor was covering any of its apertures (the openings for the protrusion of individual polypides). This procedure follows that of Barnes and Dick (2000a,b).

At each Cook's Bay site, I also observed Bryozoa on artificial substrates. On three dock pilings per site, I noted all bryozoans and their overgrowth interactions in a 5 cm by 5 cm quadrat placed at 20 cm intervals along a 1 m transect from the water's surface ($n = 5$ samples per transect). I also collected ten fronds of *Turbinaria* spp. (Phaeophyceae) from sites C1 and C2 and examined 10 blades from each frond at regular intervals along the length for bryozoans and overgrowth interactions.

For each bryozoan species found, I measured zooid length (ZL), zooid width (ZW), orifice length (OrL) and orifice width (OrW). If relevant, I also measured ovicell length (OvL), and ovicell width (OvW). Unless otherwise noted, sample size for these measurements was $n = 3$. I also included a physical description of the colony structure and, when possible, a stereomicroscope image (Appendix A).

Predation Experiment

I used PC-11 marine grade epoxy (Protective Coating Co., Pennsylvania, USA) to secure adult colonies of *Rhynchozoon* spp. to Petri dishes, which were attached to 15 cm by 15 cm ceramic tiles for weight. This species was the only one that was sufficiently abundant and with large colonies that could be collected with minimal damage. I had 10 dishes each of three densities: single colony, two colonies and three colonies. I took scaled photographs of each dish before I secured a 1 mm mesh cage around five dishes of each density. I then placed the dishes in random order at 15 cm intervals on a line parallel to shore at Cook's Bay site one. After one week, I collected the dishes and took pictures in the same manner as before. I then used ImageJ software (Rasband 2009) to calculate colony area before and after plates were placed in the field.

Statistical Analyses

Distributional Survey and Overgrowth Interactions

To compare mean number of colonies and richness of bryozoans on coral rubble, *Turbinaria* spp. and dock pilings across sites, I used one-way ANOVA. I repeated this test for both depths for coral rubble. I also tested for a difference between the two depths in mean number of colonies on rubble (summed for all sites) using one-way ANOVA. For *Turbinaria* spp., I used linear regression to test for a relationship between frond length and total number of colonies. I also tested for a relationship between blade age (using proportional distance from distal end of frond as a proxy) and number of colonies using linear regression. I tested for a difference in mean frond length between sites using one-way ANOVA. For dock pilings, I tested for relationships between depth and richness/number of colonies.

I created a standard interaction matrix (Barnes and Dick 2000a) describing the overgrowth interactions between species (Appendix B). For each bryozoan species at each site, I calculated win:loss ratios whenever more than five interactions occurred (see Barnes and Dick 2000b). This applied to 10 cheilostomates, 1 cyclostomate and 1 ctenostomate. I built a hierarchical ranking of the 10 cheilostomes according to their win:loss

ratios, but, due to the taxonomical disharmony encountered, the other two orders were not included. With these groupings, I also tested for relationships between richness/total number of colonies and depth/site using ANOVA. I compared the win:loss ratios of cheilostomates and cyclostomates (those with enough replication to calculate a mean) using one-way ANOVA.

Predation Experiment

I calculated the area lost for each plate by subtracting the initial area from the final area. For both caged and uncaged treatments, I tested for a difference in mean area change using ANOVA. I tested for density dependence by running two-way ANOVA for the three density treatments.

RESULTS

Distributional Survey

The mean number of colonies found per

for sites C1 and C3 ($F_{7,72} = 2.717$, $P = 0.015$). Deeper water was positively associated with mean number of colonies per rubble ($F_{1,78} = 6.194$, $P = 0.015$) and mean richness per rubble ($F_{1,78} = 7.208$, $P = 0.009$).

The same analyses run at the taxonomical level of order demonstrated effects of site on per rubble abundance of cheilostomates ($F_{3,72} = 2.877$, $P = 0.042$) and ctenostomates ($F_{3,72} = 7.333$, $P < 0.001$), but not cyclostomates ($F_{3,72} = 0.862$, $P = 0.465$). Depth affected per rubble abundance of cheilostomates ($F_{1,72} = 5.182$, $P = 0.026$) and cyclostomates ($F_{1,72} = 4.175$, $P = 0.045$), but not ctenostomates ($F_{1,72} = 0.417$, $P = 0.417$).

I found no colonies at the Temae site, but was only able to collect rubble from 1 m depth before there was no location at 3 m depth before the barrier reef.

On *Turbinaria* spp., site affected per frond mean richness ($F_{1,19} = 6.425$, $P = 0.02$) and mean number of colonies ($F_{1,19} = 19.133$, $P <$

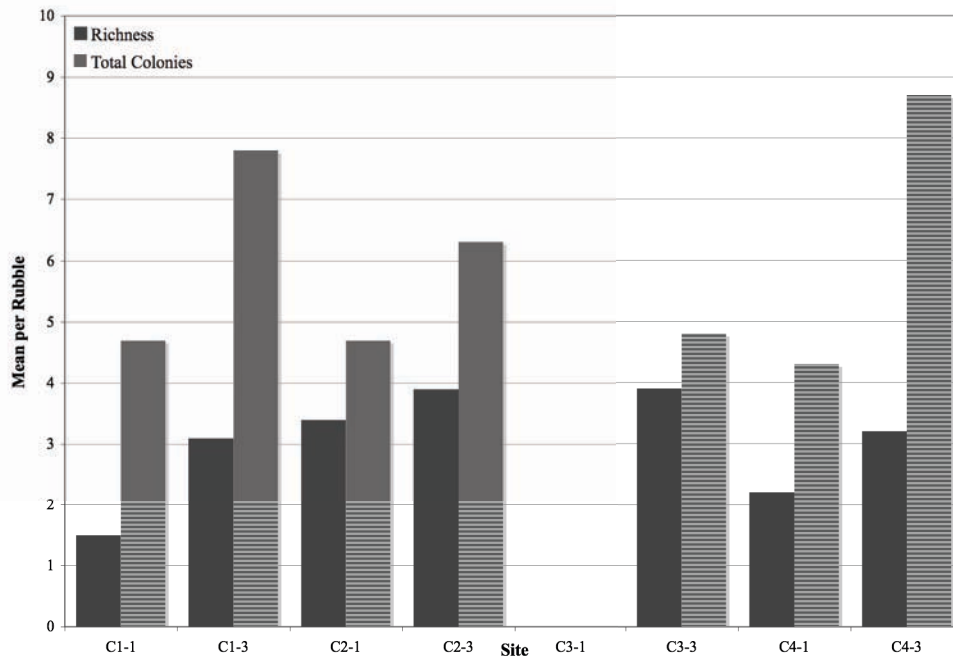


FIG. 2. Bryozoa on coral rubble in Cook's Bay, Mo'orea. Greater richness and total number of colonies was found near the mouth of Cook's Bay and in deeper waters.

piece of coral rubble was 39% greater at the base of Cook's Bay (sites C2 and C4), though the effect of site on total colonies per rubble was not significant ($F_{7,72} = 1.792$, $P = 0.102$, Figure 2). The richness per rubble averaged for sites C2 and C4 was 49% greater than that

0.001). Site C1 had 67% greater richness and 2.9 times the number of colonies than site C2. Mean frond length was not different between sites ($F_{1,18} = 1.225$, $P = 0.3$). The number of colonies per frond was significantly proportional to frond length at site C1 ($F_{1,8} =$

8.813, $P = 0.018$) but not at C2 ($F_{1,8} = 0.147$, $P = 0.712$) or overall ($F_{1,18} = 0.313$, $P = 0.583$). The number of colonies per blade was not proportional to distance from the distal end of the frond (a proxy for blade age; $F_{1,8} = 0.023$, $P = 0.883$; Figure 3).

On dock pilings in Cook's Bay, there was no effect of site on richness ($F_3 = 0.4495$, $P = 0.45$) or number of colonies ($F_3 = 0.914$, $P = 0.44$). There was greater richness with more depth, though this effect was not significant ($F_{1,48} = 3.42$, $P = 0.07$). Greater depth had a significant effect on total colonies found ($F_{1,48} = 4.40$, $P = 0.04$).

Overgrowth Interactions

I found 2 genera in order Cyclostomata, a single genus in order Ctenostomata, and 17 genera in order Cheilostomata across all habitat types. The total number of interactions for each order was: 19, 1 and 194, respectively (see Appendix B for interaction matrix). Thus, only the win:loss ratios of cyclostomates and cheilostomates were analyzed. There was no difference between the mean win:loss ratio of cyclostomes (mean = 0.872) and that of

interactions yields a hierarchy of competitive ability: *Metacleidochasma* spp. > *Rhynchozoon* spp. > *Scrupocellaria* spp. > *Robertsonidra* spp. > *Cosciniopsis* spp. > *Celleporaria* spp. > *Mucropetraliella* spp. > *Torquatella* spp. > *Fenestrulina* spp.

Predation Experiment

Density did not have a significant effect on change in colony area over the course of the experiment ($F_{2,27} = 0.763$, $P = 0.476$). Overall, there was no difference between the mean initial area and the mean final area (t -ratio = -0.857, $df = 29$, $P = 0.20$). After removing the replicates that were damaged or that had lost whole colonies, there was no difference between mean change in area between cage and non-cage treatments ($F_{1,28} = 0.254$, $P = 0.62$).

DISCUSSION

The diversity of bryozoans on coral rubble in Cook's Bay was higher than expected given the results of a previous settlement study, which found specimens from only five families (Berkson 2002). The hypothesis that

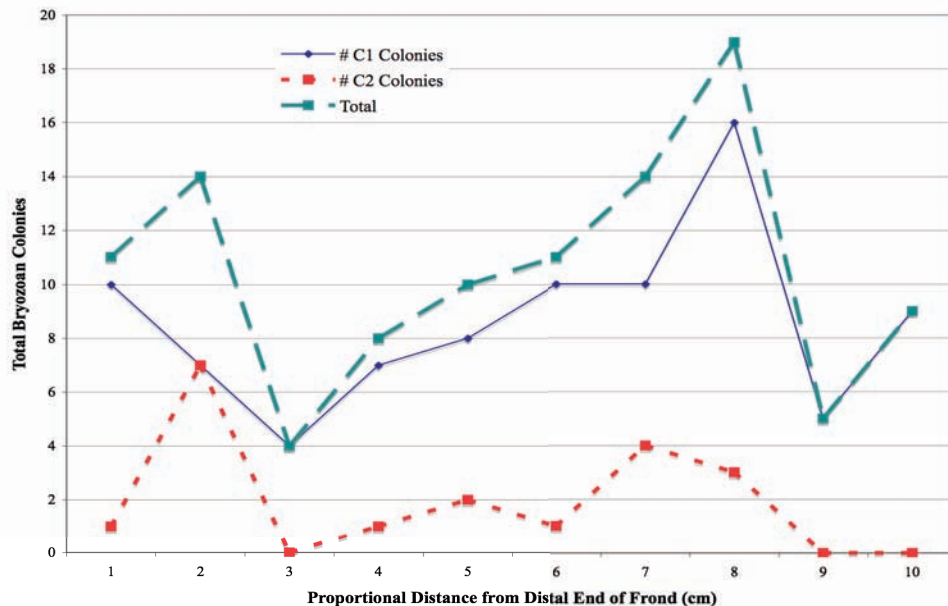


FIG. 3. Epifaunal bryozoan colonies as a function of blade age. No relationship was found between a proxy for blade age and the number of bryozoan colonies present in an attempt to establish patterns of succession.

cheilostomes (mean = 0.846; $F_{1,11} = 0.068$, $P = 0.8$). Comparing overall win:loss ratios of the nine cheilostomates with five or more

more genera would be found on rubble than in other habitats is supported by my results. However, the causes of spatial heterogeneity

and distributional patterns remain uncertain. The patterns found in this study could be explained by a number of non-mutually exclusive factors (Menge et al. 1999). The greater number of colonies and richness at the two interior Cook's Bay sites reflects a rejection of my hypothesis. Although it is generally expected that richness is greater near the barrier reef (the ultimate source of propagules), it is possible that bryozoans, which are considered competitively inferior to many other sessile invertebrates (Barnes and Dick 2000a), are excluded from outer habitats. This would help explain the anomalous lack of Bryozoa at the Temae and C3-1 sites. It is likely that a number of factors limit bryozoan recruitment and/or survival on fairly small spatial scales (Dudgeon et al. 1999). These factors may include biotic interactions, but the results of my predation experiment show that, at least in the case of *Rhynchozoon* spp., it is unlikely that predation plays a major role. It seems more likely that abiotic factors, especially sedimentation and wave action cause the localized absence of bryozoans in the Mo'orea lagoon. The potential effects of sediment were made apparent by the near coating that had settled on the plates used in the field for the predation portion of this study. Sediment is known to smother sessile invertebrates, especially soon after metamorphosis (Young and Chia 1984), and wave action can perturb coral rubble and make survival of delicate colonies impossible. These factors are also likely explanations for the increases in richness and abundance of bryozoans in deeper water, a pattern that held for artificial substrates as well and which opposes my hypothesis. Wave action, which is closely tied to turbidity as well as mechanical disturbance of mobile substrates like coral rubble, has less of an impact at depth. In general, it is unclear which factors are relatively more important in limiting bryozoans' distributions, but some combination of abiotic factors and competitive exclusion are the likely to be most important.

Interestingly, only six total bryozoan genera (all cheilostomates) were found on *Turbinaria* spp. fronds. Of those, four were found on three or fewer blades. Thus, two genera, *Fenestrulina* spp. and Bugulidae (identified to family only), were dominant. Richness and abundance of colonies followed the pattern I hypothesized, with site C1 having significantly greater of both quantities. This pattern is probably not an artifact of sampling since there was no difference in the

size of algal fronds between sites. The dominance of only a few taxa and the distributional patterns serve as a basis for asking a number of questions about epibiotic bryozoans in French Polynesia. Of particular interest is the efficacy of an epifaunal bryozoan in dispersing between islands (since algal fronds will break from holdfasts and may drift for extended periods of time). If there is a notable difference in dispersal ability that correlates with the frequency with which a species is found as epifauna, insights into the evolutionary history and adaptive radiation of French Polynesian Bryozoa might be gained. Further work will need to be done to determine the successional patterns of epifaunal bryozoans since my results showed no pattern of number of colonies and blade age. A colonization study could shed light on this question and could be applied to a number of habitat types. Information regarding the successional status of Bryozoa would yield valuable insights into their competitive ability. More comprehensive factorial ecological studies will be needed to parse out the relative effects of life-history traits and interactions on community assemblage, a recognized gap in knowledge for colonial invertebrates (Winston 1981).

Although my sampling methods proved inadequate for a full analysis of overgrowth interactions on coral rubble, the sheer abundance of Cheilostomata relative to the other two orders serves as some evidence that this group might be competitively dominant in French Polynesia (at least in relatively shallow waters). This pattern has been found in other regions (Dick et al. 2006, Pachut et al. 2009). However, factors inherent to island biogeography may also explain this pattern. For instance, it is unknown whether this group has better dispersal ability or arrived by chance earlier than the other two orders. However, it has been suggested that some genera, including *Parasmittina*, *Celleporaria* and *Rhynchozoon*, are more opportunistic and early-successional than most (Dick et al. 2006). Nevertheless, the species characteristics that lead to these distinctions merit future evolutionary research to understand the degree of radiation of French Polynesian cheilostomates. Only then could any strong conclusions be made about their potential to competitively exclude or regularly overgrow either ctenostomates or cyclostomates. The interaction matrix demonstrates support for previous work (e.g. Barnes and Dick 2000a), in terms of the competitive superiority of both

sponges and colonial ascidians over bryozoans.

The present study provides a sound basis for asking numerous questions about the ecology of French Polynesian Bryozoa. I have cataloged a number of bryozoan genera and provided one of the first studies examining their distributions as related to both depth and location in the Mo'orea lagoon. Further work could approach the patterns I have found from an evolutionary standpoint or continue with the framework for understanding interspecific interactions that I have built. While some patterns I have discovered are stronger than others, the results of my study prompt further research into this surprisingly diverse group in Mo'orea.

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APPENDIX A

Species of Bryozoa found in the Mo'orea lagoon

Format after Dick et al. 2006

Measurements:

Zooid length (ZL) is the distance from the posterior to anterior ends of the zooids skeleton (the zooecium). Zooid width (ZW) is the distance across the zooecium at the widest point. Orifice length (OL) is the distance across the orifice parallel to the primary axis of the zooid (e.g. parallel to the zooid length measurement). Orifice width (OW) is the distance across the orifice orthogonal to the primary axis of the zooid. Ovicell length (OvL) is the distance across the ovicell parallel to the primary axis of the zooid. Ovicell width (OvW) is the distance across the ovicell orthogonal to the primary axis of the zooid. All measurements are in mm.

Glossary:

- Zooid-** Individual bryozoon that divides asexually to form a colony
- Orifice-** Opening generally towards one end of zooid from which the lophophore is protruded for feeding and gas exchange
- Lophophore-** Semi-circular tentacular feeding appendage
- Avicularia-** Specialized, highly muscularized zooids which defend colony with mandible like appendages
- Unilaminar-** Zooids grow in a single plane (e.g. all orifices are oriented in the same direction)
- Multilaminar-** Zooids grow in many planes or in all directions around an erect columnar primary axis (as with *Margaretta* spp.)

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder UMBONULOMORPHA
Superfamily LEPRALIELLOIDEA
Family LEPRALIELLIDAE
Genus *Celleporaria*



Measurements

Zooid Length (ZL), average: 0.29 (range: 0.27-0.32); Zooid Width (ZW), 0.20 (0.18-0.22); Orifice Length (OL), 0.13 (0.11-0.15); Orifice Width (OW), 0.14 (0.11-0.15)

Description

Colonies encrusting, often raised in the center and white, sometimes partially translucent. Zooids distributed patchily among large calcareous spines. Orifice generally slightly ovular. Avicularia not present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder LEPRALIOMORPHA
Superfamily SCHIZOPORELLOIDEA
Family GIGANTOPORIDAE
Genus *Cosciniopsis*



Measurements

ZL, average: 0.52 (range: 0.47-0.56); ZW, 0.37 (0.34-0.39); OL, 0.13 (0.12-0.14); OW, 0.14 (0.14-0.15)

Description

Orange, encrusting, well-calcified colonies. Zooids organized into fairly well defined rows. Orifice slightly raised and flattened at the posterior end. Numerous pores posterior to the orifice. Avicularia not present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder LEPRALIOMORPHA
Superfamily SCHIZOPORELLOIDEA
Family Microporellidae
Genus *Fenestrulina*



Measurements

ZL, average: 0.38 (range: .28-.44); ZW, 0.27 (0.25-0.30); OL, 0.10 (0.08-0.12); OW, 0.13 (0.11-0.15)

Description

Encrusting translucent colonies. Zooids separated by deep groove and roughly organized into radial rows. Orifice with small semicircular groove centered on posterior edge. Many small pores posterior to orifice. No avicularia present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder LEPRALIOMORPHA
Superfamily SCHIZOPORELLOIDEA
Family MARGARETTIDAE
Genus *Margaretta*



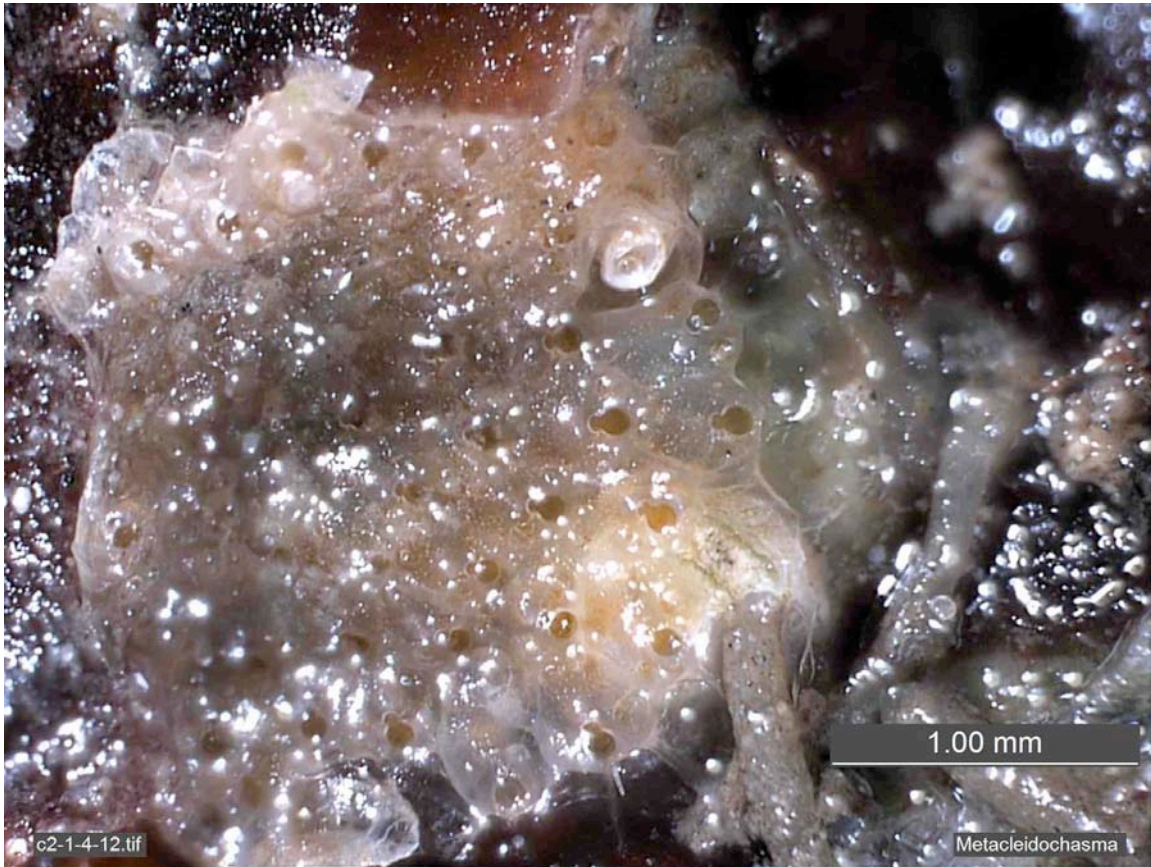
Measurements

ZL, average: 0.42 (range: 0.39-0.46); ZW, 0.17 (0.16-0.19); OL, 0.07 (0.052-0.086, n = 2); OW, 0.12 (0.121-0.123, n = 2)

Description

Colonies branching, translucent brown. Zooids narrow and elongate, multilaminar. Zooids slightly overlap. Orifice ovular (width greater than length). No avicularia present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder LEPRALIOMORPHA
Superfamily CELLEPOROIDEA
Family PHIDOLOPORIDAE
Genus *Metacleidochasma*



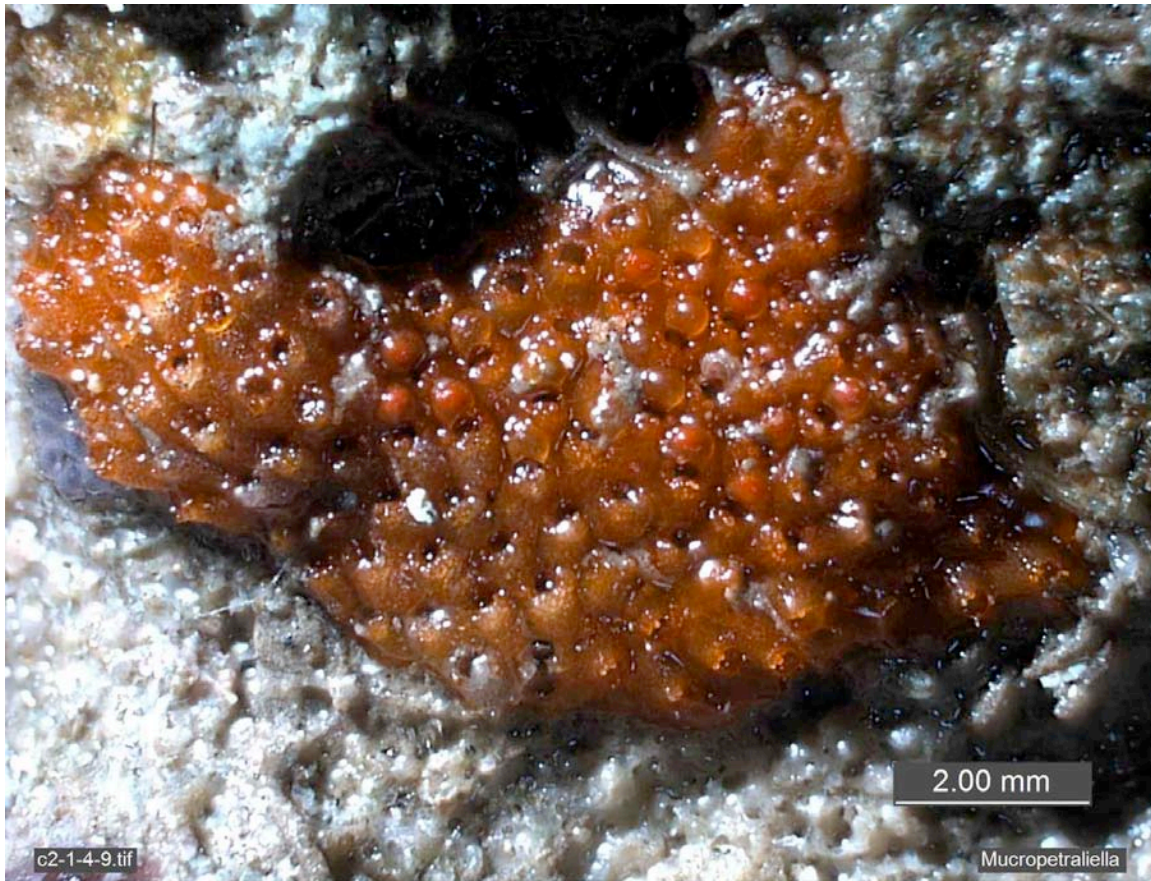
Measurements

ZL, average: 0.41 (range:0.38-0.43); ZW, 0.26 (0.21-0.30); OL, 0.14 (0.13-0.14); OW, 0.086 (0.082-0.09)

Description

Colonies encrusting, typically translucent with yellow orifice. Shallow groove separates zooids, which are organized in radial rows. Orifice has large circular groove at posterior end. Many small pores posterior to orifice. No avicularia present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder LEPRALIOMORPHA
Superfamily SCHIZOPORELLOIDEA
Family PETRALIELLIDAE
Genus *Mucropetraliella*



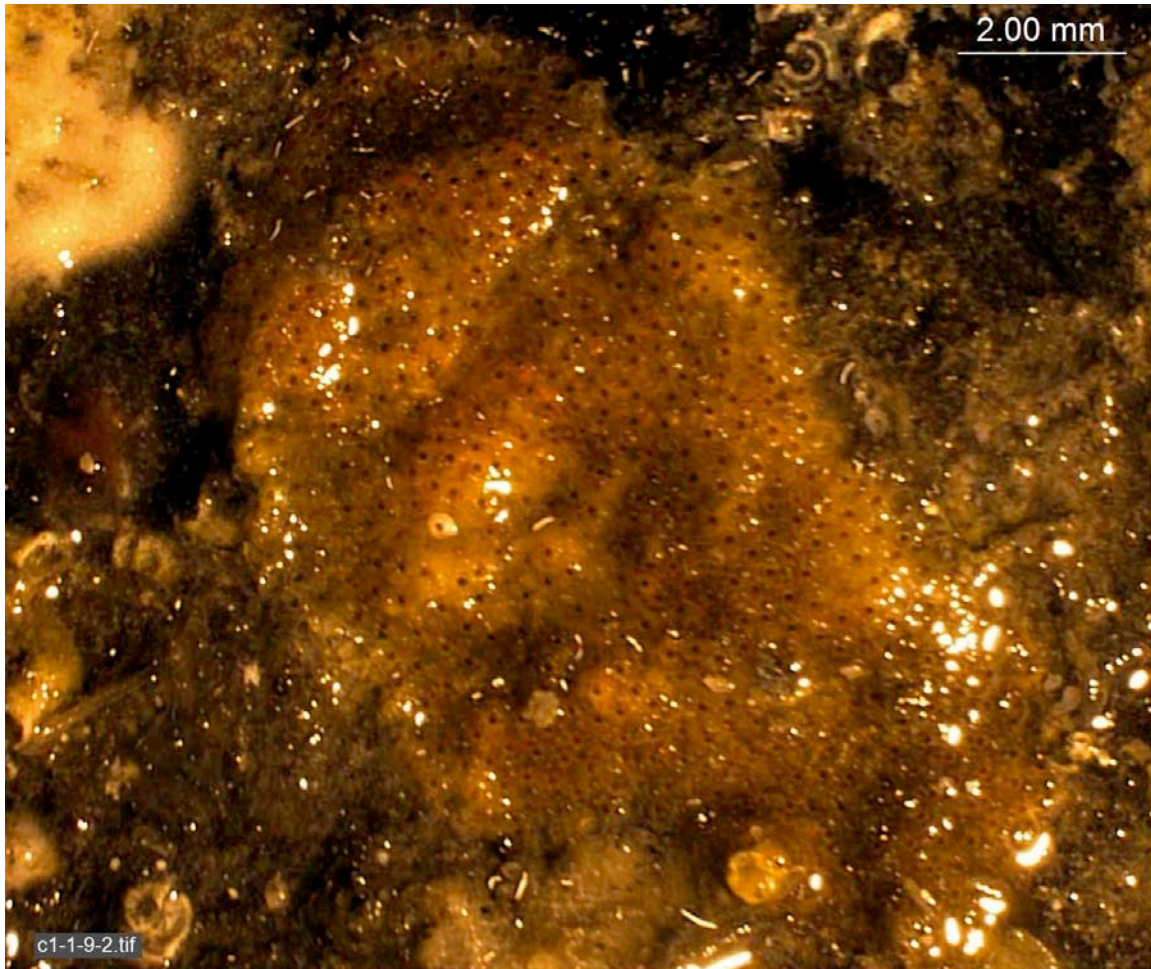
Measurements

ZL, average: 0.85 (range: 0.79-0.91); ZW, 0.61 (0.551-0.58); OL, 0.18 (0.14-0.17); OW, 0.23 (0.21-0.29)

Description

Colonies encrusting, red-orange. Zooids closely packed with deep grooves separating individuals. Anterior (orifice) end raised higher from substrate than posterior end. Two small spines protrude from the posterior base of each orifice. The posterior base of the orifice is flattened. No avicularia present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder UMBONULOMORPHA
Superfamily SMITTINOIDEA
Family SMITTINIDAE
Genus *Parasmittina*



Measurements

ZL, average: 0.25 (range: 0.23-0.27); ZW, 0.17 (0.165-0.18); OL, 0.08 (0.066-0.093); OW, 0.072 (0.068-0.078)

Description

Colonies encrusting, light brown to translucent in color with dark brown orifices. Zooids arranged in slightly offset rows. Orifice is round. Colonies only slightly calcified. No avicularia present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder LEPRALIOMORPHA
Superfamily CELLEPOROIDEA
Family PHIDOLOPORIDAE
Genus *Rhynchozoon*



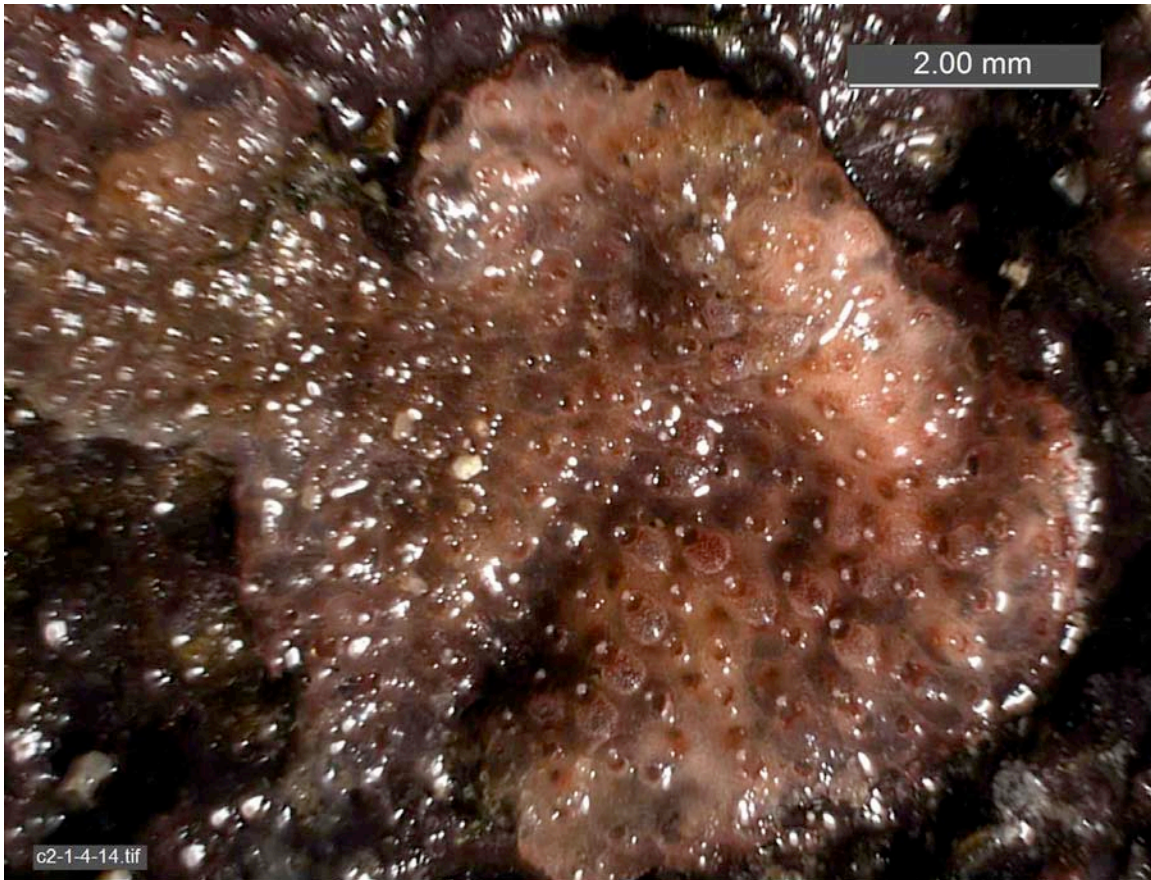
Measurements

ZL, average: 0.25 (range: 0.24-.262); ZW, 0.16 (0.154-0.168); OL, 0.096 (0.082-0.117); OW, 0.083 (0.077-0.09)

Description

Colonies encrusting and white. Zooids organized into alternating radial rows separated by shallow grooves. At posterior end of orifice, raised calcareous zooidal wall with two short spines. Orifice typically round. No avicularia present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder [UNPLACED]
Genus *Robertsonidra*



Measurements

ZL, average: 0.29 (range: 0.47-0.49); ZW, 0.30 (0.284-0.382); OL, 0.094 (0.08-0.11); OW, 0.12 (0.1-0.3); OvL, 0.093 (0.09-0.10); OvW, 0.077 (0.075-0.079)

Description

Colonies encrusting and pink in color with darker pigmentation around the orifice. Zooids organized in unidirectional rows and separated by shallow grooves. White ovicells are located just anterior to orifice. Orifice is approximately round and zooids generally ovular in shape. No avicularia present.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder FLUSTRINA
Superfamily BUGULOIDEA
Family CANDIDAE
Genus *Scrupocellaria*



Measurements

ZL, average: 0.322 (range: 0.29-0.36); ZW, 0.17 (0.15-0.19); OL, 0.10 (0.086-0.12); OW, 0.13 (0.12-0.14)

Description

Colonies branching, unilaminar, light brown to translucent in color. Darkly pigmented zooids visible on surface that is nearest to substrate. Orifice ovular- significantly wider than long.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder FLUSTRINA
Superfamily MICROPOROIDEA
Family ONYCHOCELLIDAE
Genus *Smittipora*



Measurements

ZL, average: 0.484 (range: 0.5-0.53); ZW, 0.30 (0.23-0.40); OL, 0.12 (0.11-0.13); OW, 0.13 (0.12-0.14)

Description

Colonies encrusting, translucent in color with dark avicularia (mandibles) pointing in all directions and originating from some but not all zooids. Zooids flattened with minimal grooves separating individuals; they are not organized into rows but rather radiate in a general primary growth direction but with significant variation in orientation. Orifice is fairly round but with flattened posterior end.

Class GYMNOLAEMATA
Order CHEILOSTOMATIDA
Suborder ASCOPHORA
Infraorder LEPRALIOMORPHA
Superfamily SCHIZOPORELLOIDEA
Family TETRAPLARIIDAE
Genus *Tetraplaria*



Measurements

ZL, 1.112 (n = 1); ZW, 0.534 (n = 1)

Description

Colonies branching, bilaminar and brown to translucent in color (green-blue coloration in photo is dye). Zooids become narrow at base. Lophophore of each zooid protrudes opposite attached based of subsequent zooid.

Class STENOLAEMATA
Order CYCLOSTOMATA
Suborder TUBULIPORINA
Family DIAPEROECIIDAE
Genus *Nevianipora*



Measurements

ZL, average: 0.438 (range: 0.41-0.49); ZW, 0.16 (0.15-0.17); OL, 0.13 (0.11-0.15); OW, 0.11 (0.09-0.12)

Description

Colonies branching, rigidly calcareous and dark brown in color. Zooids branch from primary axis to form tube shaped openings in multilaminar organization. Orifice may be wider than mid-section of zooid and is circular.

Class STENOLAEMATA
Order CYCLOSTOMATA
Suborder TUBULIPORINA
Family TUBULIPORIDAE
Genus *Tubulipora*



Measurements

ZL, average: 0.242 (range: 0.19-0.27); ZW, 0.09 (0.08-0.11); OL, 0.09 (0.07-0.10); OW, 0.072 (0.06-0.09)

Description

Colonies encrusting, multilaminar, translucent with zooids protruding in all directions. Zooids may be straight or slightly curved with little organization. Orifice is mostly circular except for a small groove.

Not Pictured: *Bugula* spp., *Poricella* spp., *Chaperiopsis* spp.

APPENDIX B

Interaction Matrix

Displays overgrowth interactions for all taxa encountered in this study. Each pairwise interaction is characterized by three numbers. The top right number is the number of wins for the taxon in the column. The bottom right number is total interactions between the row and column taxa. The bottom left number is the number of wins for the taxon in row.

	CELLARIIDAE	BUGULIDAE	Bugula	Celleporaria	Chaperiopsis	Cosciniopsis	Exechonella	Fenestrulina
CELLARIIDAE								
BUGULIDAE								
Bugula								
Celleporaria								
Chaperiopsis								
Cosciniopsis				1 0				
Fenestrulina								
Margaretta								
Metacleidochasma		1 0						
Mucropetraliella				2 0				0 1
Poricella								
Rhynchozoon				0 1		1 2		0 1
Robertsonidra								
Scrupocellaria								
Smittipora								
Tetraplaria								
Torquatella								
<i>Nolella</i>				0 1				0 1
Nevianipora								
Tubulipora								
Corraline Algae		1 0	1 0	17 2		29 30		5 6
Colonial Ascidian				1 2		0 2		
Sponge		1 0		3 4		1 2		1 0
Halimeda				1 0	1 0			1 0
Coral								

	Margaretta	Metacleidochasma	Mucropetraliella	Poricella	Rhynchozoon	Robertsonidra	Scrupocellaria
CELLARIIDAE							
BUGULIDAE							
Bugula							
Celleporaria							
Chaperiopsis							
Cosciniopsis							
Fenestrulina							
Margaretta							
Metacleidochasma							
Mucropetraliella							
Poricella							
Rhynchozoon							
Robertsonidra			0 1				
Scrupocellaria			0 1		0 1		
Smittipora							
Tetraplaria							
Torquatella						1 0	
<i>Nolella</i>							
<i>Nevianipora</i>							
<i>Tubulipora</i>		1 0					
Corraline Algae	4 0	9 9	17 19		16 16	5 5	19 19
Colonial Ascidian						0 1	
Sponge			1 3	4		2 0	5 7
Halimeda	3 0				1 1		2 2
Coral							0

	Smittipora		Tetraplaria		Torquatella		Nolella		Nevianipora		Tubulipora	
CELLARIIDAE												
BUGULIDAE												
Bugula												
Celleporaria												
Chaperiopsis												
Cosciniopsis												
Fenestrulina												
Margaretta												
Metacleidochasma												
Mucropetraliella												
Poricella												
Rhynchozoon												
Robertsonidra												
Scrupocellaria												
Smittipora												
Tetraplaria												
Torquatella												
<i>Nolella</i>												
Nevianipora												
Tubulipora												
Corraline Algae	1	1	7	1	4	6						
	0 1	0 1	0 7	0 1	0 4	0 6						
Colonial Ascidian											0	
											2	2
Sponge			0			1						1
			3 3			3 4						
Halimeda									1			1
								0 1		0 1		
Coral		1							1			
	0 1							0 1				