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Coral Mucus: The Properties of Its Constituent Mucins

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The gel-forming properties of mucus are closely related to its functioning; although there is limited information available relating to coral mucus gels. The present study investigates coral mucus glycoprotein using rheological methods. We demonstrate the presence of a high-molecular-weight polymeric glycoprotein similar to that found in vertebrates, capable of forming a gel. The milked mucus exuded mostly from the oral cavity of corals is not a gel; however, it does show a tendency to form a gel upon concentration. Such results indicate the potential for corals to produce two different kinds of mucus, each potentially capable of performing different functions.

Introduction

Corals are facing an unprecedented challenge of maintaining themselves from the global climate change (http://www.ipcc.ch/). In recent times, frequent outbreaks of epizootics[1−4] and bleaching[5−7] events have been reported on the reef ecosystem, which pressed for the need to study immune-related stress response of corals. Mucus is a detectable, immediate response known in corals to the changed environmental conditions,[8] and this article attempts to explain the functions of the coral mucus based on their rheological properties. Therefore, the present study offers new insight into the protective mucus layer of corals.

The surface mucus layer (SML) in corals is frequently exposed to a variety of environmental insults such as physical damage,[9] microbial invasion,[10,11] aerial exposure, sediment overload,[12,13] and pollutants.[14] During these adverse conditions, the role of coral mucus as a protecting and lubricating layer, preventing the underlying epithelium from desiccation and infection, has been speculated but not thoroughly investigated. Human mucus studies have revealed that the protecting and lubricating properties of mucus are largely governed by the composition and properties of mucus glycoproteins.[15,16] This polymeric high-molecular-weight mucin is responsible for the gel-forming properties of the mucus.[17] Rheological measurements are often used to describe the gel-forming properties of the mucus, which includes determining viscosity, gel strength, and calculating the degree of polymerization present in mucus.[15,18] Changes in the rheological properties of mucus can greatly affect the protective and lubricating function. For example, if the mucus becomes too thick, dehydrated (e.g., cystic fibrosis and chronic obstructive pulmonary disease), difficulty in mucus clearance is observed in humans, likewise, if it becomes too thin with low levels of polymeric mucin.[19] Therefore, the "correct consistency or gel-forming property" of mucus is necessary for maintaining good health.[16,18−20]

Recent studies on the coral surface microbial communities have renewed interest in the SML, and its inherent protective (antibacterial) properties.[21,22] The healthy coral surface mucus harbors a distinct microbial community compared with the surrounding water column.[10] This healthy microbial community has been reported to change during disease conditions.[10,23] An increase in the number of bleaching-associated *Vibrio* species prior to bleaching[22] and a loss of antibiotic properties of mucus during the summer bleaching event has been demonstrated.[21] However, these studies focus on determining the changes in the antimicrobial properties of mucus and shaping of microbial community structure in response to different environmental stressors rather than understanding mucus/mucin interactions and the mucus composition that could lead to this change.

In the latter part of last century, major work was carried out in an attempt to understand the biochemical composition of coral mucus. Although biochemical analysis of various species of coral mucus revealed that newly secreted mucus consists of varying proportions of protein, lipid and polysaccharide along with coral tissues, zooxanthellae, bacteria, nematocysts, planktons, filamentous algae and sediments,[8] no common dominant component could be established in the coral mucus. These inconsistencies in biochemical composition of coral mucus are not surprising given the adoption of widely different sample collection, methods, and analytical techniques.[8] Thus neither a consistent composition of mucus has been described nor have the roles of its components been identified in the functions of the mucus.

The function of mucus is demonstrated to be closely related to its biophysical properties in vertebrates.[24] The present manuscript characterizes the functional component (mucin), which is responsible for versatile behavior of the coral mucus gel using the solution viscosity measurements, gel rheology measurements, and sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS PAGE).

Experimental Section

Sample Collection and Solubilization. The corals *Goniopora djiboutiensis*, *Acropora millepora*, *Fungia fungites*, and *Montastrea faveolata* were collected from Phuket Island, Thailand in February 2007. The corals were collected by detaching the bases of the skeleton from the substrate with a hammer and chisel without touching the live tissue as far as possible. The collected colonies were aerially exposed and kept inverted on a funnel and a beaker immediately to promote mucus secretion for 20−30 min. The exuded mucus was immediately frozen

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at −20 °C and then stored at −80 °C until further use. This method of mucus collection is referred to as "milking of corals".[8,25] A colony of *Goniopora stokesi* was ordered from Tropical Marine Centre, Manchester, U.K., and a sample from this colony was obtained by snap-freezing the coral directly in liquid nitrogen in the laboratory and preserving it at −80 °C until further use. The volume of coral mucus samples was measured, and then they were briefly homogenized on ice. The sample was mixed with the inhibitor buffer (10 mmol·L^{-1} EDTA (ethylenediaminetetraacetic acid), 100 mmol·L^{-1} α-aminocaproic acid, 10 mmol·L^{-1} *N*-ethyl melimide, 1 mmol·L^{-1} iodoacetamide, 5 mmol·L^{-1} benzamide HCl, and 1 mmol·L^{-1} PMSF (phenylmethylsulfonyl flouide) in PBS (phosphate buffer saline) (pH 7.3) to inhibit any proteolytic activity. Coral mucus samples and the proteolytic inhibitors solutions were mixed in a 1:9 ratio. PMSF and benzamide HCl were added to the rest of the buffer just before adding the sample to the buffer. A further 25 mL of PBS (pH 7.3) was added to this mixture, and the solution was stirred at 4 °C for 24 h. The samples were then centrifuged at 13 000 g for 1 h at 4 °C, and supernatants were extensively dialyzed against distilled water. Different methods of solubilization were tried for *G. stokesi* (PBS and 4 M Guanidinium chloride), whereas for all other species mucus, PBS was used to extract the mucin from the collected samples.

Isolation of Coral Mucin. *Cesium Chloride (CsCl) Equilibrium Density Gradient Ultracentrifugation.* To obtain purified mucin, CsCl equilibrium density gradient centrifugation was performed. The dialyzed samples were weighed, and CsCl was added equivalent to approximately 60% of the total volume of sample. Samples were adjusted to a starting density for the mucin isolation of 1.42 mg·mL^{-1}.[26] The samples were then centrifuged for 48 h at 100 000*g* at 4 °C in a Centricon T-1170 centrifuge. After centrifugation, we recovered eight fractions from the gradient by piercing the bottom of the tubes and collecting equal fractions. The density of the fractions was measured, and then they were dialyzed extensively against distilled water. The dialyzed samples were then subjected to Periodic Acid Schiff's assay (PAS) to determine glycoprotein distribution and concentration.[15,27] We also determined the presence of protein in the samples by calculating the 260/280 nm ratio. The glycoprotein-rich fractions were pooled and lyophilized.

Reduction of Native Goniopora stokesi Mucin. We reconstituted a mucin solution by dissolving 5 mg of lyophilized material in 10 mL of distilled water. The solution was dialyzed against 0.2 mol·L^{-1} NaCl and 0.03 mol·L^{-1} sodium azide with 0.2 mol·L^{-1} β-mercaptoethanol at 4 °C and incubated for 24 h. The reduced material was then dialyzed for 24 h against 0.2 mol·L^{-1} sodium chloride containing 0.03 mol·L^{-1} sodium azide and 0.22 mol·L^{-1} iodoacetamide. This reduced and blocked glycoprotein preparation was finally dialyzed against distilled water at 4 °C for 24 h and then freeze-dried.

Sodium Dodecyl Sulfate Polyacrylamide Gel Electrophoresis. SDS PAGE was conducted using the Pharmacia gel system (Pharmacia Ltd.). The isolated freeze-dried coral mucin samples and standards were solubilized in 0.0625 mol·L^{-1} Tris buffer, pH 6.8, containing 2% (w/v) SDS, 10% (v/v) glycerol, and 0.001% bromophenol blue. Samples were heated to 100 °C for 2 min in a water bath before being applied to the gels (PhastgelTM gradient 4−15%). Gels were run at a constant current of 10 mA for 260Vh.

Periodic Acid Schiff's Staining (PAS) for 4 −15% SDS PAGE Gel. The gels were fixed overnight in 7% acetic acid, followed by a 1 h oxidation step using periodic acid (0.2% (v/v) periodic acid in 7% (v/v) acetic acid). Sodium metabisulphite (0.4 g) was added to 24 mL of Schiff's reagent (Sigma) and was incubated at 37 °C for 1 h in a water bath. This activated Schiff's solution was then added to the oxidized gel and again incubated for 30 min at 37 °C. The gels were then scanned using a Biorad GS-800 densitometer. We calculated the amount of polymeric material present in a sample by determining the amount of material that remained at the point of application compared with the amount that had moved from the point of application to the interface between the stacking and running gel and just into the running gel. This SDS PAGE method for determining the polymeric structure has previously been validated.[28,29]

Solution Viscosity Measurements. Solution viscosity measurements were carried out using a Contraves low shear 30 viscometer (Contraves A.G.). The equipment consists of a Couette rotating cup and a bob. For solution viscosity measurements, 20 mg of the *Goniopora* species mucin was dissolved in 2 mL of the PBS solution. Viscosity was determined from the gradient of deflection versus the shear rate plot, that is, relative viscosity (η_{rel}), and was expressed as specific viscosity (η_{sp}).

Using specific viscosity, reduced viscosity (η_{red}) was obtained as follows

$$\eta_{red} = \eta_{sp}/C \quad (C = \text{concentration in mg·mL}^{-1})$$

To obtain intrinsic viscosity, serial dilutions were made of the stock mucin solutions, and ln η_{rel}/C was plotted against glycoprotein concentration and extrapolated to infinite dilution (Kramer plot). Alternatively, a value for intrinsic viscosity can also be obtained by plotting η_{red} versus C extrapolated to infinite dilution (Huggins plot). Both Kramer and Huggins plots can be used together or independently to obtain the intrinsic viscosity. The molecular weight of the mucin was calculated using the intrinsic viscosity [η] from the Mark−Houwink equation which is

$$[\eta] = KM^{\alpha}$$

where K and α are Mark−Houwink constants that depend on the type of mucin polymer, solvent, and the temperature of the viscosity determinations and the exponent α is a function of polymer geometry and varies from 0.5 to 2.0. Because no values were available for coral mucin, constants determined experimentally by measuring the intrinsic viscosities of several pig gastric mucin samples for which the molecular weight has been determined by light scattering and sedimentation methods were used. For pig gastric mucin, K and α were 3.4865×10^{-5} and 0.56, respectively.

Gel Rheology Measurements. These measurements were carried on Bohlin CV050 rheometer using serrated plates set to a gap of 0.150 mm. The samples were subjected to control electronically sinusoidal deformations at a frequency of 1 Hz at 25 °C to determine viscoelastic region, that is, "the shear independent plateau", where the moduli G' (elastic moduli) and G'' (viscous moduli) remain constant over a range of shear stress. Once the viscoelastic region was determined, a frequency sweep was performed at 25 °C between 0.1 and 10 Hz with the rheometer operating in auto stress mode. The initial stress was set in the middle of the viscoelastic region with the target strain also set in this region.

Centrifugal Concentration of M. faveolata Mucus Sample. The *M. faveolata* milked mucus sample (120 mL) was thoroughly mixed, and then 2 mL of sample was used to obtain the initial solution viscosity measurement on the viscometer. Samples were concentrated at 2000 g at 10 °C using a Centricon filter device with a cut off limit of 50 000 Da in a stepwise manner until 120 mL of mucus sample was concentrated to 2.7 mL. After every step, solution viscosity measurements were recorded. A gel rheology measurement was carried out on this concentrated sample, followed by the isolation of mucin using the equilibrium CsCl purification method, as described earlier.

Results

Molecular Weight Determination. It has been previously reported in vertebrates that CsCl equilibrium density gradient centrifugation concentrates the mucin in the density range of 1.4 to 1.5 mg·mL^{-1}.[30] *Goniopora* species CsCl fractions at density 1.4 to 1.5 mg·mL^{-1} showed an increasing amount of PAS positive material, which reached a maximum in the fifth fraction and then declined (Figure 1). Therefore, in corals,

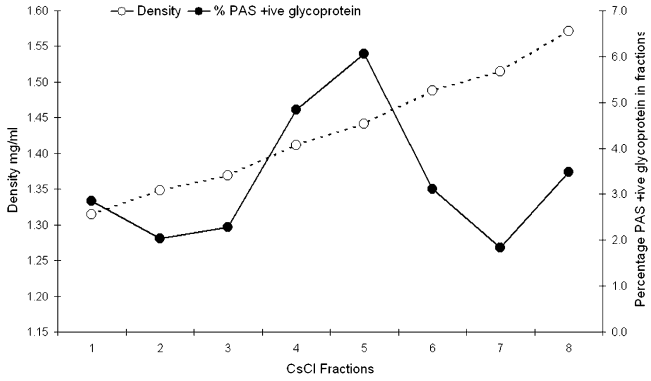

Figure 1. CsCl equilibrium ultracentrifugation fractions. The eight fraction of centrifugation showing the PAS positive glycoprotein concentration along with the density of fractions in mg·mL^{-1}. A density of 1.4 to 1.5 mg·mL^{-1} is recommended for mucin isolation.

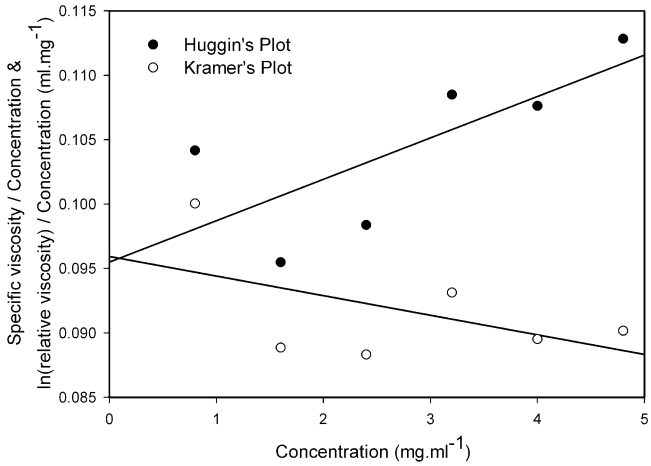

Figure 2. Intrinsic viscosity determination. Huggins and Kramer plot for the *Goniopora stokesi* PBS solubilized mucin. The values obtained from Kramer plot were used as intrinsic viscosity.

fractions 4 to 6 of CsCl centrifugation showed the correct density for mucin and were rich in glycoprotein. To collect all potential mucin fractions, 3 and 7 were included even though they were slightly outside the 1.4 to 1.5 density range. This confirmed that the distribution of PAS positive glycoprotein in corals mucus is similar to those of the vertebrates.

Molecular weight was determined for purified *Goniopora* species mucin. Huggins and Kramer plots were produced and extrapolated to infinite dilution to obtain the intrinsic viscosity and hence molecular weight. Ideally, Kramer and Huggins plot should be a straight line, but the plot deviated at a lower concentration (<2 mg·mL^{-1}) in the case of coral mucins, and this deviation was present in plots generated from the other coral mucin samples (Figure 2). The *Goniopora* species mucus extracts obtained by PBS solubilization showed the presence of high molecular weight ((1.39 to 2.45) $\times$ 10^6 dalton) glycoprotein (Table 1). This glycoprotein molecule consisted of subunits (360 000 Da) presumably joined by the disulfide bridges, as seen by the change in molecular weight on reduction. The use of PBS first on *Goniopora* mucus may have solubilized all of the available very high-molecular-weight glycoproteins; then, extracting the remaining material in guanidinium chloride may have resulted in solubilization of previously undissolved mucus glycoprotein such as incompletely biosynthesised mucin, as indicated by the lower molecular weight. Therefore, the molecular weights indicate a polymeric structure of *Goniopora* mucus glycoprotein consisting of an average of four monomers of size ~360 $\times$ 10^3 dalton.

Table 1. Molecular Weight of *Goniopora* Species Mucin. Table Showing the Various Parameters and Calculated Molecular Weight of the *Goniopora* Species Mucin

mucin sample	Huggins plot value (mL·mg^{-1})	Kramer plot value (mL·mg^{-1})	molecular weight (dalton)
Goniopora djiboutiensis	0.148	0.132	2.45 $\times$ 10^6
Goniopora stokesi (PBS extract)	0.095	0.096	1.39 $\times$ 10^6
Goniopora stokesi (GuCl extract*)	0.070	0.074	8.73 $\times$ 10^5
reduced *Goniopora stokesi**	0.046	0.045	360 000

* means limited amount of mucin available (mucin concentration range for intrinsic viscosity determination 3 to 0.5 mg·mL^{-1}).

An *M. faveolata* milked mucus sample of unknown mucin concentration was subjected to solution viscosity measurements in a stepwise manner while concentrating the 120 mL of sample to 2.7 mL. The concentrations of the solution were back-calculated from the amount of lyophilized material obtained from the CsCl equilibrium density gradient purification of the 2.7 mL sample. Molecular weight was determined from the solution viscosity measurements based on two different assumptions: (1) Mucin was present only in fractions numbered 3−7 of the CsCl gradient, as shown in the vertebrate mucins.[26,30] (2) Mucin was present only in fractions numbered 3−7 of the CsCl gradient, but the values were corrected for the glycoprotein content determined by PAS assay (Table 2). Nearly 80% of the weight of pig gastric mucin is PAS positive. The adjacent hydroxyl groups present on the sugar backbone in pig mucin are oxidized and therefore stain with PAS. On the basis of this criterion, it is possible to estimate the amount of mucin present in the pig mucin. In the case of *M. faveolata*, only 7.5% of total lyophilized material has been found to be PAS positive (Table 2). Using the concentration derived from the total freeze-dried weight in fractions 3−7 the glycoprotein in the milked extract from *M. faveolata* had a molecular weight of 30 $\times$ 10^6; however, if the solute concentration is determined from the PAS positivity, then the molecular weight is much larger, 12.7 $\times$ 10^8 (Table 2).

Sodium Dodecyl Sulfate Polyacrylamide Gel Electrophoresis. The amount of material present in *A. millepora* that had moved from the point of application to the interface between the stacking and running gel and into the running gel was 36% of the total, whereas 64% remained at the point of application of the SDS PAGE gel (Figure 3). Polymeric high-molecular-weight mucin has previously been shown to remain at and around the point of application, whereas the material at the interface and in the running gel had represented the degraded or the smaller subunits of the mucin. The standard used was native pig gastric mucin, which also showed the same kind of the trend (62% polymeric and 38% degraded), confirming that the degree of polymerization in the pig mucin and *A. millepora* mucin were similar.

Gel Rheology Measurement. The gel rheology measurements carried out directly on the milked mucus samples showed an absence of gel properties (results not shown), but when the gel rheology measurements were performed on the concentrated *M. faveolata* mucus samples, data revealed that concentrated mucus samples were starting to behave like a gel. The amplitude sweep shows an initial fall and variation in the values of the moduli at low shear rates. This eventually plateaus into a linear viscoelastic region. In this region, the ratio of induced strain to applied stress remained constant. The initial variation in the moduli is characteristic of mucus gels and relates to the loading

Table 2. Molecular Weight of *M. faveolata* Mucin. Table Showing Molecular Weight of *M. faveolata* Milked and Concentrated Sample along with Various Criteria Adopted to Obtain It

Montastrea faveolata mucin	criteria	lyophilized material mg	concentration of milked (120 mL) sample ($mg \cdot mL^{-1}$)	concentration of final (2.7 mL) sample ($mg \cdot mL^{-1}$)	Kramer plot value	molecular weight
3−7 fractions	lyophilized mucin fraction 3−7	13.41	0.113	4.96	0.54	30.3×10^6
3−7 PAS positive fractions	mucin fractions (3−7) calculated using PAS positivity	1.80	0.015	0.66	4.37	12.7×10^8

[a] Note that the Kramer plot value has been used to calculate the molecular weights.

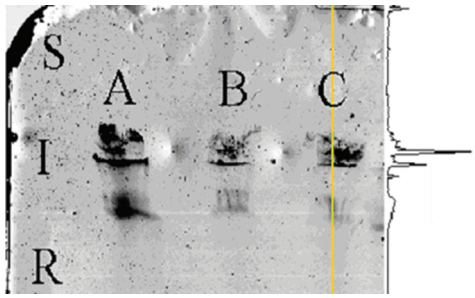

Figure 3. Scan of SDS PAGE of *A. millepora* mucin compared with the native pig gastric mucin. (A) pig mucin and (B,C) *A. millepora* mucin. I; interface between stacking and running gel; S: stacking gel; R; running gel.

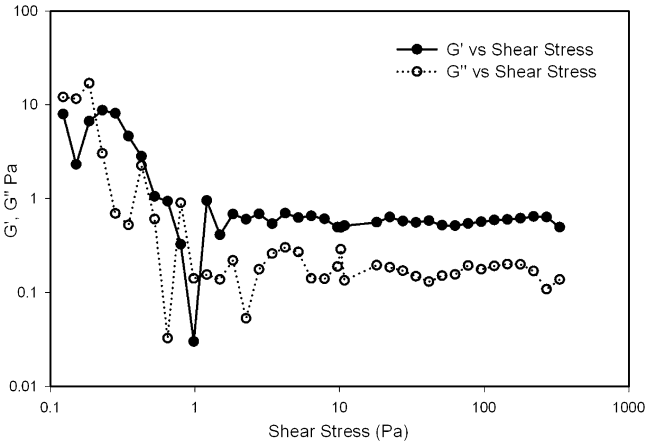

Figure 4. Amplitude sweep of coral mucus. Concentrated sample of *M. faveolata* subjected to an amplitude sweep with shear stress ranging from 0.1−330 Pa. G' and G'' appear to be nearly constant between 22 and 270 Pa showing shear independent region.

procedure, where a lump of gel is squeezed to the required thickness between the rheometer plates (Figure 4). The amplitude sweep was carried out at shear stress of 0.1−330 Pa. At shear stress (1.2−330 Pa), the value of elastic moduli (G') is greater than viscous moduli (G'') (Figure 4). G' and G'' appear to be nearly constant between 22 and 270 Pa. This was taken as the shear-independent region. A shear stress of 63 Pa was selected ($G' = 0.5$ Pa and G'' 0.2 Pa), and the sample was subjected to a frequency sweep at 0.1−10 Hz at 25 °C (Figure 5). The target strain 3.65 was achieved at $G' = 0.6$ Pa and $G'' =$ 0.1 Pa. Figure 5 shows that the moduli are frequency-dependent, increasing with increasing frequency. These results suggest that there is evidence of shear independent region; however, the moduli are extremely low. Pig gastric mucin forms a strong gel at a concentration above 20 $mg \cdot mL^{-1}$ with G' and G'' values around 100 Pa. In *M. faveolata*, a very weak gel would be expected based on the values of G' and G'' moduli.

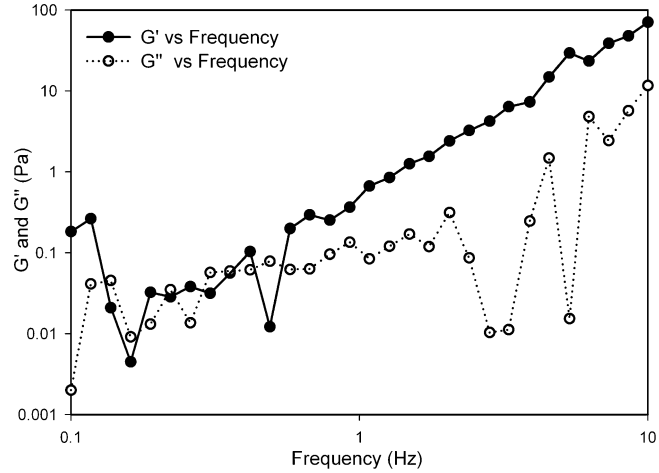

Figure 5. Frequency sweep of *M. faveolata* mucin. It shows a very weak gel that is frequency dependent with the moduli increasing as the frequency increases. G' is almost 100 Pa at 10 Hz, and G'' is around 10 Pa at 10 Hz.

Discussion

There are four characteristic features needed for a glycoprotein to be identified as a mucin. These criteria are (1) the isolation of glycoprotein in a density range of 1.4 to 1.5 $mg \cdot mL^{-1}$ in the CsCl ultragentrifugation, (2) PAS positivity, (3) a high molecular weight, usually in million dalton, and (4) a polymeric structure. The isolated coral mucus glycoprotein displayed all of these characteristics; however, it did show a difference in PAS staining. The *M. faveolata* results suggest that the PAS positivity of coral mucin is different from that of pig mucin, and this fact needs to be considered in the study of gel-forming properties of coral mucin. The possibility of coral mucus possessing some sugar chains that are totally different from the mammalian mucin is expected because a large quantity of arabinose (a plant associated sugar) has been reported in corals.[31−33] Although the sugar groups present in coral mucus are known to a large extent from their biochemical composition,[25,32] further investigation is needed to determine the exact chemical linkages between the sugar molecules and which sugars are mucin-specific.

Goniopora species demonstrated a molecular weight of (1.5 to 2) $\times 10^6$ daltons, which is in the range of molecular weights reported for vertebrate mucin molecules,[15,34,35] whereas *M. faveolata* mucin displayed a molecular weight of 30×10^6, but this mucin was isolated from material milked from the mouth and gut of the coral as opposed to that extracted from the whole coral and as such may represent a different mucin population.

The most important parameter for gel formation lies in having an appropriate amount of dissolved mucin with an intact polymeric structure.[15,16,36] The pig gastric mucin, which was used as a standard, forms a gel only after it reaches a concentration >20 $mg \cdot mL^{-1}$.[15] The amount of lyophilized coral

mucin recovered and initial values of viscous and elastic moduli suggested a very low concentration (0.2 mg mL^{-1}) of coral mucin in the milked samples. This low concentration of mucin is not sufficient to form a gel on the coral surface but with an increase in the concentration of mucin (8.82 mg·mL^{-1}), an increase in solution viscosity and gel rheology was observed. Pig mucus gel rheology studies suggest intermolecular interactions and specific arrangements of molecules within the gel system ($G' > G''$) during gel formation.[37] It is observed that during excess shear stress or strain, the value of viscous moduli (G'') becomes greater than elastic moduli (G'), resulting in the gel becoming a viscous fluid that recovers its optimum gel properties after the removal of mechanical disruption.[24] The elastic modulus for *M. faveolata* mucus was very low compared with pig mucus ($G' = 0.6$ Pa and $G'' = 0.1$ Pa), but the fact that G' was higher than G'' suggested a gel. The behavior of G' during a frequency sweep (i.e., it is frequency-dependent) (Figure 5) implied some contribution from entanglements to the bulk gel properties. The behavior of coral mucus during the amplitude sweep showed a feature uncharacteristic of a weak mucus gel which breakdown and flow at shear stress values of ~10 Pa, the coral mucus gel appears to remain a gel up to 400 Pa. Care must be taken in interpreting this because the moduli are so low, and further studies are needed with a gel with larger moduli values. These data do, however, suggest that *M. faveolata* mucin is capable of forming gel provided that an appropriate quantity of mucin is present in the mucus.

In the present study, all coral species revealed a lower yield of mucin from the milked mucus samples. The milked mucus sampling technique was used to reduce the possibility of contaminants, which may act as gel inhibitors[39] and to obtain the clear sticky mucus from the surface of the coral. The functional role of the mucus may explain the lower concentration of mucin in the coral mucus samples. It is now apparent that the majority of milked mucus is probably released from the mouth of the coral polyp (John Bythell per communication) with this exudate consisting of mainly the coelenteron (gut) seawater, tissue debris, and mucin. This viscous fluidlike mucus released from the coral mouth seems to explain a functional role of ciliary feeding in which corals produce mucus that covers the mouth and surrounding area. The food gets entangled in this mucus, and corals have been reported to ingest the food-entangled mucus strings.[8,40−42] Therefore, for feeding purposes, the mucus required by a coral should be more fluid for easy flow and does not necessarily need gel-like behavior. Also, the mucus released onto the epithelium during low tide must be fluid enough to spread over the surface of polyp to prevent desiccation during long hours of aerial exposure.

When a mucin molecule is released onto the epithelium in humans, it undergoes hydration and mucin gene products anneal to form a mucus gel.[43] Therefore, mucus obtained by the milking technique in corals could be a combination of the exuded SML and mucus released from the oral cavity. There is the possibility of different kinds of mucin or mucin molecules encoded by different mucin genes in the collected samples similar to those of humans. (For example, the MUC5AC and MUC6 are found in human stomach.) Therefore, the potential for more than one gel-forming mucin gene in corals cannot be overlooked.

Conclusions

Coral mucus contains high-molecular-weight polymeric mucins similar to those found in vertebrates. The rheological measurements indicate that the corals have the potential to produce at least two different kinds of mucus by varying the concentration of the mucins. The milked mucus that has been studied does not possess gel properties but can become a gel at higher mucin concentrations. Therefore, there is a possibility that such a gel-forming mucus could be present on the general body surface in corals.

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