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Biology and ecology of coral mucus release

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ABSTRACT

There has been an exponential increase in coral mucus research over the last 5 years, attracting attention from coral biologists and reef ecologists. The most active area has been the study of microbial structure and function associated with mucus, and very recent findings have increased our understanding of the roles of microbes in coral health and disease, and also on the ecosystem level. Here we overview some of the latest findings, but also identify scientific gaps. A priority area for future research is understanding the structure and dynamics of the surface mucus layer in relation to microbial community development. Environmental factors including climate change impacts affect the release of mucus/organic matter by the coral engineer and may therefore also have profound effects on entire reef ecosystem function, so it is vital that we also gain a better understanding of these responses.

1. Introduction

Since 2005 when the biology of coral mucus secretion was reviewed by Brown and Bythell (2005), there have been over 100 ISI-Web of Knowledge-listed papers published that refer to coral mucus. However, relatively few of these (<7%) address the structure and function of mucus itself. By far the majority of publications in this area (58%) address the emerging field of coral-associated microbiology, a field that has increased exponentially in activity since 2000 (Fig. 1). This area has emerged as a priority largely because of the urgent need to understand coral–microbial interactions in health and disease (Lesser et al., 2007; Littman et al., 2010; Mao-Jones et al., 2010; Rosenberg et al., 2007; Rosenberg and Ben-Haim, 2002), particularly in an era of climate change impacts. Activity has also increased due to the widespread availability of culture-independent DNA technologies that have allowed large-scale, replicated assessments of microbial communities associated with reef corals (for example, Bourne and Munn, 2005; Guppy and Bythell, 2006; Hansson, et al., 2009; Koren and Rosenberg, 2006; Kvennefors, et al., 2010; Lampert, et al., 2008; Reis, et al., 2009; Rohwer, et al., 2001; Sunagawa, et al., 2009).

Here we review what we have learnt of the microbial ecology of coral-associated microbes, but also argue that our understanding of the biology of mucus secretion has lagged behind and that this is a critical gap in our understanding of coral–microbial interactions. Alongside coral–microbial interactions, there have been a number of papers (about 36% since 2005) that address other aspects of coral biology that are influenced by mucus secretion, including the reef ecosystem effects of mucus release and subsequent mucus-induced and facilitated organic matter recycling. We therefore also review the important functions and reef ecosystem processes that are influenced by coral mucus post-release. Mucus release is a dominant part of the natural biogeochemical processes on coral reefs. Although the direct impacts of climate change on these processes have been little studied to date, we conclude that coral bleaching will likely reduce the rate of mucus release into the environment and thereby have profound effects on reef ecosystem function.

2. Coral mucus structure and function in coral biology

The coral surface mucus layer (SML) is central to many aspects of coral biology, including feeding, protection from pathogens, sediment cleansing, and myriad other hypothesised and observed roles (reviewed by Brown and Bythell, 2005). The SML offers protection to the underlying epithelium whilst allowing gas and metabolite exchange. It is interesting to note that a functionally similar mucosal surface is present in every phylum of multicellular animals that evolved after the sponges, and yet most zoology texts still refer to the evolution of a blind gut and well-integrated, diploblastic tissues as the major evolutionary advances of the Cnidaria. It is doubtful that either of these advances would have been possible without the development of the surface mucosa.

Despite the central role of the SML in coral biology, there is still confusion and 'sloppy practice' in terminology and methodology that hinders understanding of the ecology of mucus in corals and reef systems. Mucus, *sensu stricto*, refers to a complex mixture of polymeric glycoproteins called mucins and other exudates such as lipids

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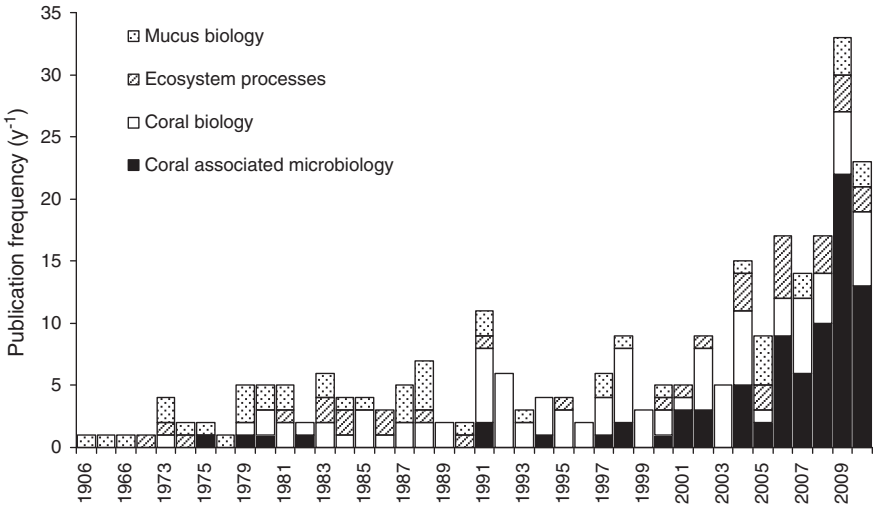

Fig. 1. ISI-listed publications citing coral and mucus as keywords, divided amongst four areas of research. 'Mucus biology' = papers addressing the structure, function or composition of cnidarian mucus; 'Ecosystem processes' = papers concerned with post-release effects in the reef environment; 'Coral biology' = papers that address biological processes of the coral such as feeding and sediment rejection that rely on mucus secretion (except microbial interactions); 'Coral associated microbiology' = studies that address the *in situ* microbiology and microbial ecology of the coral colony (excluding post-release processes). Note that the 2010 listing is not complete.

that are secreted by mucocytes of the epithelium (Brown and Bythell, 2005). The mucins, large glycoproteins that are responsible for the gel-forming properties of the mucus, may not be the major fraction of the carbon released by the coral. In fact, Crossland (1987) showed that 'mucus-polysaccharides' accounted for only about 20–30% of the total carbon secreted, with the rest composed of DOC-lipids, mainly wax esters. However, it has never been established whether this DOC-lipid is released from the mucocytes along with the mucus glycoproteins (and therefore should be accounted as a part of mucus release) or is a separate process, or processes, of secretion by the coral. It has become a common practice to refer to the total carbon released by the coral as 'mucus', but the biological basis for this is largely unknown. To understand the ecology of mucus secretion, however, we need to first understand the composition of mucus.

2.1. What is 'mucus'?

Mucus is a complex mixture of secreted materials, and the composition of coral mucus has been recorded to vary temporally (Crossland, 1987; Crossland, et al., 1980; Ferrier-Pages et al., 1998), between coral species (Meikle, et al., 1988), with water depth and irradiance levels (Crossland, 1987) and with ageing and trapping of exogenous materials upon release into the seawater environment (several references, reviewed by Brown and Bythell, 2005). However, the biophysical characteristics of mucus that are important to its function, namely the ability to form gels of varying viscosity and elasticity that lubricate and protect the underlying epithelia, are dependent on glycoproteins known as mucins.

Mucins are extremely large glycoproteins (0.5–20 MDa) formed from a central protein core with heavily glycosylated side-chains (Bansil and Turner, 2006) (Fig. 2). The levels of glycosylation vary, even within the same type of mucin molecule, as the post-translational modification of glycosylation is not an exact process, but the carbohydrate composition of mucins is typically around 80% (Bansil and Turner, 2006). Very little is known about the biochemical structure of coral mucins, however the basic domain structure of the secreted, gel-forming mucins is conserved throughout metazoan evolution (Desseyn, 2009; Lang et al., 2007). Mucins consist of a protein core (~200–500 kDa) with a central 'mucin domain' rich in proline, threonine and serine (PTS) arranged in a variable number of tandem repeats (hence it is often referred to as the PTS-repeat or

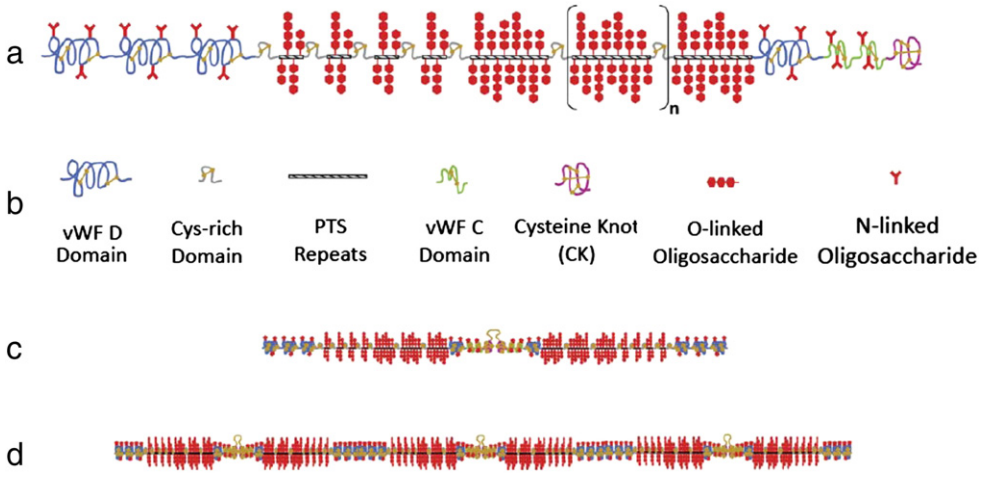

Fig. 2. Schematic structure of a generalised mucin, taken from a pig gastric mucin example. (a) Monomer consisting of glycosylated PTS repeat region flanked by vWF (von Willebrand Factor) D-domains and, at the C-terminus, a vWF C-domain and a Cystine Knot (CK); (b) symbols representing the different domains in (a); (c) a dimer formed by two monomeric subunits linked via disulfide bonds in the non-glycosylated regions, and (d) dimers that are further disulfide linked to form higher multimers. Redrawn from Bansil and Turner (2006) with permission of the authors.