

FUNCTIONAL IMPORTANCE OF BIODIVERSITY FOR CORAL REEFS OF BELIZE¹

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ABSTRACT

A thriving coral reef results from an intricate collaboration among many different kinds of animals, plants, and micro-organisms. Some of the key collaborators include nearby seagrasses and mangroves that capture and control sediments and transform dissolved nutrients into plant biomass, and herbivorous fishes and sea urchins that prevent quickly growing algae from overwhelming reefs. But most central to the building and maintenance of the reefs are corals and sponges, and the microbial collaborators that live within their bodies. Reef-building corals deposit solid carbonate skeletons as they grow, building a sturdy 3-dimensional framework within which fishes, crustaceans, and other animals shelter and find food, while sponges glue living corals onto the reef frame and protect them from excavators, facilitate regeneration of damaged reefs, and keep the water clear by efficiently filtering bacteria and phytoplankton. All of these functional roles must be played for a reef to remain healthy and capable of recovering from damage.

Coral reefs, as shallow-water tropical ecosystems, have always been challenged by physical damage due to hurricane-charged water movement, and more recently, pulses of freshwater and sediment due to heavy coastal rains, and temporarily extreme temperatures. Recovery from effects of these challenges is a normal part of the dynamics of healthy coral reefs. High species diversity of corals and sponges is essential to successful recovery because species differ in their ability to: a) resist challenges (physical disturbance, disease, high or low temperatures, sediment, etc.), b) recover from challenges (by regeneration, regaining symbionts after bleaching, halting the advance of disease, etc.), c) recover in the sense of recolonization by the next generation, and d) host symbionts and engage in other interactions that increase survival of participants. As well, individuals within a species vary in their ability to resist or recover from challenges and to interact positively with other organisms. When high biodiversity is protected, there are always at least some species capable of performing each of the roles essential to the functioning of the reef - even when other species are temporarily diminished by their vulnerability to a particular environmental challenge. However, when multiple challenges occur together, or when the challenges are novel (i.e., exposure to substances that humans have manufactured or released from inside the earth), too many species may be diminished or deleted simultaneously, impairing the natural growth and recovery processes.

INTRODUCTION

Coral reefs, as shallow-water tropical ecosystems, have always been challenged by physical damage due to hurricane-charged water movement, and more recently by pulses of fresh-water and sediment due to heavy rains on deforested coasts, and temporarily extreme temperatures. Recovery from effects of environmental challenges is a normal part of the dynamics of healthy coral reefs. High species diversity of corals and sponges is essential to successful recovery because species differ in their ability to: a) resist challenges (physical disturbance, disease, high or low temperatures, sediment, etc.); b) recover from challenges (by regeneration, regaining symbionts after bleaching, halting the advance of disease, etc.); c) recover in the sense of recolonization by the next generation; and d) host symbionts and engage in other interactions that increase survival of participants. As well, individuals within a species vary in their ability to resist or recover from challenges and to interact positively with other organisms. When high biodiversity is protected, there are always at least some species capable of performing each of the roles essential to the functioning of the reef—even when other species are temporarily diminished by their vulnerability to a particular environmental challenge. However, when multiple challenges occur together,

¹ Cite as: Wulff, J., 2011. Functional importance of biodiversity for coral reefs of Belize. *In*: Palomares, M.L.D., Pauly, D. (eds.), *Too Precious to Drill: the Marine Biodiversity of Belize*, pp. 52-56. Fisheries Centre Research Reports 19(6). Fisheries Centre, University of British Columbia [ISSN 1198-6727].

or when the challenges are novel (i.e., exposure to substances that humans have manufactured or released from inside the Earth, such as oil), too many species may be diminished or deleted simultaneously, impairing the natural growth and recovery processes.

CORALS AND SPONGES

Corals and sponges spend their adult lives attached to the substratum on which they settle as waterborne larvae, and they illustrate great variety in shape and size, facility at asexual propagation and regeneration, and tendency to host microbes within their bodies. Corals and sponges differ from each other in important ways that underlie the compatible roles they play in building, maintaining, and repairing coral reefs.

Corals

Corals deposit rock-like calcium carbonate skeletons as they grow, creating the basic building blocks of the reef structure. Among the 45 reef-building corals inhabiting the Belize Barrier Reef (Bright and Lang, 2011) are a great variety of shapes, including branching, plate-shaped, pillar, massive mounds, and encrusting forms. Whatever the overall shape of a colony, the living tissue is always a very thin layer over the surface. Thus even shallow wounds expose skeleton, making it vulnerable to colonization by quickly growing algae that can inhibit regeneration, and also by excavating organisms which can bore into the solid carbonate of the coral skeleton, weakening its attachment to the reef frame. Although coral polyps can capture plankton with their tentacles, they acquire most of their food from the single celled algae, zooxanthellae that live at high densities within their tissue. Like all plants, zooxanthellae convert sunlight energy into food energy. Their position within the corals enhances their access to nutrients due to recycling of metabolic wastes. Although this collaboration is unquestionably beneficial to the corals, as their chief food source, dependence on zooxanthellae makes corals vulnerable to the possibility that the association may break down under stressful environmental conditions. In particular, abnormally high sea surface temperatures cause zooxanthellae to be expelled by their coral hosts. Moderation of temperatures can allow recolonization of corals, but bleaching can weaken corals, making them more vulnerable to other threats such as diseases. If zooxanthellae are unable to recolonize quickly, the corals die.

Sponges

Most of the over 800 species of sponges (Diaz and Rützler, this volume) that inhabit Caribbean coral reefs and associated habitats have soft bodies with living tissue throughout. Their skeletons, which homogeneously pervade the living tissue, are made of fine meshworks of protein fibers, generally augmented by silica spicules. Sponges are also pervaded by a system of canals through which they pump water, from which they filter bacteria and other very small particles extremely efficiently. The extraordinarily simple internal structure of sponges bestows on them great flexibility in growing around obstacles, adjusting to changes in orientation, and accommodating close associations with other organisms. Because sponges are living tissue throughout, wound healing can be achieved quickly, by simply reconstituting the layer of specialized cells that cover the surface; thus sponges are masters of regeneration after damage or fragmentation (Wulff, 2011).

ROLES OF CORALS AND SPONGES IN BUILDING, MAINTAINING, AND REPAIRING CORAL REEFS

Growth of corals is required for generating the solid carbonate building blocks of reef framework. But, even as they accrete, coral skeletons are also eroded by grazing fishes and sea urchins, and by a handful of bivalve and sponge species that transform solid carbonate to fine sediment, as they excavate burrows for themselves. Excavations can erode coral basal attachments to the point that corals relinquish their grip on the reef frame, often perishing in the surrounding sediments or cascading into deeper water. Fortunately, sponges associated with corals can increase coral survival by gluing them to the reef frame. Experimental removal of sponges from fore-reef patches resulted in 40% of the corals becoming disengaged from the reef frame; while on similar patch reefs with intact sponges coral mortality was only 4% (Wulff and Buss, 1979). This collaboration of solid rock-generating corals with sponges capable of adhering corals to the reef frame is further enhanced as the sponges filter the entire water column above the reef each day, maintaining water clarity that allows corals to receive adequate sunlight for their zooxanthellae.

Physical damage to coral reefs, on scales ranging from small patches to many square kilometers, is inevitable given the coincident geographic distribution of coral reefs and tropical storms. The ability to recover is a normal part of the life histories of coral and sponge species, and repair and regeneration is a

normal part of coral reef growth. At any moment portions of a reef system have been recently damaged by a storm, so the process of regeneration of rubble mounds into solid reef frame onto which living corals can flourish once again is required for continued growth of coral reefs to keep pace with rising sea level. Large pieces of damaged or dead coral may remain stable where they fall at the end of a storm, but smaller rubble pieces can continue to be churned by foraging fishes or water motion, impeding their incorporation into a stable structure. Coral larvae that settle on loose rubble tend to be smashed, as rubble pieces are moved against each other. Because sponges can adhere quickly to solid carbonate with any part of themselves, the same gluing capability that allows them to bind living corals to the reef frame also allows them to bind piles of loose rubble into continuous structures. Once loose rubble pieces are stabilized, crustose coralline algae can grow from one piece of rubble to the next, cementing them together, rendering them more hospitable to small corals (Wulff, 1984). Sediment generated by grazing and excavating organisms fills in the holes in the frame, increasing solidity. Growth of corals continues the cycle.

Tropical storms have challenged coral reefs as long as they have existed, but additional challenges have been increasing in importance: pulses of freshwater and sediment running off of deforested land, bleaching due to increased sea surface temperatures, coral predators that are no longer kept in check by their larger predators that have been overfished, and diseases that are poorly fended off by animals that are stressed by other challenges. Each of the many species of corals and sponges that participate in reef building and re-building is characterized by a unique set of strengths and vulnerabilities, and no single species is the best at coping with all environmental challenges. Species that rebound gracefully after a storm may succumb to disease, while species that resist bleaching may be overwhelmed by uninhibited predators, and those most resistant to predators may be devastated by storms. In the following section, examples illustrating the wide range of variation in resistance to and recovery from a few of the challenges faced by sessile animals on reefs are drawn from the diverse species inhabiting the Belize Barrier Reef.

VARIATION AMONG SPECIES IN RESISTANCE TO, AND RECOVERY FROM, CHALLENGES

Physical damage by storms

Massive corals, such as *Montastraea* species, are champion survivors of hurricanes, remaining standing amidst a litter of fragments of branching species and broken off corals with small basal attachments. Branching species of both corals and sponges, although readily broken tend to be especially adept at recovering from breakage, as fragments can reattach to the substratum, and branching patterns adjust to their new orientation as fragments continue to grow. Thus moderate storms can result in propagation, but the violent water motion of major hurricanes can overdo breakage to the point of destruction (e.g., Woodley *et al.*, 1981). Corals with smaller forms and shorter life spans may be readily damaged by storms, but tend to be successful at replenishing their populations by efficient settlement of larvae (e.g., Bruckner and Hill, 2009).

Sponge species also balance resistance to damage with recovery in a variety of ways. After Hurricane Allen in Jamaica in 1980, monitoring of nearly six hundred sponges over 5 weeks for recovery revealed an inverse relationship between ability to resist damage and ability to recover from damage (Woodley *et al.*, 1981; Wulff, 2006b). Erect branching species suffered the most damage, but they were also most adept at recovering; while at the opposite extreme, many sponges of species that live confined to cryptic spaces within the reef frame eluded damage altogether in their protected microhabitat; however, those that were exposed as the framework was ripped apart did not recover at all. Massive sponges with tough skeletons were highly resistant to being damaged, but when they were damaged, recovery was elusive. These massive, tough species were able to recoup their substantial losses, however, by recolonizing the battered reefs with their next generation (Wilkinson and Cheshire, 1988).

Bleaching

Variation in susceptibility to bleaching varies with the coral species, clade of zooxanthellae hosted, and habitat details (e.g., Baker, 2003). Variation among species can be extreme, as in a 2005 bleaching event during which 85% of colonies of the relatively small massive coral *Porites astreoides* were resistant, but fewer than 5% of the colonies of the large massive corals in the *Montastraea annularis* species complex remained unbleached (Bruckner and Hill, 2009). Closely related coral species can differ in vulnerability, for example the plate-shaped *Agaricia agaricites* tends to be able to cope with higher temperatures better than closely related *Agaricia tenuifolia* (Robbart *et al.*, 2004). The net result of bleaching is a combination

of susceptibility to bleaching and ability to recover. Ultimate results of very similar rates of severe bleaching in the brain coral *Colpophyllia natans* and the short thickly branched *Porites porites* (92% and 97% of colonies, respectively) were very different, with 88% of completely bleached *Colpophyllia* recovering, but only 28% of completely bleached *Porites* recovering (Whelan *et al.*, 2007). Individuals within a species also vary in their ability to cope with environmental challenges. In the case of species that are capable of propagation by fragmentation, it is possible that relatively resistant genotypes will be able to quickly increase in abundance. Genotypes of staghorn and elkhorn coral that have demonstrated particular resistance are currently being propagated in nurseries in Laughing Bird Caye National Park, Belize, in order to bolster natural replenishment of reefs (Carne, in press).

Disease

Coral diseases are not generally specific to a single species, but there are patterns in the tendency of a particular disease to affect certain corals (Bruckner, 2009), complicated by the recent history of bleaching and other weakening circumstances. For example, the ultimate fates of the *Porites porites* and *Colpophyllia natans* colonies in the bleaching recovery study mentioned in the previous paragraph were high mortality all around, because the *Colpophyllia* colonies that recovered from bleaching succumbed to White-plague type II disease (Whelan *et al.*, 2007). Diseases have disproportionately influenced populations of some of the most important and abundant Caribbean reef coral species. The near demise of the *Acropora* species, staghorn and elkhorn corals, that contributed rapid growth and facile recovery from damage to shallow reef zones, has been attributed to white band disease; and populations of the large, long-lived massive *Montastraea* species, so highly resistant to physical damage, have been heavily influenced by yellow band and white plague diseases. Short-lived, smaller-colony species have been less affected (e.g., Bruckner *et al.*, 2009). Sponge diseases by contrast tend to be quite specific to particular species. Disease may be having a profound effect on sponge species diversity. By the end of a 14 year study on a shallow reef at a remote site, 20 of the 39 sponge species present at the start had vanished, with disease the most likely culprit (Wulff, 2001, 2006a).

CONCLUSIONS

Complementary roles played by corals and sponges in reef building, maintenance, and repair are all required to the point that if any are not performed, the entire enterprise can fail. But, why do we need to be concerned about keeping more than a few species of each alive and well? Species of corals and sponges that build, maintain, and repair coral reefs have evolved in a context that has provided the selective impetus for an effective balance between resistance to, and recovery from, physical disturbance by tropical storms. Species less resistant to damage make up for that by effective individual recovery by regeneration or by population level recovery by recolonization. When threats are relatively novel, as are bleaching and disease, strategies that compensate for lack of resistance are much less evident, perhaps reflecting the lack of time for evolution in response to these threats. Species that appear especially vulnerable are failing to exhibit effective recovery.

Oil is not a substance to which corals and sponges have had a chance to evolve strategies for either resistance or recovery. In 1986, an oil spill in Bahia las Minas, near the Caribbean terminus of the Panama canal, killed many corals outright, resulting in an immediate decrease in coral cover by 76% at 3 m depth or less, and 45% at 9 to 12 m depth (Jackson *et al.*, 1989). After 5 years, recovery was still not apparent. Corals on oiled reefs had slower growth and higher injury rates, and there was practically no recruitment of the next generation (Guzmán *et al.*, 1994). Effects of oil on sponges are much less understood, in large part because sponges vanish so quickly after they are killed that they are invisible to any monitoring that is not immediate. Highly efficient filtering of large volumes of water may render sponges especially vulnerable to oil that has been broken into fine suspended droplets with chemical dispersants. Lingering effects of the Panama oil spill were in part due to continual re-oiling, every time sediments in which oil had become buried were resuspended by water movement (Levings *et al.*, 1994).

High biodiversity ensures functional redundancy of species that differ in how gracefully they cope with temperature extremes, disease, and physical damage so that there are always at least some species capable of performing each of the roles essential to the functioning of the reef - even when other species are temporarily diminished by their vulnerability to a particular environmental challenge. However, when multiple challenges occur together, or when the challenges are novel, as oil is, too many species may be diminished or deleted simultaneously, impairing the natural growth and recovery processes. Given the

inability of slow-recovering species to resist novel threats, it seems rash to risk the addition of oil to the many other threats currently facing corals and sponges of the Belize Barrier Reef.

ACKNOWLEDGEMENTS

My funding sources for research in Belize are the Caribbean Coral Reef Ecosystems Program (CCRE) of the US National Museum of Natural History, the Marine Science Network of the Smithsonian Institution, funded in part by the Hunterdon Oceanographic Research Endowment, and the National Science Foundation (Grant number 0550599). I am grateful to Deng Palomares and Daniel Pauly for organizing the symposium on the Biodiversity of the Belize Barrier Reef of which this paper is a part. This is CCRE Contribution #907.

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