Control of the fungal parasite Aspergillus sydowii in the Caribbean Sea

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Parasite Ecology, Professor Chelsea Wood, Fall 2020

Abstract: Coral reef ecosystems are facing a multitude of threats due to climate change. As the temperature of seawater rises, coral immunity is compromised. This leads to emerging diseases, such as aspergillosis, a disease of gorgonian corals caused by the fungal parasite *Aspergillus sydowii*. This paper proposes two management strategies for control of the parasite in the Caribbean Sea: ecosystem vaccination and top-down control of the vector. First, I advocate ecosystem vaccination, a widespread implementation of assisted evolution. Second, the parasite is vectored by the flamingo tongue snail, which can be reduced in abundance by regulating the fishing of the snail's predators. Both of these strategies address the larger problems of climate change and overfishing in coral reef ecosystems.

Introduction

Coral reef ecosystems are facing a multitude of threats due to climate change. Coral bleaching, ocean acidification, and increased storm prevalence leading to structural damage all contribute to the decline of coral reefs (EPA 2018). As the temperature of seawater rises, coral immune systems are impaired due to heat stress (Harvell et al. 2001). This reduced immunity is contributing to disease emergence by opportunistic pathogens (Harvell et al. 1999, Harvell et al. 2004, Kim and Harvell 2004). Gorgonian coral species are ideal targets for one such pathogen, *Aspergillus sydowii*.

Gorgonians are a group of soft-bodied corals adapted to filter feeding. While they are not reef-building corals, they are considered ecosystem engineers (Pascual 2015). Gorgonians produce several antimicrobial compounds and are mined for drug targets (Matulja et al. 2020). They are the dominant taxa on Caribbean reefs (Chiappone and Sullivan 1994), which is where outbreaks of aspergillosis are occurring (Nagelkerken et al. 1997a, 1997b, Kim and Harvell 2004).

Aspergillosis is an emergent disease of gorgonians caused by the terrestrial fungus *Aspergillus sydowii* (Smith et al. 1996, Geiser et al. 1998, Kim and Harvell 2004). It is known to affect eight species (Smith and Weil 2004). This soil fungus can act as an opportunistic parasite, traditionally infecting crops, livestock and even humans (Sweeney et al. 1976, Pier and Richard 1992, Perrone et. al 2007, Seyedmousavi et al. 2015). The fungus cannot reproduce in the marine environment, making the coral a dead-end host (Kim and Harvell 2004), but new spores are continuously introduced from local terrestrial runoff and possibly by large-scale dust storms (Rypien 2008). The disease was first detected in the Bahamas in 1995, and has since spread through the whole Caribbean (Nagelkerken et al. 1997a, 1997b). Evidence suggests that the

spores themselves have always been present in the ocean, but that changing conditions due to global warming has now created an opportunity for *A. sydowii* to overcome the corals' defenses (Kim and Harvell 2004). The higher temperatures of the water both weakens the immune system of the coral and promotes the growth of the fungus (Alker et al. 2001).

Increasing coastal runoff (Howarth et al. 2000, Jones and Boyer 2000, Lapointe et al. 2002) further facilitates aspergillosis and increases its severity by providing sufficient nitrogen for the usually nitrogen-limited fungus to increase its fitness and therefore virulence (Olutiola and Cole 1977, Bruno et al. 2003). Managing a marine disease presents a challenge because the standard terrestrial strategies of culling, quarantine and vaccination are not options (Bruno et al. 2003). Therefore, managing water quality may be an important consideration for conservation of coral reefs. I have not explored this option further in this report because I believe sufficient mitigation of nutrient enrichment to be an unlikely outcome given the human response to climate change thus far.

Gorgonians are good targets for infection because they are filter feeders with a large surface area angled into the current, making them likely to come in contact with a floating spore (Kim and Harvell 2004). When the coral encounters a spore, a large lesion develops at the point of infection, resulting in a hole in the fan (Nagelkerken et al. 1997a, 1997b). The tissues surrounding the lesion turn purple, a distinctive calling card of the disease which is caused by an innate immune response of the coral called melanization (Petes et al. 2003). The hole compromises the structural integrity of the fan and can lead to pieces of the fan breaking off. This breakage is particularly damaging if it occurs close to the base, because the coral colony loses all of the healthy tissue above (Kim and Harvell 2004). Larger sea fans are more likely to come in contact with a spore both because of their size and because they have lived longer and so

have accumulated more pathogen hits over time (Kim and Harvell 2004). Larger colonies also have lower antifungal defenses than smaller colonies, making them more susceptible in general (Kim et al. 2000, Dube et al. 2002). The largest sea fans are the most mature individuals and are responsible for the bulk of the population's reproduction (Beiring and Lasker 2000), which is significantly repressed by the parasite even without mortality (Petes et al. 2003, Kim and Harvell 2004). Thus, recruitment only occurs when disease prevalence is low, a large barrier to recovery (Kim and Harvell 2004).

Outbreaks of aspergillosis are particularly prolific and damaging to corals because the parasite's population is not controlled by the decline of the coral host's population (Kim and Harvell 2004). Beginning in 1997, a six-year outbreak of aspergillosis in the Florida Keys was monitored from start to finish to understand the disease ecology of this emergent fungal epizootic. Kim and Harvell (2004) found that these outbreaks are so devastating to corals because the parasite population is not being regulated by the host population's decline. This terrestrial fungus, incapable of reproducing in the ocean, is ending up in the water by accident and maintains a massive reservoir on land independent of coral hosts. This means that the parasite cannot evolve to be less virulent to the coral hosts as successful pathogens normally do. The naïve coral host is thus required to evolve resistance quickly, before the fungus can completely wipe the population out. This is a serious challenge for the corals while simultaneously facing pressures from climate change. Aspergillosis is now thought to have emerged once before, in the 1980s in Central America (Guzmán and Cortéz 1984, Kim and Harvell 2004). It wiped out the gorgonians there (Guzmán and Cortéz 1984), proving that management is necessary.

Eradication and elimination of this parasite in the marine environment is not possible. This fungus is highly successful terrestrially, ranging across the world (Raper and Fennell 1965, Klich 2002), making eradication of reservoir populations unfeasible. This genus also has free-living roles on land (Raper and Fennell 1965, Klich 2002) and is useful in commercial fermentation (Perrone et. al 2007), meaning elimination may have unintended ecological consequences (Wood and Johnson, 2015). New spores will continue to be introduced to the ocean from terrestrial sources, making oceanic eradication equally unfeasible. Therefore, this paper will explore two strategies to control the outbreak of aspergillosis in corals.

Management Part 1: Ecosystem vaccination

The classic conservation strategy I would like to build on centers around increasing the recruitment rate, the chances of a baby coral successfully settling, of wild corals. Gorgonian populations reproducing now have survived multiple warming events over the past few years, and already show some resilience to climate change due to natural selection (Goulet et al. 2017). However, these coral's rely on asexual fragmentation to maintain their population, while sexual reproduction does not have much of an effect on their population growth (Lasker 1991, Lasker et al 1998). Sexual reproduction is essential to evolve as a population. While corals have a low reproductive rate due to predation and abiotic factors (Lasker et al, 1996), they have a high reproductive potential which we can exploit.

Some Caribbean gorgonians are spawners (Brazeau and Lasker 1989, Beasley et al. 2003), meaning they release their gametes into the water to do external fertilization. During general coral spawning, all members of a species release their gametes into the water at the same

time, an event frequently synchronized to the phase of the moon. These gametes float to the surface, where, if they are extremely lucky, they will encounter each other and fuse to form a zygote. This zygote then sinks to the bottom and tries to establish itself wherever it has the fortune, or misfortune, to land. At every point in this process, the various components of an embryo are susceptible to predation. Because this event is highly synchronized, the reproductive effort of that entire species, sometimes for the whole year, delicately hinges on several environmental factors. For example, a rainstorm could decrease the surface salinity to a level fatal for gametes (Hédouin et al. 2015, Wijayanti et al. 2019). Due to these biotic and abiotic factors, the recruitment rate for a population in the wild can be very low (Lasker et al, 1996). But since the corals have the biological capacity to produce a large number of offspring, increasing their recruitment rate can be achieved relatively simply.

The non-profit organization SECORE (SExual COral REstoration) is working on a method to increase recruitment rates and distribute coral embryos on a practical scale (Chamerbland et al. 2016, Chamberland et al. 2017). To approach this challenge, they developed their methods using wild populations of brain corals, a type of hard-coral (Chamberland et al. 2016). Brain corals participate in spawning events triggered by the full moon. Parrotfish cluster around the brain corals right before they spawn, because they eat the gametes. The parrotfish cluster can also indicate to scientists which corals to target. Researchers put a tent over the coral to catch all released gametes, which are funneled up into a small inverted collection tube at the top of the tent. These tubes full of gametes are then taken back to the lab, where scientists assist in the fertilization process by ensuring the gametes encounter one another. The larvae are then settled on cheaply produced, handheld seeding units. The shape of these concrete seeding units, called tetrapods, is designed to increase coral survival and self-stabilize when sown on the reef,

reducing labor by eliminating the need to secure them down. These tetrapods, seeded with viable coral larvae, can be easily distributed along the reef wherever they are needed (Chamberland et al. 2017). Future goals include making it possible to deploy these seeding units en masse from a boat or drone instead of seeding each by hand, further reducing required labor (SECORE 2020). These tetrapods are intrinsic to scalability because they are easily and cheaply produced, and are easily deployed, making this solution both practical on a large scale and economically feasible for the communities where they are most needed.

In theory, this work could be applied to natural populations of gorgonian corals in the context of aspergillosis as well as climate change. The Florida Keys corals that survived the 1997 epizootic represent a prime target. The outbreak appears to have ended due to increased abundance of naturally resistant individuals (Dube et al. 2003, Kim and Harvell 2004), shown by a shift in the population's age structure (Kim and Harvell 2004). Individuals from this population could in theory be similarly propagated and potentially even dispersed to equivalent reefs. Further, this population and these methods of distribution should be coupled with assisted evolution.

Ruth Gates, founder of the Gates Coral Lab, was a pioneer in coral restoration using the process of assisted evolution (van Oppen et al. 2015, van Oppen et al. 2017). The goal of the Gates Coral Lab is to help corals build resilience to climate change to prevent bleaching (van Oppen et al. 2015, van Oppen et al. 2017). First, fragments of individual colonies shown to have some resistance to the effects of climate change are collected from the damaged reefs. In the lab, these corals are put onto "environmental treadmills" (Braverman 2016), meaning they are subjected to increasingly stressful conditions that replicate projected environmental conditions. Transgenerational acclimatization is achieved in a shorter period than adaptation would be

(Donelson et al. 2011, Putnam 2012, van Oppen et al. 2015), through induced heritable epigenetic resilience within the coral host (Brown and Cossins 2011) and genetic evolution in the coral's short-lived endosymbionts (Berkelmans and van Oppen 2006, Middlebrook et al. 2008). The most resilient of these individuals are mated, ideally hybridizing, to produce "super-corals" (Willis et al. 2006, Fogarty 2012, Putnam et al. 2020). Hybrid corals have been shown to have greater thermal tolerance (Rinkevich 2014, van Oppen et al. 2015, Chan et al. 2018, Wood et al. 2019). The overall goal is to reseed the natural environment with these super-corals, giving coral reef ecosystems heightened resistance to climate change (van Oppen et al. 2015, van Oppen et al. 2017).

In theory, these methods could be extended to include fostering resistance to aspergillosis, both directly and indirectly. Directly, the addition of spores into the suite of stressors would weed out those most susceptible. Indirectly, aspergillosis is becoming a problem now due to the decreased immunity in corals brought on by climate change (Harvell et al. 1999, Harvell et al. 2004, Kim and Harvell 2004). Fostering resilience to climate change alone could increase the coral's resistance to aspergillosis by eliminating this decline in immunity, immunity that was sufficient to prevent outbreaks before climate change. The population of corals studied in the Florida Keys represents a great pool of candidates for assisted evolution, given that they survived an outbreak in the face of climate change (Kim and Harvell 2004). Resultant supercoral larvae could then be distributed to reefs in need using SECORE's cement tetrapods.

Assisted evolution, still in its proof-of-concept phase, faces double controversy. First, there is debate over whether altering the population's gene pool through assisted evolution is the right move versus preserving natural genetic pools (Coleman et al. 2020). Critics cite possible unintended consequences, such as maladaption and decreased resilience to non-target stressors

(Hereford 2009, Anderson et al. 2014), as well as ethical concerns (Sandler 2013, Filbee-Dexter and Smajdor 2019). However, this process does not represent a departure from natural processes, it just represents a speeding up of these processes (van Oppen et al. 2015) to match the projected future conditions that we will not be able to sufficiently mitigate (Sgrò et al. 2011, Aitken and Whitlock 2013, van Oppen et al. 2017, Breed et al. 2018, Ralls et al. 2018, Breed et al. 2019, Wood et al. 2019, Anthony et al. 2020). Corals both hybridize in the wild (Willis et al. 2006, Fogarty 2012, Chan et al. 2018) and are starting to adapt to climate change naturally (Goulet et al. 2017). Over time natural selection will increase the abundance of these resilient genes in the population (Kim and Harvell 2004). Unfortunately, the natural rate of adaptation among current coral populations is not sufficient for the corals to persist given the much faster rate of climate change (van Oppen et al., 2015). Ethical concerns over the hubris of meddling with nature can be refuted by the consideration that humans have a moral responsibility to use all tools available to us to solve the problem we created (Douglas 2003, Coleman et al. 2020).

Second, there is controversy regarding the range over which these genetically modified organisms should be introduced in regards to the range of the parent species (Hoegh-Guldberg et al. 2008, Ricciardi and Simberloff 2009a and 2009b, Richardson et al. 2009, Riegl et al. 2011, Thomas 2011) In response, I would advocate for seeding reefs with species of super-gorgonians that have high functional redundancy with the dominant gorgonians. Functional redundancy refers to two different species that perform the same function in the ecosystem and are therefore roughly equivalent in terms of the health of the reef (McWilliam et al. 2018). Unmodified corals are already threatened with extinction (van Oppen et al. 2015), regardless of possible competition with super-gorgonians. Therefore, possibly replacing a single, susceptible species with an ecologically equivalent gorgonian that has the resistance required to persist would be

better for the ecosystem as a whole. Further, because gorgonians do not secrete calcium carbonate skeletons, they will not be directly competing with reef-building species for this resource, an important distinction in the context of ocean acidification.

Empirical studies are needed to assess functional redundancy among gorgonian corals. I would expect there to be a high level of functional redundancy within gorgonians because most of the function these corals perform is structural complexity (Steinberg et al. 2020). Defining functional groups within gorgonians, and subsequently adding a metric to select for subsets of functional redundancy when evaluating potential candidates for assisted evolution, could address this issue of range.

Some argue that due to the controversial nature of assisted evolution, these techniques should only be applied to damaged reefs and species under direct threat of extinction (Coleman et al. 2020). However, I advocate for seeing both damaged and healthy reefs with supergorgonians. Seeding healthy reefs with resistant, functionally redundant individuals might not save specific threatened species, but could preserve and ensure the continued function of the reef ecosystem as a whole as climate conditions worsen in the future. Introductions of super-corals to healthy reefs would function as an ecosystem vaccination. Similar to how a doctor would vaccinate a healthy person against a disease instead of only treating the sick, so too should we vaccinate healthy ecosystems that will be threatened in the future instead of only conserving the damaged reefs.

In summary, I advocate that wild populations of gorgonians that have developed greater resistance to aspergillosis should be bred and seeded into naïve populations to avoid catastrophic epizootics such as in Central America. This could be thought of as a vaccination of the ecosystem. Where traditional vaccines provide an individual organism with a mechanism of

resistance, here an ecosystem is provided with a mechanism of resistance through the introduction of resistant individuals. To achieve this goal, assisted evolution should be implemented for gorgonians, and existing dispersal methods fine-tuned to these super-gorgonian larvae.

Management Part 2: Control the vector by reducing overfishing

The flamingo tongue snail (*Cyphoma gibbosum*), a micropredator specializing in gorgonian corals, has been shown to be capable of successfully vectoring aspergillosis among sea fans (Rypien 2008). When this snail feeds, they plow along the rows of polyps, leaving behind an open wound that leaves this part of the coral colony very susceptible to infection. If the snails have recently been feeding on parasitized coral tissue, then they deposit feces full of viable spores and hyphae into the open wound, allowing the fungus to bypass some host defenses. These snails have shown a preference for eating infected coral tissue (Rypien 2008), supported by previous observations of them aggregating on diseased sea fans (Nagelkerken et al. 1997a, Slattery 1999). In addition, Rypien suggests the coral's might be exhibiting a trade-off, a reduction in anti-predation defenses in favor of more antifungal compounds (Kim et al. 2000), thus encouraging the snails further. This feeding preference increases their likelihood of harboring infective agents which they can vector to uninfected fans.

The flamingo tongue snail is not the sole mechanism of transmission for *Aspergillus*. The snails' patchy distribution alone disqualifies it (Birkeland and Gregory 1975, Hazlett and Bach 1982, Harvell and Suchanek 1987, Lasker and Coffroth 1988, Botero 1990, Chiappone et al.

2003), and the spatial patterns of aspergillosis suggest multiple modes of transmission (Jolles et al. 2002). Further studies are needed to determine the relative importance of the snails as vectors.

Certain reefs may be more affected than others by the snail. Rypien (2008) suggests that the snail's presence on a reef with an active outbreak of aspergillosis may generate a positive feedback loop in terms of transmission due to their feeding preference for infected tissue. Further, the snail's might be more important on reefs with a low input of spores, or a low host density, where they could increase the likelihood of an outbreak despite low encounter rates. Special attention should be paid to those reefs with *C. gibbosum* that are being overfished.

The flamingo tongue snail is one of the only natural grazers of these corals, and the impacts of its predation are minimal in a healthy ecosystem (Birkeland and Gregory 1975, Harvell and Suchanek 1987, Lasker et al. 1988). The snail population is controlled by their predators, mainly large fish. If large predators are excluded from a range, the snails are both more abundant and more active and do significant damage to the gorgonian corals there (Burkepile and Hay 2007). Overfishing of the snails' predators indirectly leads to significant physical damage to the corals, damage compounded by the snail's ability to vector *Aspergillus*.

I advocate that fishing regulations incorporate monitoring of *C. gibbosum* abundance to limit the vectoring of aspergillosis. In theory, this could even provide a new metric to quantify overfishing in general. Alternately, this species is heavily over-collected by divers for its ornate shell (Sterrer 1986). This confounding variable would need to be considered in regulatory decisions.

Conclusion

Control efforts of any parasite are more successful when the solution is multifaceted. In keeping with this, aspergillosis can be best controlled in the marine environment by investments in assisted evolution, ecosystem vaccination, and new regulations against overfishing. Each of these solutions work to combat larger threats facing coral reefs related to fishing and climate change.

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