Comparison of extinction threats to coral-reefs during the devonian and today

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Coral reefs are “holobionts,” composed of coral-forming species, numerous algae, and bacterial species that live symbiotically with their coral hosts (Roik et al., 2022). Predominantly found in tropical and subtropical waters of the Atlantic, Pacific, and Indian Oceans, these holobionts serve vital roles in marine ecosystems, acting as protective barriers and food reservoirs for approximately one third of marine species (Plaisance, 2011). Among those marine species are coral-dwelling fish, which one-third gain 80% of their diet from coral reefs (Cole et al., 2008). Other fish species utilize coral reefs as breeding grounds and nurseries for their young (Verweij et al., 2008). Despite overwhelming evidence suggesting fish utilize coral reefs for multifold purposes, it is unknown the extent to which they would be impacted if coral reefs went extinct.

Some coral species act as ecosystem engineers, such as those belonging to the genera Scleractinia, by secreting calcium carbonate to build coral reef structures (Von Euw et al., 2017). However, this process may be halted due to environmental change. Low oceanic pH or high ocean temperatures cause available oceanic carbonate ions to be converted to carbonic acid (Mollica et al., 2018). With less carbonate ions available, coral species struggle to form their carbonate skeletons (Mollica et al., 2018). Additionally, ocean acidity can degrade remaining coral structures or cause coral bleaching, the death of the coral’s symbiotic bacterial and algal species (Mollica et al., 2018). Overall, environmental pressures are a determinant in the speed at which a coral’s carbonate skeleton can be produced and resulting coral reef habitats are vital to marine and terrestrial life.

By forming carbonate skeletons that serve as marine habitats, corals are crucial for promoting high marine diversity and productivity, to the extent that biologists analogize coral reefs to tropical rainforests. Coral reefs also assist terrestrial ecosystems, safeguarding coastlines from vehement storms and possessing medicinal agents useful for composing antiviral drugs and cancer therapies (Bruckner, 2002).

Economically, coral reefs are beneficial to society — on average generating $482,000 per square kilometer annually, with some generating up to $7 million per square kilometer, from tourism alone (Bruno et al., 2019). While corals serve multifaceted purposes today, their functionality was minimized throughout history.

Some of the first corals, namely Stromatoporoidea, are thought to have evolved during the Ordovician Period, nearly 485 million years ago (Webby, 2002). During this time, corals transitioned from microbial-based metazoan symbionts to algal and microbial-based symbionts (Webby, 2002). While the Ordovician is surely an important marking for the first appearance of coral species, the Devonian Period displays mass-scale population shifts which are of interest to coral extinction literature. During the Devonian, coral species faced mass expansion, the formation of the first coral reef networks, and the demise of such networks (Wendt & Kaufmann, 2006, Bridge et al., 2022). Overall, the history of corals, particularly during the Devonian, provide insight into the interactions between corals and their environments even today.

The Devonian Period of the Paleozoic Era is characterized by an explosion of aquatic life, thus commonly referred to as “The Age of Fishes”. Alongside other marine life, coral life multiplied in increasing numbers, with one of the largest reef complexes being created by the middle of the Devonian Period (Wendt & Kaufmann, 2006). By the end of the period, these same reef ecosystems collapsed, a period referred to as the Late Devonian Mass Extinction (Bridge et al., 2022). The exact factors that may have led to this collapse are unknown, although eutrophication, anoxia, hypersalinity, red tide and algal blooming may have contributed (Gong et al., 2002). Nonetheless, while the Devonian holds remarkable developments in coral-reef complexes, it also holds the extinction of coral reef species in such complexes.

Similar to the Devonian, present-day predictions suggest corals are under threat. It is estimated there are approximately 1,670 coral species up to date (Hoeksema, 2023), and according to the IUCN Red List of Threatened Species, of those species, 31 are critically endangered (CR), 30 are endangered (EN), and 207 species are vulnerable (VU) (The *IUCN Red List of Threatened Species*, 2023). Some carbon emission models estimate that 99% of the world’s coral reefs will disappear or become bleached by the end of the century (Strona et al., 2021). Despite how beneficial coral species are to marine and human life, large-scale measures necessary to save them are not being implemented, resulting in credible extinction-level threats.

While the extinction of coral species is not novel nor modern, the contemporary factors contributing to their demise are. Natural environmental processes, such as climate change, have threatened, reconstructed, and eliminated coral populations during the Devonian. Today, however, climate change accelerated by anthropogenic effects threatens living corals and coral-reef networks. In this paper, I will investigate threats posed to coral reefs by comparing and contrasting such threats from the Devonian Period and today, and discuss implications of future coral reef extinction on coral-inhabiting fish species.

It is important to understand the differences in what is threatening coral populations today compared to the Devonian Period so effective conservation efforts can be developed. Some of these differences arise in the composition and climate of Earth during the Devonian Period, as compared to today. During the Devonian, nearly 85% of the world was covered in seawater, and large landmasses comprising North America, Europe, and Greenland formed the supercontinent of Laurussia (House, 2023). While Earth cycled through glacial and interglacial periods, interglacial periods were on average warmer than today’s climate, supporting few polar ice caps and moderate global temperature gradients (Bridge et al., 2022). These interglacial and glacial periods, which resulted in the Frasnian-Famennian biodiversity crisis, impeded speciation and growth of living species, and left marine ecosystems in peril or extinct (Zapalski et al., 2017). Today, however, the Earth is comprised of seven continents, some separated by large bodies of oceanic water. Earth’s climate gets progressively warmer, supporting few existing ice caps, due to average annual land and water temperatures increasing. Understanding Earth’s climatic cycling during the Devonian has allowed for extrapolation of possible attributions to coral demise, including thermal stress brought on by global warming, global cooling, and volcanic outgassing.

Coral stress is caused by fluctuations in the coral’s external environment pertaining to light, temperature, or pH level. One resulting mechanism of coral stress is coral bleaching, in which corals undergo whitening events upon the death of their bacterial and algal symbionts, primarily brought on by the expulsion of such symbionts from the corals. Expulsion serves as a mechanism of preservation— allowing corals to avoid further tissue damage by oxidation during periods of thermal stress (Buddemeier & Fautin, 1993). Simply, if corals rid the photo symbiotic zooxanthellae living on them, they remove the reactive oxygen species they produce. Coral’s tolerance for thermal stress declines below oceanic temperatures of 20°C and above oceanic temperatures of 30-32°C, thereby prompting zooxanthellae expulsion (Zaapalski et al., 2017, Buddemeier & Fautin, 1993). With average sea surface temperatures of the late Frasnian hovering 30°C, this threshold was surpassed during its interglacial periods suggesting one possible cause of tabulate coral extinction during the Devonian to be global warming (Joachimski et al., 2009). This hypothesis is supported by the extinction of photo symbiotic coral taxa correlating with rising sea temperatures and levels during the Devonian (Bridge et al., 2022, Zapalski et al., 2017). Although bleaching events do not kill the living coral, they render them susceptible to disease and malnourishment, which may accelerate death (Zapalski et al., 2017). Ultimately, adjoining the understanding of coral bleaching biology and the Devonian climate allows analysts to suggest global warming may have led to Devonian coral extinction.

Contrarily, global cooling is thought to be a principal driver of coral extinction during the Paleozoic Era (Stanley, 1988). During the Late Devonian, rugose corals, found in benthic environments, dominated, and replaced reef-building corals, found in shallow marine environments (Pedder, 1982). The stable coldness of the seafloor allowed benthic rugose corals to be better adapted to colder oceanic temperatures than coral species found in superficial water levels (with direct access to sunlight). The shift from reef-building corals, found in shallow marine environments, to rugose corals, suggests broader climatic cooling which disproportionately affected shallow coral species (Stanley, 1988, Pedder, 1982). While not all rugose coral survived global cooling, it is suggested nearly 30-40% did survive, compared to only 4% of shallow coral species surviving (Pedder, 1982). Coral population shifts are not the only body of evidence supporting global cooling as a mechanism of coral demise. Records show the Late Devonian correlated with the onset of glaciation at the polar regions of Earth (Stanley, 1988). The presence of mass glacial sheets, dated from the Famennian Age of the Devonian suggests global temperature decreased, allotting for glacial formation and the possibility of induced thermal stress for coral species (Stanley, 1988). If global cooling did affect Devonian corals, their induced thermal stress would have rendered them susceptible to similar threats as global warming, including malnourishment and disease.

While global warming and cooling theories correlate with the history of glacial and interglacial periods of the Devonian, the question remains of what caused these fluctuations in global temperature. The Frasnian-Famennian boundary of the Late Devonian suffered a series of comet showers that hit current-day Nevada and Germany (Sandberg et al., 2002). The initial impact of these comets may have prompted volcanic eruptions (Sandberg et al., 2002, Chen et al., 2005), thereby propelling sulfate aerosols into the stratosphere in the form of ash. The addition of such toxins in the stratosphere causes chemical weathering like acid-rain, adding sulfide and irons into the Earth's oceans (Chen et al., 2005). This would have prompted microbial blooms, preventing photo symbionts on faunal species from thriving (Chen et al., 2005). Equally important, the presence of ash in the stratosphere blocks sunlight from reaching Earth's surface, causing global surface cooling and possibly glaciation (Chen et al., 2005). While volcanic eruptions by comet showers may have initially caused global warming, the long-term effect of them results in global cooling. We may correlate these global warming and global cooling theories with interglacial and glacial periods, suggesting a synergistic effect of coral demise across the Devonian.

In summary, comet showers raining on Earth during the Frasnian-Famennian boundary of the Late Devonian likely caused mass-scale volcanic eruptions, putting Earth through a cycle of interglacial and glacial periods (Sandberg et al., 2002, Chen et al., 2005). Such climatic fluctuations likely promoted coral thermal stress, causing them to expel photosymbiotic coral taxa, become bleached, and remain susceptible to their changing environment. Certainly, comet showers and volcanic eruptions are not threats to modern-day corals, however, the effects of them, such as global warming, contributes to coral demise even today.

While threats posed to coral reefs during the Devonian are not known in their entirety due to dating obstacles, threats posed to coral reefs today are certain and substantial. Such threats include disease, anthropogenic effects, and most recently noted, global warming.

Similar to terrestrial animals, marine animals can face a plethora of diseases. Two diseases corals face are Stony Coral Tissue Loss Disease (SCTLD) and White Plague Disease. Once faced with disease, coral health is compromised and acts as a selective pressure, thereby contributing to coral reef loss and prompting susceptibility to other extinction threats. Stony Coral Tissue Loss Disease (SCTLD), first reported in the coast of Florida in 2014, is a highly virulent coral disease with exact modes of transmission not yet known (Alvarez-Filip et al., 2022, Shilling et al., 2021). Researchers hypothesize a viral-component which infiltrates the algal symbionts, promoting the development of white lesions and death within weeks of symptom onset (Alvarez-Filip et al., 2022, Shilling et al., 2021). SCTLD has infected 30 different coral species up-to-date and has been the demise of 60% of coral reefs in the Northern Florida Coast (Shilling et al., 2021). To determine the effects of SCTLD on coral reef communities, researchers introduced SCTLD to a 450-km reef track in the Mexican Caribbean and compared functional data (such as skeletal density growth rate) prior to and after the introduction of SCTLD (Alvarez-Filip et al., 2022). They found SCTLD caused widespread mortality in the corals, causing <10% but up to 94% of species-specific populations to perish (Alvarez-Filip et al., 2022). Some genera of corals, such as the maze corals (Meandrinadae) suffered >50% population mortality (Alvarez-Filip et al., 2022). Without such corals to act as main functional diversity contributors, total reef system functionality declines (Alvarez-Filip et al., 2022). SCTLD is just one of many diseases that weakens coral species and depletes coral populations.

Another prominent disease of coral species is White Plague Disease, also known as White Band Disease. As suggested by its name, the disease leaves visible banded- white lesions on the corals, and thus is commonly confused with coral bleaching. However, while coral bleaching leaves live tissue white, White Band Disease renders the coral dead, preventing it from supporting its symbionts (Jones et al., 2021). Reef-building corals belonging to the genera Acropora can be particularly susceptible to White Band Disease, with nearly 80% of the Acropora palmata population falling victim to it in the 1970's (Alvarez-Filip et al., 2022). In past years, some Caribbean Acropora reefs have lost a staggering 98% of their population (Shilling et al., 2021). It is the amalgamation of coral disease with other coral threats (like thermal stress), that may result in potential coral extinction in the near future.

Disease prevalence can increase in severity when paired with anthropogenic effects. Most ecologists assert we are now living through the sixth mass extinction, commonly titled the "Anthropocene". Titling this epoch the Anthropocene attributes blame to humankind for the mass extinction of species. Similarly, by attributing the extinction or death of a species to "anthropogenic effects," suggests mortality was avoidable if human actions like pollution, fossil-fuel burning, or improper disposal of pesticides were minimized. Researchers found thermal stress by anthropogenic stressors, paired with White Plague Disease, heightened disease transmission and severity for coral species (Jones et al., 2021). Following bouts of thermal stress in Southeast Florida during 2014 and 2015, pillar coral survivor hood subsided immensely, revealing a positive relationship between mean water temperature and White Plague Disease prevalence and mortality (Jones et al., 2021). Other studies found that disappearances in Acropora corals during the 1980's to 1990's can be attributed to anthropogenic behaviors such as overfishing and land-based pollution (Cramer et al., 2022). Run-off from land-based nutrients and agricultural development may have polluted nearby waters, thereby decreasing water quality which corals reside (Cramer et al., 2022). Other listed stressors include fishing, coast development, and land-based sedimentation, which all may act synergistically to contribute to coral degradation and coral bleaching (Cramer et al., 2022). The additive collection of anthropogenic effects can lead to a larger issue at hand, global warming.

Climate change is a common theme among the Devonian Period and the Quaternary Period. While global cooling may have largely contributed to coral extinction during the Devonian period, global warming is steering modern corals into extinction. The main mechanism by which global warming occurs today is through increased global carbon emissions, or the burning of fossil fuels. Increasing global temperatures have prompted thermal stress in corals, thereby transitioning them to a net negative carbonate budget in the Florida Keys (Toth et al., 2022). The net carbonate budget quantifies the rate of coral-reef construction versus the rate of corrosion (Toth et al., 2022). A net positive carbonate budget suggests a coral-reef builds its carbon skeleton faster than it erodes, whereas a net negative carbonate budget asserts the carbon skeleton degrades faster than it can be built. Only a mere 15% of coral reefs in the Florida Keys had a net positive carbonate budget in 2019 (Toth et al., 2022). This was not the case nearly 7,000 years ago, where most coral reefs had a positive carbonate budget, suggesting they produced more carbonate than they lost (Toth et al., 2022). This increasing rate of coral erosion is attributed to ocean warming, thereby entering the corals into a state of thermal stress similar to one that Devonian corals entered (Bruno et al., 2019). Ocean warming is not the only threat posed to coral reefs. Often, stress by ocean warming goes hand in hand with stress by ocean acidification. Red corals, Corallium rubrum, are ecosystem engineers that are particularly vulnerable to ocean acidification. As partial pressure of carbon dioxide (pCO2) in seawater continues to rise due to increased global carbon emissions, corals are hindered from performing calcification (Cerrano et al., 2013). The rate of their calcite-skeletons degrades faster than it can be built, once again diminishing their functionality for the ecosystem (Cerrano et al., 2013). Substantial changes in global temperature will continue to weaken coral populations until the global efforts to minimize carbon emissions are enacted.

Coral reefs have faced considerable threats between the Devonian Period and the Quaternary Period of the Anthropocene. Facing comet showers, volcanic eruptions, and glacial and interglacial periods during the Devonian, corals predominantly face disease and anthropogenic effects today. The similar threat to corals of global warming transverses through both periods, but it is accelerated today due to anthropogenic effects like the burning of fossil fuels. The effects of global warming on coral reefs have been studied for decades, yet literature discussing the implications of coral reef's mortality on marine ecosystems remains underserved.

Coral reefs house nearly 600,000 to 9 million species worldwide (Plaisance, 2011). From those, coral-dwelling fish species rely extensively on coral-reefs for protection from predators and access to food (Plaisance, 2011, Cole et al., 2008).Therefore, it is important to project how marine communities, specifically coral-dwelling fish species, might respond if coral extinction were to occur in the future. Some fish species are obligate coral species, meaning they rely on corals for survival, whereas other species earn facultative benefits from corals. Therefore, the consequences of coral extinction might differ among marine ecosystems.

Fish primarily utilize coral reefs by using their trabeculated coral branches as shelters from larger predators (Boström-Einarsson et al., 2018). However, as coral branches die, they become overgrown with algae, thereby minimizing available space for hiding and shelter (Boström-Einarsson et al., 2018). Researchers found as available shelter decreases, fish are more likely to seek live coral, crossing large areas of open water between coastlines and increasing their likelihood of encountering a predator (Boström- Einarsson et al., 2018). They found a positive relationship between coral death and predation-induced mortality of coral-reef dwelling damselfish, Pomacentrus moluccensis (Boström-Einarsson et al., 2018). The loss of available trabeculated coral branches may be particularly harmful for the 126 species of coral-dwelling fish who use coral branches as shelter from predators during their infancy (Coker et al., 2013, Jones et al., 2004). In the case of coral extinction, we may use these findings to suggest coral-reef dwelling fish populations would suffer higher mortality rates due to their increased risk of finding shelter in open waters.

It is also suggestive that coral reef fish communities would be reshaped completely if coral reefs went extinct, potentially threatening species abundance and ecosystem functioning (Jones et al., 2004, Cheal et al., 2008). Fish species diversity at the Great Barrier Reef was measured over an eleven-year period (Cheal et al., 2008). Despite coral abundance decreasing following coral bleaching and mortality events, diversity remained the same (Cheal et al., 2008). It is important to note, however, community diversity is not necessarily indicative of communal change in species presence. As coral mortality increased, so too did the abundance of herbivorous fish who do not depend on corals for survival (Cheal et al., 2008). Coral-dependent fish species and other fish species abundance declined with coral mortality, thereby reducing overall ecosystem functioning (Cheal et al., 2008). This shows that coral bleaching and coral decline can reshape fish species abundance at coral reefs, reducing the extent to which coral reefs can provide natural services and products to the surrounding environment (Cheal et al., 2008). Overall, although community diversity (the number of coral-dwelling fish interacting at coral reefs) may not decline, species composition surely does.

Some literature suggests coral-dwelling fish are not necessarily impacted by coral bleaching and degradation, and thus would not suffer exceedingly from coral extinction. Between 2016 to 2018, researchers recorded changes in coral and coral- dwelling fish populations at Lizard Island in Australia (Wismer et al., 2019). Over this period, the island suffered two mass coral bleaching events attributed to seasonal cyclones and crown-of-thorns starfish outbreaks (Wismer et al., 2019). They found that despite >40% of coral coverage declining, obligate coral-dependent fishes continued using bleached coral-reefs (Wismer et al., 2019). Although this research provides hope that fish species will not be negatively impacted by coral bleaching to the extent previously thought, researchers found that global thermal fluctuations will disproportionately eliminate Acropora corals— forcing them into extinction (Wismer et al., 2019). Acropora corals are reef-building corals that are vital to coral-reef functionality, forming large branching structures for other marine species to seek residence in (Cramer et al., 2022). The extinction of such corals, rather than their bleaching, can have profound effects on fish populations. Coral degradation and coral bleaching are separate events with distinct consequences. While the effects of coral bleaching may not be as detrimental as coral extinction, bleaching acts as a channel by which coral extinction can occur.

It is undeniable that coral species today are facing extinction-level threats, similar to the ones they have faced in the past (such as climate change) and others entirely new and correlated to human activity. One commonality between all threats from the Devonian and now, however, is that such threats exploit biological and life-history traits of corals. Corals can only thrive in ocean temperatures between 20-30°C before entering states of thermal stress and a net negative carbon budget (Zapalski et al., 2017, Buddemeier & Fautin, 1993, Toth et al., 2022). Once in a state of thermal stress, they resort to expelling their symbionts to prevent any further tissue damage (Buddemeier & Fautin, 1993). Whether it be due to volcanic eruptions, glaciations, anthropogenic effects, or global warming, coral species have, and will continue to remain susceptible to their global environment, entering them in a state of thermal stress. This does not, however, rid humans of their duty to prevent coral reef extinction. Coral reef disappearances have been correlated with entirely preventable human actions like overfishing, land-based pollution, and global warming (Cramer et al., 2022). Given that coral reefs provide shelter and food for marine and terrestrial animals, alongside economic and medicinal benefits for humans (Bruckner, 2002), the benefits of their maintenance far outweigh the benefits of their exploitation. How then do we prevent coral reefs from going extinct?

Wide-scale efforts of reducing carbon emissions and protecting coral communities are needed to save the corals. The implementation of coral-reef managers has been seen to help restore coral production in the Keys (Toth et al., 2022). Coral- reef managers are personnel tasked with maintaining the ecosystem's functionality by promoting reef resilience (Anthony et al., 2014). This consists of predicting risks posed to corals, assessing influences of bleaching events or other threats like natural disasters on coral reefs, and responding to those threats accordingly (Anthony et al., 2014). However, these managers can only make-up ground once anthropogenic effects have been mitigated or addressed (Toth et al., 2022). Other conservation efforts include enacting marine protected areas, fisheries management, marine bioengineering, or minimizing greenhouse gas emissions (most notably through using renewable energy techniques) (McLeod, 2020). There remains hope regarding conserving coral species, especially at the Great Barrier Reef. However, it requires proper measuring of ecological functioning, as well as wide-scale efforts to minimize anthropogenic effects. Although the extinction of coral species during the Devonian may not have been preventable, it is entirely avertible today and would have large-scale implications for marine ecosystems. Corals are prime ecosystem engineers, and the marine ecosystems they create, at a minimum, are reflective of the beauty in biodiversity we see on Earth today and warrant saving.

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