A literature study on the consequences for coral reefs if corallivorous fish become extinct.

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DISCLAIMER

Title

A literature study on the consequences for coral reefs if corallivorous fish become extinct.

Subtitle

An investigation into the most likely consequences for coral reefs if corallivorous fishes become extinct.

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In cooperation with

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Preface

In front of you lies the research paper on the consequences for coral reefs if corallivorous fish become extinct. It was written as part of my graduation phase at Aeres hogeschool Almere for Applied Sciences.

Last year, in 2020, I went to Australia for an internship abroad for a period of eight weeks. I stayed in Cairns which is one of the best places to visit the Great Barrier Reef from. Here, I got the chance to see the reef in all its beauty.

Although The Great Barrier reef is still full of life and color, bleached coral patches can clearly been seen. I had already heard about coral declines, but also about changes in reef communities. Both inspired me into wanting to know more about reefs. This is why I started to read up on many papers and publishments, until I found a suiting and interesting topic that would not only match my interests, but would also give the opportunity to approach a fitting knowledge gap.

I want to thank my coach, Dinand Ekkel, for his guidance during the writing process.

I sincerely hope that you will enjoy reading this study, and might even find some inspiration from it yourself,

With kind regards,

The author,

Tessa van Noord

June 2021

Table of contents

Summary in Dutch

Dit literatuuronderzoek is geschreven voor iedereen die zich bezig houdt met de bescherming van oceanen, riffen en de gemeenschappen maar ook voor eenieder die zich hierin interesseert. Deze literatuurstudie richt zich op het beantwoorden van de vraag 'Wat zijn de consequenties voor koraalriffen als koraal etende vissen zouden uitsterven?' Door versnelde trends in koraal verbleking, verzuring van de zeeën en overbevissing is dit een mogelijk scenario. Om de hoofdvraag goed te kunnen beantwoorden is onderstaande informatie in de literatuur verzameld.

Er zijn zes verschillende soorten eet-methodes die koraal etende vissen kunnen aanwenden. Zo bestaan er ''excavators, scrapers, browsers, grazers, mucus eters en bioeroders''. Bij obligate koraaleters bestaat het dieet voor meer dan 80% uit koraal, waarbij de facultatieve koraaleters hun dieet ook verrijken met andere organismen of algen.

Koraal dat wordt beschadigd door koraal etende vissen kan gevoeliger worden voor ziektes, kennen een langzamere groei, hebben verminderde voorplanting en herstellen slechter na verbleking. Tegelijkertijd zijn er ook positieve gevolgen van koraal-eters; ze voorkomen overgroei van dominante koralen waardoor diversiteit wordt bevordert. De meer dieet-gevarieerde vissen voorkomen verder ook algen overgroei en houden het rif schoon, wat koraalgroei bevorderd.

De koraal etende vissen hebben naast hun rol betreffende hun eet-wijze, ook andere rollen in het ecosysteem. Zo dienen ze als prooidieren voor de top predatoren en verschillende koraal-eters houden populaties in toom van lagere soorten, zoals de Crustacea, Annelida en Echinodermata, welke schadelijk kunnen zijn voor koraalriffen mochten deze de overhand krijgen. Verder verspreiden koraal etende vissen levende symbionten in hun ontlasting over het rif, welke koralen gebruiken in hun cellen. Dit helpt bij opbouw van beschadigd weefsel en koralen blijken hierdoor beter te kunnen herstellen na verbleking.

Er zijn niet veel andere diersoorten die de taken van koraal etende vissen kunnen overnemen mochten deze dieren uitsterven. Andere diersoorten voeden zich wel op koraal, maar vervullen niet op dezelfde schaal de andere waardevolle ecologische functies.

Het verlies van koraal etende vissen zou lijden tot het verlies van de negatieve maar ook van de positieve effecten van de dieren. De positieve effecten wegen zwaarder dan de negatieve omdat koralen vooral de schoonmaak functies nodig hebben van de facultatieve koraal eters, degene met een gevarieerder dieet welke alg competitie verminderen, het koraalrif schoon houden en populaties van invasieve soorten laag houden. De conclusie is dat het verlies van de dieet-gevarieerde vissen het meest gevoeld zal worden op het rif.

Summary in English

This literature review is written for those concerned with the protection of oceans, reefs and communities as well as anyone interested in it. The literature study focuses on answering the question ‘what are the consequences for coral reefs if corallivorous fish become extinct?’. Accelerated trends in coral bleaching, acidification of the seas and overfishing makes extinction a possible and relevant scenario. In order to answer this question properly, the following information has been gathered from the literature.

There are obligate and facultative coral eaters. In the case of obligate corallivores, more than 80% of the diet consists of coral, whereas facultative coral eaters enrich their diet with other organisms or algae. There are six different types of eating methods that these fish can use. There are excavators, scrapers, browsers, grazers, mucus eaters and bioeroders.

Coral that is damaged by corallivores can become more susceptible to diseases and have slower growth, reduced reproduction and slower recovery after bleaching. There are also positive effects of coral eaters; they prevent overgrowth of dominant corals which promotes diversity. The more diet variated fish also prevent algae overgrowth and keep the reef clean, which promotes coral growth.

Besides their dietary roles, corallivorous fish have other roles in the ecosystem. They serve as prey for the top predators and various facultative corallivorous fish keep populations of lower species, such as Crustaceans, Annelids and Echinoderms, in check, which could be harmful to coral reefs would they become dominant. Also, corallivorous fish spread symbionts in their faeces over the reef, which corals use in their cells. This helps rebuild damaged tissue and corals seem to be able to recover better after bleaching.

There are not many other species that can take over the tasks of corallivorous fish. The other animals that feed on corals feed the same way, but do not perform other valuable ecological functions on the same scale as the corallivorous fish.

The loss of the coral eating fish would lead to the loss of the negative, but also of the positive effects of the animals. The positive effects outweigh the negative effects because corals mainly need the cleaning functions of the facultative coral eaters; the fishes with a more varied diet that reduce algae competition, keep the coral reefs clean and keep populations of invasive species low. The conclusion is therefore that the loss of the facultative corallivores will be felt most on the reef.

Chapter 1. Introduction

Since 1800, the atmospheric CO^2 levels have risen from the preindustrial value of 280ppm up to 410ppm in present time. The total of methane content has since then more than doubled (Steffen, Crutzen, & McNeill, 2007). Consequently, earth's generic atmospheric temperature rose with 0.6 to 0.9 degrees Celsius between 1906 and 2005 and is expected to keep rising with 0.15 to 0.20 degrees per decade (Nasa Earth Observatory, 2010). Along with this temperature rise, the oceans are warming (Dye *et al.,* 2013). The oceans absorb most of the excessive heat that can no longer radiate back into the atmosphere due to greenhouse gas pollution (Laffoley & Baxter, 2016). Over 90% of the total warming on earth of the past 50 years took place in the oceans (Cheng *et al.*, 2020). Because the oceans are storing heat, the atmosphere has for now been largely spared of global warming. Eventually, the overheated oceans will release its warmth and from then on, exponentially contribute to warming up the planet (Upton, 2014). A paper by Levitus *et al.* (2012) revealed that the deep ocean absorbs one third of the total increase of the planets heat. For the past 30 years, an upward warming trend of 0.1 degree Celsius per decade has also been measured in surface water (Johnson & Xie, 2010; Rhein *et al.,* 2013). Due to CO^2 emission, the pH of the ocean waters has decreased with 0.1 pH unit and although this does not seem like much, since the scale for pH is logarithmic, a change of 0.1 unit equals a 30 percent increase in ocean acidity (NOAA, 2020a).

Due to elevated ocean temperatures, the amount of heat stress on coral reefs has largely increased over the past century and this has resulted into mass-bleaching events like never seen before (Readfearn, 2020). Since temperatures are only expected to rise, heat stress is one of the most threatening factors for shallow coral reefs (Oliver, Berkelmans, & Eakin, 2009). In the last large coral bleaching event from 2014 to 2017, heat stress caused a massive bleaching event in which 75% of global coral reefs were affected, of which 30% suffered permanent mortality. This event was noted as the longest and most destructive event known to men to this day (Blunden & Arndt, 2019). Although coral is found all over the ocean floor, reef building corals are only found in shallow tropical waters in which they prefer clean, moving water (NOAA, 2020b). The CO^2 greenhouse gas emissions are causing acidification of these shallow waters and this also threatens coral reefs. Acidification reduces the availability of carbonite ions which the corals need for composing their skeletons. Bleaching and acidification may lead to the loss of coral diversity and complexity as well as change the species dynamics (Spalding & Brown, 2015; Loya *et al.,* 2001).

Going back in time, in 1842, Charles Darwin visited the Cocos Islands, where he caught and dissected parrotfish that resided in the shallow, coral rich ocean waters. Darwin noticed that these fish had coral-remains in their stomachs and was hereby the first to discover the existence of coral consuming organisms, called corallivores (Darwin, 1845). These corallivorous organisms are quite rare, only three percent of known fish species are corallivorous, along with four families of crustaceans and gastropods and a few echinoderms (Claremont, Reid, & Williams, 2011). There are 128 corallivorous fish species, belonging to 11 different families. Most of these fish are facultative corallivores, meaning they have a balanced diet of coral along with other food sources. Only one third of these fish have a diet primarily existing of coral, making up 80% or more, which makes them obligatory corallivores. (Cole, Pratchett, & Jones, 2008)

Due to stressors causing bleaching and ocean acidification, the coverage of preferred feeding corals of these fish are decreasing, resulting into a shrinking food supply for these corallivorous fish. These declines may result into the disappearance of the more specialised corallivores and an increase of the more generalist species (Rice, Ezzat, & Burkepile, 2019; Clavel, Julliard, & Devictor, 2011).

Considering the degree of pressures threatening coral reefs and reef communities, the importance of understanding the dynamics and forces interacting with coral reef health and corallivorous fish are key elements in the efforts of protecting them (Rice *et al.*, 2019). The ecological significance of corallivores and their way of feeding is not yet fully understood, and the effect that corallivorous fish have on coral communities are still mostly unappreciated (Cole *et al.,* 2008). The many interactions between corallivorous fish and their habitat are unclear, and an improvement is necessary to understand how coral-corallivore communities are changing (Rice *et al.,* 2019).

It is known that there are small advantages on coral health implemented by corallivorous fish due to their specific feeding pattern, however these fishes are also reducing the health of already stressed coral reefs by reducing growth, tissue damage and making them more susceptible to events like bleaching. Conversely, bleaching and coral mortality induced by heat stress also lowers food availability for these fish (Cole *et al.,* 2008). The specific ecological role these corallivorous fish fulfil causes vulnerability of these animals under the current circumstances. This has left to wonder, what do these fish provide for their habitat and how much do they take, and would the possible disappearance of these fish leave an imperative mark on how the ecosystem functions? Ultimately, questioning the cruciality of these organisms in relation to their inherent ecological habitat.

Combining these thoughts and questions while taking the gaps in present knowledge into consideration, the following main research question has been composed: What are the consequences for coral reefs if corallivorous fish become extinct?

To be able to articulate a well-funded answer, the following sub-questions have been lined up:

1. What are the different corallivorous feeding strategies?
2. How do these different feeding strategies impact coral?
3. What function do corallivorous fish have, aside from their feeding-habits, in relation to the ecosystem?
4. Are there other organisms that can take over the function of corallivorous fish, would they become extinct?

Answering these questions will give insight into what is known about coral reefs, corallivorous fish and the communities they are part of, and what is not. Recent literature and findings will be presented here. This study also approaches the large knowledge gap with the intention to clarify and elaborate on the impacts of stressors and shed light on the prospects for coral and these fish. Although definitive knowledge on corallivores and how they relate to their habitat is still being researched, combining information and discussing what is known about the role and niche of such specialised species helps in getting a better understanding and can ultimately be used in deciding how - and if - to protect these species along with their ecosystems. Social values on attitude towards species is mostly determined by what people know and like about them. Some species receive more protection than others due to this tendency (Ainsworth, Aslin, Weston, & Garnett, 2016).

This literature study is meant for those that are devoted to marine life protection, coral reef conservation, and marine community safeguarding. It is also meant for those who are looking for clear information on the most recent findings on this topic. Lastly, this study can be used to highlight the importance of healthy ecosystems, knowledge on community dynamics, and raise awareness of the impact of human stressors through investigating the ways life around us is affected.

Without diving too deep into the literature that will be used to answer the main and sub-questions, hypothesized on forehand is that all life in every ecosystem evolved to fulfil a certain function. Hinchliff *et al.* (2015) came up with an evolutionary tree with 2.3 billion tips, connecting almost all animals, plants, microbes and fungi attempting to prove that everything is connected. It can even be visualized as a puzzle, in which every piece has its own specific place and together it forms a unity. The extinction of species will thus always affect surrounding organisms and dynamics. To what extent this is the case for corallivorous fish and their habitat, will be discussed in this paper.

Chapter 2. Method

In this chapter, the methods that are used to compose this literature study are discussed, starting with the literature style. This chapter will clarify why certain decisions were made, along with why data sometimes was included, or why it was not. On the terminology and searches is also elaborated.

2.1 Style

This literature study is a qualitative study. Meaning that the results are expressed in words and not numbers. The paper is produced by desk research and no field research has taken place. For this paper relevant literature was collected, and specific cases and methods were critically reviewed. Different sides of the data was highlighted to allow thoroughness.

2.2 Inclusion and exclusion criteria

The sources used in the introduction of this literature study could be no older than 30 years. In the introduction one exception on this principle is made; Darwin (1845) is referred to many times in other papers and serves as a baseline for other research, making it indispensable to mention. It was decided to not include sources dating back over 30 years due to the possibility of the information becoming outdated, caused by aging and more recent discoveries and technologies.

In the remainder of this literature study, information obtained to answer the main- and sub-questions could not be older than 20 years, due to the same possibility of the information becoming obsolete. This means that the information should be published in 2001 or later. A smaller time frame of 20 years was used, because it was believed that the most recent data will provide the most conclusive answers to topics that are very relevant in present time. Long-term research, with a starting period prior to 2001, was still included into this paper if the publishment was no older than 20 years. Used sources had to be written in English to qualify for this literature study, sources in different languages were excluded.

2.3. Sources

Sources used include peer reviewed books, research papers and literature studies. Any other source that is not peer reviewed must meet the following standards:

- It must be written by an organisation or individual with proven knowledge on the subject (for example NOAA, National Oceanic and Atmospheric Administration, an institution on oceanography or Upton (2014), article written and produced with permission of Scientific American.
- Must be published in 2001 or later.
- Information in non-peer reviewed sources needs to align with those that are peer-reviewed, meaning that the information cannot be completely contradictory from official publishments.

2.4 Types of searches

In this paper, forward and backward searching was used along with keyword, phrase and subject searching. Citation searching was also used, including author citation searching. Search words were connected by 'and' and 'or' or excluded by using 'not'- which is also known as nested searches. Double quotation ''….'' in some cases was applied to make the results more relevant. Search words for this literature study were combined as desired and include one or multiple of the following:

Anthropocene, climate change, temperature rise, atmosphere, ocean, warming, acidification, stressors, pollution, greenhouse gas emission, coral, prey, reef, bleaching, health, damage, mortality, generalist, specialist, species, communities, corallivores, feeding-method, food source, strategies, obligatory, facultative, habitat, niche, role, fish, dynamics, population, change, effect, impact, positives, negatives, extinction, function, protection, management, importance, future, prospects, protection, conservation, *name fish species*, * name coral reef* & *name coral species*

A few examples of possible sentence and keyword searches:

- Impact warming on coral
- Effect ocean acidification
- Corallivorous fish and coral bleaching
- Feeding strategies corallivores / *name fish species*
- *name coral reef* protection and management

For each sub question a different choice for specific keywords was made, therefore a more detailed overview is presented in Table 1 to specify possible search words per sub-question:

Table 1. Keywords per sub-question

Sub question	Search words and examples
What are the different corallivorous feeding strategies?	Feeding modes, corallivorous fish, coral, reef, generalist, specialist, obligatory, facultative food source, strategies, *name coral species*, *name fish species *, prey. Example: *Name fish species* feeding strategies.
How do these different feeding strategies impact coral?	Corallivorous fish, feeding strategies, coral, reef, specialist, effect, impact, habitat, impact, damage, negatives, positives, generalist, specialist, health *name fish species*, *name coral species*. Example: Impact corallivores on coral health.
What function do corallivorous fish have, aside from their feeding-habits, in relation to the ecosystem?	Corallivorous fish, species, communities, role, function, niche, coral, reefs, dynamics, community, importance, impact, effect, species, future, prospects, change, population, dynamics, *name fish species*. Example: Corallivore extinction effect community.
Are there other organisms that can take over the function of corallivorous fish, would they become extinct?	Coral, reef, specialist, species, communities, corallivores, habitat, niche, role, dynamics, extinction, population, change, function, extinction, future, prospects, *name species*, *name coral species* Example: Community change extinction corallivorous fish.

In all searches, the difference between English and American spelling was considered, resulting into sometimes using different spelling for certain keywords in order to obtain all accessible information in used databanks. If information was found in an interview, article or (online) newspaper, the original source is traced back to the original publishment.

Google scholar was often used to get access to literature, along with SpringerLink, PubMed and ResearchGate. Firefox was used as main browser.

2.5. Reliability

This literature study is based on reliable sources, their requirements are addressed in chapter 2.2. Without any prejudices or biases from the author, the main question was answered by factual evidence and by exploring multiple perspectives. This means that if one would repeat a similar process of collecting and reviewing literature, the conclusions would most likely be similar.

Chapter 3. Results

In this chapter the results will be presented, meaning that all information that was collected and retrieved is summarized here. This process will follow the same order as the four different sub-questions, which leads to the following arrangement:

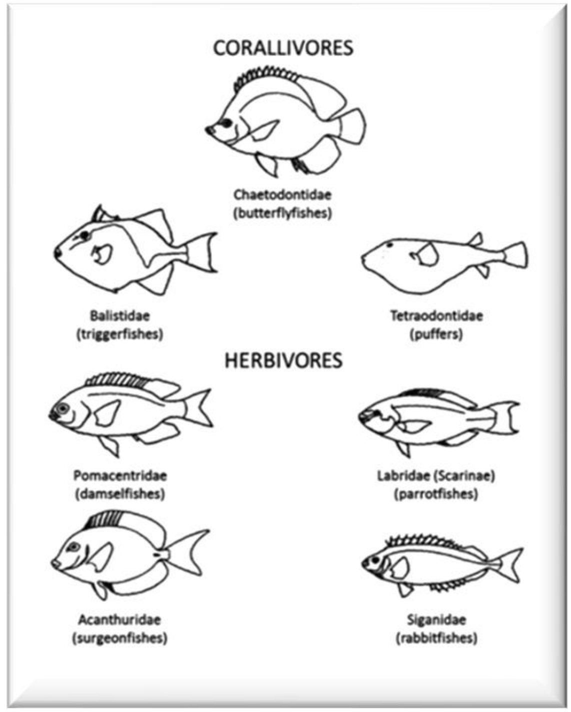
- What are the different corallivorous feeding strategies?
- How do these different feeding strategies impact coral?
- What function do corallivorous fish have, aside from their feeding-habits, in relation to the ecosystem?
- Are there other organisms that can take over the function of corallivorous fish, would they become extinct?

3.1 Different corallivorous feeding strategies

As described in the Introduction, corallivorous fish can be divided into the facultative feeders and the obligatory feeders. The difference between these two is the assembly of the amount of coral in their diet. Some species supplement their food intake with invertebrates, sponges and algae (Cole *et al.,* 2008). Whilst diving deeper into the literature available on these animals, it became clear that there is no distinct separation between corallivorous fish and herbivorous fish. The term corallivorous fish includes both corallivorous- and some partially herbivorous fish (Green, Bellwood, & Choat, 2009). The terms are often used interchangeably indicating the same concept; most corallivores eat algae that has developed on coral structures, and some herbivores participate in coral feeding due to algae growth on corals. Lastly, some species of fish just inherently feed on both resources. Whether algae or coral makes up most of one's diet, depends on the fish being facultative or obligatory corallivorous (Hixon, 2015).

Further research on this topic, made it clear that a large portion of the available research on reef fish feeding strategies took place on 'herbivores', or in other words, the often only partially corallivorous fish. To ensure thoroughness, the different classifications of these herbivores among corallivores will also be elaborated on in this paper.

In figure 1, the larger bodied reef fish that include most corallivores and herbivores are presented. The article (Hixon, 2015) in which this figure was published made a statement that not all members of the listed corallivore families feed on corals, and that about half of the species of the damselfish are not corallivorous at all. Also, many smaller-bodied coral- and algae feeders in multiple other families are not included into the figure. This prudence seems to validate the vague line between herbivorous and corallivorous fish.



▲ Figure 1. Classification of herbivores among corallivores (Hixon, 2015)

The different corallivorous feeding strategies can be broken down in to six categories which are used to classify a large variety of coral feeders, not restricted to fish only but also used for the Crustaceans, Gastropods and Echinodermata. Some of the six terms are more often used for the corallivorous fish, others are reserved for the more herbivorous fish among corallivores.

The different corallivorous feeding strategies will be discussed from most, to least invasive for coral. Firstly, there are the so-called excavators (1), then there are corallivorous and herbivorous scrapers (2), browsers (3), territorial and roving grazers (4), mucus-feeders (5) and bioeroders (6). Each of these feeding strategies has a different consequence for the coral prey. (Rice *et al.,* 2019)

Excavators are corallivorous fishes that feed on coral by removal of live coral tissue along with breaking of large portions of the underlying skeletons. Some Parrotfish *(Scaridae),* Pufferfish *(Tetraodontidae)*, Triggerfish (*Balistidae)*, and Damselfish (*Pomacentridae*) have the ability to do so. Parrotfish (*Scaridae*) make up a largest portion of the classification of excavators. These fish have over a thousand individual teeth arranged in up to 15 rows, forming an almost beak-like shape (figure 2A). Glenn Roberts, a biophysicist and professor at the University of Wisconsin-Madison, he stated that these teeth are the stiffest, among the hardest and most resistant to fracture ever measured due to their interwoven crystal structure. These types of fishes can apply a tremendous force on hard corals; over 530 tons per square inch (Roberts, 2017). Most parrotfishes are documented to consume live coral along with algae (Rotjan & Lewis, 2008).

The scrapers are known for scraping of live tissue of coral and with that also often remove a thin layer of the underlying hard coral skeleton. Other than the excavators, they mostly do not break off coral pieces, but they do sometimes tear off new growing polyps of abundant prey coral colonies (Palacios, Munos, & Zapata, 2014). An example of a major scraper is the *Arothron meleagris,* also known as the Golden puffer. In the literature, this fish is labelled as a species that consumes large amounts of coral. These fish are particularly well adapted to their niche due to their sharp teeth, which are slightly tilted forward (Jayewardene, Donahue, & Birkeland, 2009) (Figure 2B). Corallivorous scrapers can switch food-source when preferred prey coral abundance declines; they then often switch to a more algae rich diet (Hempson, 2017). The more herbivorous scrapers often use the same tactics as the corallivorous scrapes, their teeth are well adapted for scraping off algae from hard surfaces such as rocks and coral as well. Surgeon fishes (*Acanthuridae*) belong to this class. Other than the corallivorous scrapers, Surgeon fishes move along coral reefs in large groups, and are only rarely seen alone. Moving in a pack is a strategy to overwhelm the highly defensive damselfish, that often aggressively defend good feeding patches (Basford *et al.,* 2016)

Browsers are described as the corallivorous fish that also eat from the living tissue of coral, but do not touch the skeletons of their coral prey. Approximately half of the corallivorous fish species belong to the family of butterfly fishes (*Chaetodontidae*). These fish are mostly browsers and often have fleshy lips with which they can remove coral polyps or other tissues (Figure 2C). It is known that these fish have a dual role; reducing coral- and algae overgrowth (Rotjan & Lewis, 2008). Some species have been seen to feed on 51 different coral species from 24 different genera (Pratchett, 2005).

Then there are two types of grazers. The first group are the territorial grazers, and secondly the roving grazers. The first group, the territorial grazers, consists of solitary fishes that defend a certain habitat and stay here. These fishes, for example the Damselfish, actively defend their territory against other grazers, and although these fish mainly feed on algae, they are known to also bite live coral tissues and disturb corals directly. Some species feed of algae living directly on live coral colonies (Jones, Santana, McCook, & McCormick, 2006). The other group, the roving grazers are the more mobile fishes. These fish often move around in large schools, which protects them from predators. The roving grazers mostly feed on macro algae. Fishes belonging this class are often from the classification of *Siganidae,* or rabbitfishes (Green *et al.,* 2009).

Healthy coral produces mucus, which can help them catch organic matter and fight of diseases (Bythell & Wild, 2011; Bauman *et al.,* 2017). Only a small portion of the corallivorous fish are mucus-feeders. These fish only consume coral mucus and leave the live tissue and skeleton intact. Fish that are especially known to use this strategy are the so-called Wrasse's (*Labridae).* These fishes have lips that are modified to only suck off the coral mucus material (Figure 2D). The shape of their mouth and lips is designed to be able to create a lot of suction-force. Their lips also have a special layer of epithelium that secretes mucus on its own, which reduces damage and stings from nematocysts of some coral or anemones species. (Huertas, Bellwood, 2017).

Lastly, the bioeroders are corallivorous fish whose diet exists primarily out of dead coral substrate (Rotjan & Lewis, 2008). There are two types of bioeroders: the internal- and the external bioeroders. Most bioeroders are small bodied and depend on in coral structures for shelter. These fishes are called the internal bioeroders. The larger bodied animals are often more visible and present on coral reefs are thus called the external bioeroders (Glynn & Manzello, 2015). Fish like the Green humphead parrotfish (*Bolbometopon muricatum)* from the parrotfish family, with a body size up to 130 centimeters, is an example on these larger bodied animals. (Bellwood, Hoey, & Hughes, 2012).

The make-up of the diet is determined by either geographical location, habitat, or as a response to the availably of coral prey (Berumen, Pratchett, McCormich, 2005). The amount of coral eaten by corallivores can also be influenced by mutual competition between species, some of which are known to fiercely defend good coral patches (Pratchett, 2005). Normally, species stick to a few preferred corals, but due coral bleaching and rapid coral decline, are now often forced to consume other species (Home, 2018). Because some species are very dietary specific, not all are able to alter their food source. (Alwany*,* Thaler, & Stachowitch, 2003)

The way corallivorous fish feed can at times be hard to identify, making it challenging to chart the preferred coral prey (Nagelkerken *et al.*, 2009). Known is that different types of corallivorous fish prefer different types of coral. This distinct coral preference usually limits itself to only a small portion of the six thousand existing coral species (National Geographic Society, 2019).
There are two overall classifications of corals; Scleractinian and Alcyonarian corals. The first one being the hard corals, and the second being the soft corals. Most species target hard corals, but some fish, like the black-backed butterflyfish, prefer soft corals. Still, there are no obligatory soft coral corallivores known. (Pratchett, 2005)

The coral genera *Acropora*, *Pocillopora* and *Porites*, are the corals mostly fed on by corallivorous fish (Cole *et al.,* 2008). *Acropoda* corals are small and polyp-like, but are the most diverse genus of reef-building corals (Figure 2E). These corals are responsible for building the most calcium carbonate structures supporting the reef (Wallace, & Rosen, 2006). *Acropora* species also offer the most optimal combination between food and shelter for protection, by which the availability of this coral species can influence the distribution of species. (Schoepf, Herler, & Zuschin, 2010)

The *Pocillopora* are widespread and can be seen in the Pacific and Indian Oceans (Veron, 2002) (Figure 2F). In the Indo-Pacific, the *Acropora* and the *Pocillopora* are the preferred species for most corallivorous species (Pratchett, 2005) whilst in the Caribbean the *Porites* are eaten the most (Rotjan, & Lewis, 2008) (Figure 2G). This difference is probably due to the underrepresentation of some coral species in different oceans, implying that preferred coral prey are often the ones that are largely represented. Other explanations for a certain coral preference may be that this is influenced by whether the corals are easy to feed on due to size or shape. The way some corals defend themselves with for example, the density or nematocysts also plays a role. (Gochfeld, 2004)

▲ Figure 2. Corallivorous fish characteristics and coral species

3.2 Impact of feeding strategies

The way corallivorous fish feed is known to have an impact on coral health and abundance. These impacts can either be negative or positive for corals and the reefs. When corals are chronically predated on, the damage can ultimately lead to a decline in coral growth, abundance, resilience and might increase corals susceptibility to bleaching (Rotjan & Lewis, 2008). Corallivory often also implies damage and causes a loss of total coral biomass. Sometimes corallivorous behaviour can even cause direct coral mortality (Lenihan *et al.,* 2011).

Corals live in a symbiotic relation with certain algae, and are depending on each other for their survival. When ocean temperatures rise, these algae are expelled from the corals tissue, leaving them white; bleached (Home, 2018). Damage done by corallivorous fish adds to the destruction that is already done by bleaching, which leads to even greater losses and further weakening of coral reefs. Roff, Ledlie, Ortiz and Mumby (2011) also noticed that feeding rates of corallivorous fish increased, when the coral density decreases, leading to an even more rapid loss of coral cover. The loss of coral seems to directly influence the rate of predation on the remaining corals. In the Caribbean it was discovered that on coral reefs with low coral density the predation on preferred corals can be 34 times greater than on other - high density - Caribbean reefs (Burkepile, 2012).

As previously explained, the scrapers and excavators are the fishes that eat live coral tissue and do often damage the underlying coral skeletons. For this reason, the type of fish that feed using one of these techniques are causing the corals the most damage. Especially the larger, obligatory species that leave deep bite marks are able to alter reef structure (Bellwood, Hoey, & Choat, 2003) In a study (Palacios *et al.*, 2014) on the Guineafowl pufferfish (*Arothron meleagris),* it was found that this fish feeds on coral on a major scale in the Eastern pacific. With an abundance of 171 fishes per hectare, and a feeding rate with an average of 1.8 bites per second, this comes down to a bite density of 366 bites per minute. This pufferfish prefers the *Pocilloporid* corals of which it can remove 15.6% of the total volume of the species in just one year. The feeding habit of these fish can cause scars and permanents bitemarks on damaged area (Green *et al.*, 2009). Another example of such an impactful species is the Green Humphead parrotfish (*Bolbo-metopon muricatum).* This species is by far the largest coral consumer - living tissue as well as dead coral - in the Indo-Pacific (Bellwood *et al.,* 2003). In this study an estimation was made that one population of Humphead parrotfish can remove 13.5 kilo of living coral per square meter per year. Not only do they consume large quantities of live coral, but they also contribute to coral bioerosion breaking down more than 5 tons of reef carbonates in total per year. This species has a large impact on coral growth and mortality of their preferred coral species.

Another example are the highly territorial butterflyfishes, they browse and graze on coral very consequently. This can result into lower coral fitness, by depleting nutrients en decreasing reproductive success. Furthermore, all corallivorous fish have the potential to pass on diseases from one coral to another via oral contact (Aeby & Santavy 2006).

When coral is damaged by predation, the organism goes trough a wound healing process. The first step in this is the detection of the wound, and to fight possible pathogens that entered through the wound. The second step is the synthesis of melanine, which is used for regenerating the lost tissue. Thirdly, apoptosis or controlled cell death of damaged tissue often occurs. Hereafter, amoebocytes can be moved in, which are the elements that cause tissue regeneration in corals (Toledo-Hernandez, & Ruiz-Diaz, 2014). This process does not only require a lot of cell resources, it also demands energy. This energy can no longer be used elsewhere, for example on coral growth or reproduction. This shows that energy distribution is a trade-off process. (Henry & Hart, 2005). In a study (Lenihan *et al.,* 2011) in which *Porites* and *Pocillopora* coral damage by predation was tracked, 20-60% of the juvenile corals were damaged after one year. The growth rates declined with increasing damage and it was stated that corallivory had an overall negative effect, changing local communities. In another study on damselfish territories, a 44% decline was seen in juvenile coral abundance (Casey, Choat. & Connolly, 2015). Conversely, protecting corals from certain corallivorous strategies was found to increase coral growth and survival (Lenihan *et al.,* 2011).

The small portion of fishes that feeds on coral mucus, have been reported to feed excessively more on corals that are damaged due to a heightened mucus production on distressed tissues, meaning that these animals profit of the damage (Huertas, & Bellwood 2017). Although it is normal for coral to produce small amount of mucus, excessive mucus production due to damage can disrupt the natural microbes present on corals, making them more susceptible to diseases (Rotjan, & Lewis, 2008).

Some species like the damselfish, often the more facultative corallivores, or partially herbivorous, tend to scrape or bite corals to create more growing space for algae (McCook, Jompa, & Diaz-Pulido, 2001). Bite marks and scars can be noticed on these damaged spots on which algae attaches. Coral and algae compete for light and other resources, and an increase in algae can limit coral growth. Direct contact between algae and corals can even lead to coral diseases due to the presence of possible harmful microbes in algae (Smith *et al.,* 2006; Nugues, Smith, van Hooidonk, & Seabra, 2004)

Although there are negatives on corallivorous behaviour, there are often also positives. Hoey and Bonaldo (2018) discovered that some corallivorous species only target fast growing coral species that are present in large quantities. This preference might reduce overgrowth by these coral species, preventing the reef from becoming monotonous and allowing more biodiversity. Grazing on algae is also a very important process on coral reefs. Grazing controls the rate at which algae are able to expand, preventing overgrowth and coral loss. The loss of grazers might disturb the balance between algae and coral, in which algae become more dominant and will eventually oppress corals (Jackson, Donovan, Cramer, & Lam, 2014).

Reef maintenance is a time-consuming process, in which algae, dead coral, dirt and waste are removed, and this is necessary to insure healthy reefs. Bioeroders and herbivorous grazers are species that provide such ecosystem services. They clean up dead coral and sculpt the reef by the production of sand and rubble. Their behaviour can stimulate coral growth and offer more diverse habitat. (Glynn & Manzello, 2015) In the literature it is also debated that the coral-corallivore relationship in the seas is comparable to plant-herbivore relations on land, meaning that it is a co-dependent cycle in which species rely on each other for their long-term survival (Home, 2018).

Whilst it is still debated whether obligate corallivorous fish are having a greater positive or negative effect on coral reefs, the positive effects of herbivorous fish, seem to outweigh the negatives of the obligatory corallivorous fishes (Knoester, Murk, & Osinga, 2019). In this research, caged and uncaged coral nurseries were monitored during a period of four months. The growth- and survival rate of corals was tracked, as well as the number of bite marks. In the caged corals, the impact was way lower but survival rate and growing speed was down to 40 percent, compared to the non-caged corals. This was probably caused by the lack of cleaning done by herbivorous fishes; coral cleaning was almost 800 percent higher on these non-caged corals. Ten percent of the uncaged corals showed bite marks from corallivorous fish, but this did not stop the uncaged corals from reaching a larger size, and ultimately be better at survival.

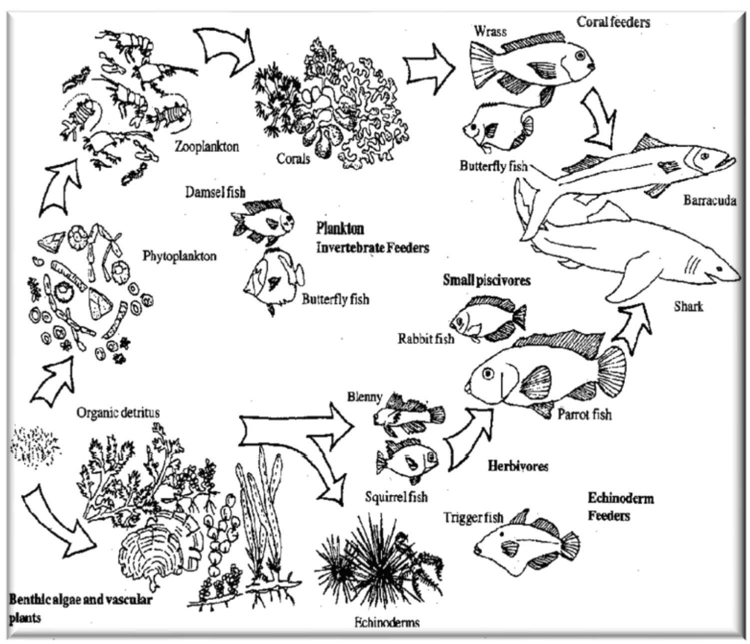
Not all research detects negative nor positive effects of corallivory. A study done by Goldberg (2020) aimed to investigate the hypothesis that corallivorous fish impair the ability of bleached corals to repair themselves. Multiple cages were set up, with in them either healthy non-bleached corals, and cages with either moderately bleached or very bleached corals to test this hypothesis. At the end of the study, the researchers had to conclude that no impairment of corallivorous fish was detected, rather, the corals had suffered more due to the use of these cage-equipment's.

3.3. Function of corallivorous fish

Apart from the positive or negative consequences of corallivorous feeding strategies on coral reefs, the fishes themselves fulfil other roles for the ecosystem as well. In this paragraph these other ecological functions are elaborated on, starting with the position of these fishes within the reefs food-web, then their capacity to control invasive species, and lastly the ability of these fish to spread beneficial materials and nutrients.

In figure 3 a simplified illustration of the coral reef food- chain is presented. When looking at this graph it becomes clear that the barracudas and sharks are on top, as top predators. They feed on the animals one trophic level below: the larger corallivores, herbivores and echinoderm-feeders, keeping their population sizes in check. Approximately 100 million sharks are caught and killed each year, and populations are rapidly declining (Worm *et al*., 2013). When animals at the top the food chain disappear, this can be felt many trophic levels lower, since each level is regulated by the organism in the level above. This is called the trophic cascade (Ames, 2019). The potential loss of these large top predators is thought to disrupt the balance of the number of corallivorous fish; when the top predators disappear, the second level now becomes the most dominant one. This might cause a temporary drastic increase in the number of corallivores due to the loss of predation pressure, but this only holds until no more coral is left to consume. This would propose a great threat for coral-reefs in the future (Lenihan *et al.*, 2011).

Other reef fishes are also caught by commercial and non- commercial fisheries, which might lead to the disappearance of key species. On the reef only surrounding Hawaii, 900.000 kilograms of fish is caught annually (McCoy, 2018). Furthermore, increased coral bleaching is also threatening corallivorous communities (Rice *et al.*, 2019). Corallivorous fish, like the Trigger fishes and Parrot fishes, feed on urchins and starfish, and in turn balance their population growth as well. Corallivorous fish can thus control population sizes of other species in the lower trophic levels.



▲ Figure 3: Tropic levels on coral reefs (International Institute for Rural Reconstruction. (n.d.)

The possible loss of these fish can have a large impact on coral communities. For example, the Crown-of-thorns starfish (*Acanthaster)* is one of the most invasive and coral destructive species known. Whilst eating coral polyps one animal can kill up to 6 square meters of coral a year (Mueller, Bos, Graf, & Gumanao, 2011). An individual with a body size larger than 40 centimetre can kill up to 60 square centimetres a day, as seen in research done on the species on The Great Barrier reef (Pratchett, 2001) where this animal is also actively managed by conservationists. There are not many species known that feed on these starfish due to their poisonous spines, but some facultative corallivores like the Triggerfish and Pufferfish, are known to prey on the juveniles (Thompson, 2020). The loss of these predatory fishes would lower the predation pressure on *Ancnthaster,* ultimately adding great additional predation pressure to the corals this starfish preys upon.

To test what would happen when larger bodied corallivores and herbivores fish would disappear, for a study on a coral reef in the Pacific Ocean these fishes were removed. Within weeks a drastic effect of the loss of them was noticed, not only did the behaviour of the prey fish change but the herbivory on algae decreased, causing more pressure on corals in the competition for light and space and the number of small benthic invertebrates decreased rapidly. This study gave some new insight into what can happen when the larger bodied fish, which are higher up in reef trophic levels, would disappear. (McCauley *et al.,* 2010). Graham, Nash and Kool (2011) were able to calculate species extinction vulnerability due to climate change, for which over the course of 9 years, 50.000 square meter of coral reef was inventoried. It was found that obligate corallivores are the most vulnerable group of reef fishes, and most prone to global extinction. These fish also have a low resilience, meaning that they are not able to adapt fast enough to their changing environment, risking the loss of all obligatory corallivorous fishes (Vinebrooke *et al.,* 2004*).* The facultative corallivores are the next group most vulnerable to extinction. They seem to have a higher diversity of response meaning that they are able to adapt better. This means the threat of climate change is not as acute for these fish, but lies further into the future. The roving grazers and scrapers including some excavators turned out to be the most vulnerable to overfishing rather than habitat loss. The specialistic wrasse's fishes were calculated to be the most vulnerable for extinction due to small populations, and small geographic range. Most of these species that have a high risk of extinction are the ones with small bodies. This would servery decrease biodiversity since diversity of reef fishes peaks in this range (Graham *et al.,* 2006).

One of the arguably biggest positive functions of corallivores, which has only been discovered this year in 2021, might be the transport of symbiotic algae in the faeces of corallivorous fish. Corals depend on these symbionts for their survival. In total, 80% of all corallivorous species have live symbiotic algae in their faeces which they discard all over the reef. Even in 30 percent of the non-corallivorous species faeces, live symbionts were found. The fish seem to export and excrete these symbionts all over the reef, making their role comparable to the function of bees on land. These symbiotic algae can be used by corals to enrich their tissues with new algae, and to help them recover after bleaching events. This innovation in understanding corallivores fish could alter the current prejudices of corallivorous being net negative for coral reefs. (Grupstra, Rabbitt, Howe-Kerr, & Correa, 2021)

Another, often overlooked, function of (all) fishes is the amount of nutrients they hold inside their bodies (Ma, 2016). Out of all reef animals, fish probably possess the largest portion. Researchers found that coral reefs with large quantities of fish, had corals with more nutrients inside their tissues; up to 50% more. This is because the pee of these fish contains a lot of nutrients, including phosphor and nitrogen, which are crucial elements for coral growth. Since reef fishes are still caught for human consumption, the total biomass of fish is shrinking, resulting in a decrease in the amount of nutrients available for the ecosystem (Allgeier *et al.,* 2020). Furthermore, the species present on coral reefs are often called a 'medicine treasure chest', since many medical breakthroughs have been made by examining species, tissues and chemicals from a variety of reef organisms. Losing them could also mean the loss of possible treatments for example cancer or Alzheimer's disease (Reef-world Foundation, 2021).

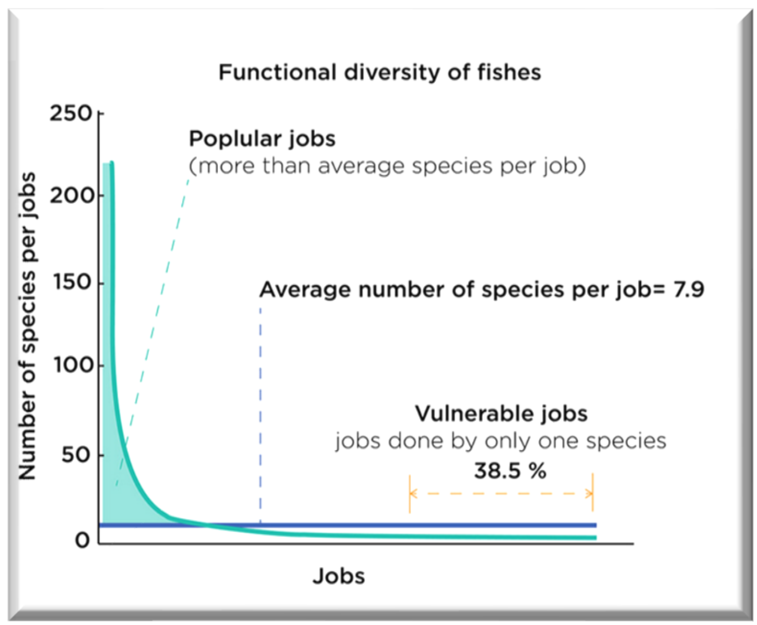
A disbalance in coral reef communities could cause serious other threat for humans too. The loss of them would imply a massive strain on the economics and resources. Over 35 million people who work in the fish-catching industry would lose their jobs and mankind would also have to deal with the loss of one fifth of all natural protein that is present in seafood. Healthy reefs also protect the coastlines because they form a barrier against large ocean waves, decreasing their impact with 97%. Estimated is that the construction of dikes with the same effect would cost more than 2.5 million per mile (1.6 kilometres) (Sharma & Reilly, 2018). Coral reefs generate a lot of tourism, and the reefs are estimated to have an economic value of $36 billion per year (Mapping Ocean Wealth, 2020).

Although the loss of healthy coral reefs and corallivorous fish would leave an impact rippling through all trophic levels, Cole *et al.* (2008) stated that the corallivores do not make up the majority of coral reef organisms, and thus add little to the energy pathways of the reefs, implying their absence would not be missed that much. However, more recent literature like the research of the forementioned Grupstra *et al.* (2021), which addressed the animals as the bees of the sea, seem to now argue otherwise.

3.4 Other organisms to fill the gap

In every ecosystem and niche, on land and in the seas, there are jobs to fulfil. Inherent ecological roles are performed by all present organisms. As presented in figure 4, most jobs have an average of 7.8 species who are able to fulfil it. Some jobs are very popular, having hundreds of species who are able to perform this. The loss of one of these species would mean that there are many others that can take its place. On coral reefs, this principle is the same, but here almost 40 percent of all coral-reef jobs, are performed by just one species only (Mouillot *et al.*, 2014). In this sub-chapter, these jobs for one-species-only will be elaborated on, as well as further investigate witch other species would be able to take over the role of corallivorous fish and what this would mean for coral, would these fish disappear.

Examples of 'single job' corallivorous species is the Green hump-headed parrotfish; the fish that can consume 5 tonnes of coral material per year. These fish remove dead corals and make room for new growth, it is the only animal who does this on such a large scale. The coral that is eaten by these fish is later excreted as the white sand that some tropic beaches partially exist out of. (AIDA, 2018) Sharks and humans are the only real predators of these largely bodied fish (Taylor, Hamilton, Almany, & Choat, 2018). Another example is the *Ctenochaetus striatus,* or striated surgeonfish. This animal is very important for the removal of sediment and rubble and can remove between 8 and 66 grams of it per day, often discarding it in other regions of the reef. This process showed to be beneficial for some specific algae communities, and creates new habitat, which is very valuable for many other species (Australian Academy of Science, 2020).



▲ Figure 4:
Jobs of coral-reef fishes
Source adapted from: Mouillot et al. (2014)

The loss of obligatory and facultative corallivorous would open these jobs on the coral reefs, meaning that a niche that was once regulated by the fish species is now available for others. Species that were once one trophic level below the corallivorous fish now do not have any predation pressure anymore nor do they have to share their resources. This would probably result in an increase of these invertebrates on the reefs (Graham *et al.,* 2011).

A species that might take over the role of a major corallivore, like the Green Hump head parrotfish, is the forementioned Crown of Thorns starfish. However, the difference between the corallivorous fish and this starfish is that it often causes guaranteed and permanent coral mortality. The animals digests coral tissue with certain intestine chemicals, leaving only the dead coral skeleton behind (Oceana, n.d). Some corallivorous fish are known to feed on this species of starfish and thereby regulating its population size. Would corallivorous fish disappear, this generalist species is likely to profit from its absence. The Giant triton snail (*Charonia tritonis*) is most likely to thrive from the rise of the Crown of Thorn population as well; these snails are one of the few animals that feed on the starfish (Australian Academy of Science, 2020).

There are more organisms with similar characteristics; the urchin *Eucidaris thouarsiiin* is able to consume large coral patches. This animal relies very heavily on live coral tissue. Some species of (partially) corallivorous reef fish, like the Wrasse's, Triggerfish and Pufferfish are known to also feed on this urchin. Also, the genus *Drupella,* which includes some obligatory corallivorous sea snails, feed on *Acropora* coral. Like the Crown of Thorn starfish, this animal can cause serious coral population declines (Cole *et al.,* 2008). Another species belonging to Annelida taxon, called the Bearded fireworm (*Hermodice carunculata*) is also a very common corallivore and they propose a serious threat to coral health. These animals are already labelled as a problematic species (Ladd, & Shantz, 2016). The larvae feed on plankton and algae, and due to coral cover decline, much more algae can be found. This would most likely increase the population size of these fireworms. The adult animal does not only consume large quantities of coral, it also 10-folds the chance for coral to fall ill to diseases that cause coral tissue loss (Grimes, 2020). Although most fish leave these fireworms alone due to their toxicity, it was also discovered that some facultative corallivorous feed on them, balancing their population growth (Ladd, & Shantz, 2016). Without these predatory fish, an increase in these Annelida is expected.

Most of these invertebrate species are generalists, meaning that they are less specific in food choice and can feed on most corals, causing a future threat to remaining corals. Some species of sea snails are known to feed on 26 different coral species without showing any distinct preference. In total there are 48 corallivorous invertebrate's species (Rotjan & Lewis, 2008).

Not all corallivorous species that would rise during the fall of corallivores fish are negatively impacting coral reefs; Arthropoda's, like the Crustacean *Trapezia* form a large taxon of species that are beneficial to coral reefs. These animals are very likely to step in once animals from the higher trophic levels disappear because many species, for example the triggerfishes, feed on these crabs. The crabs are beneficial for corals, removing dead coral and cleaning dirt of their tissues. It was reported that these crabs defend their preferred coral prey. Coral present in their territory was also recorded to survive better when under attack of urchins. When crabs like these are removed, 40 – 60 % of the coral dies due to predation, and research also showed that corals under the protection of crabs healed better after damage of bleaching. (Stewart, Holbrook, Schmitt, & Brooks, 2006)

It is also likely that when corallivorous fish disappear, more herbivorous animals of lower trophic levels, will appear. Algae and corals have always been competing for resources, and with the loss of corallivorous and herbivorous fish it becomes likely that algae start to take over. This would mean more food supply for the herbivorous organisms (Wilson *et al.,* 2006). Giant clams (*Tridacna gigas)* filter feed on algae and absorb organic matter from the ocean waters, keeping it clean. In present time, these species help in keeping the reefs clean and healthy while their population sizes are balanced by food availability and predation. When corallivorous fish disappear, lots of rubble, debris, algae, and organic matter is no longer removed. This species is probably one of them that will profit of this, filling in the gab (De Goeij *et al.,* 2013). Due to its sessile lifeform however, it cannot clean algae of corals, like the fish would and thus not provide much for coral health.

Although there are species of corallivorous and even herbivores that will step in the gap left by the disappearance of corallivorous fish, the alternative species do often not fulfil the same functions. Concluding that their dietary preferences might be similar, but the function they further fulfil for the ecosystem is not. This means that when corallivorous fish would become extinct, the other mentioned organisms would only cause further damage to coral reefs, without the counterbalance of the positive effects.

Chapter 4. Discussion

The discussion contains two sub-sections, the first part being a reflection on this research itself and secondly, a discussion on how the sub-questions have contributed to finalizing the conclusive answer to the main question.

4.1 Reflection on the study

With research like this, it is always important to keep an eye out for new publishments and research. In most oceans, along most coral reefs, continuous research is carried out and new questions will arise depending on local or global events. Efforts were made to use the latest data for this literature review. Nevertheless, it can already be seen that there are contradictions between the data of about 10 years old, with those of after 2020. In the data of the past two years, it became much more apparent that coral-eating fish can have an important, even bee-like, function in relation to coral. While the slightly older literature still often talks about these animals being of only moderate importance, sometimes even being more destructive than beneficial. Further research needs to further investigate this trend.

It is also good to keep in mind that humans have a tremendous impact on the oceans, which is not mentioned in this literature study. Pollution, acidification, (illegal) fishing, and many other factors determine the future of the oceans and thus the prospects of coral reef communities (Zaneveld *et al.,* 2016). Every year, 2.7 trillion fish are caught from the oceans, which is equivalent to 400 million pounds of fish every day. Over 40% of the revenue is caught as bycatch, which are often discarded, making them unnecessary casualties (Keledjian *et al.,* 2014) In total, 46 percent of plastic pollution in the oceans is related to the fishing industry, of which the majority are fishing nets (Parker, 2021). These nets can reach enormous sizes and damage the ocean floor. Nets can cause coral damage by getting tangled in it (Plastic Soup Foundation, 2020). The rate at which the oceans are overfished now, will leave them empty by the year of 2048 (Worm *et al.,* 2006). It is even said that fish that are involved in coral reef ecosystems are under greater direct threat of fishing, than of climate change (Graham *et al.,* 2011). The global goal for 2030 is to highly protect 30% of the ocean. Although some politicians claim that this goal is halfway reached, experts have calculated that only 2.2% of the oceans are under well-regulated and beneficial protection (Gibbens, 2021). If humans are not able to start protecting the oceans, all problems surrounding coral and change in community composition will become obsolete.

Not only fishing poses a threat, but the aquarium trade also has a big influence. Some reef fish, and even corals, are illegally taken away from the system. Special species can be sold for large amounts of money. For some species, like the golden pufferfish, it is known that their population declined due to the aquarium trade. (Shao *et al*., 2014)

Tourism, although economically beneficial, is also a threatening for coral reef health. Divers can cause coral damage, and people take pieces of coral or shells with them as relics. Very shallow corals that are at risk of trampling; they can suffer up to 100% mortality at the hands of tourism (Friedlander *et al.,* 2005*).* Damage by anchoring in reefs, especially in developing countries with less reef protection, can cause a repeatedly damaging process (Wilkinson, 2004). Even small things, like the type of sunscreen one is wearing whilst swimming, can also disrupt coral microbe balance (Zachos & Rosen, 2021).

Furthermore, after reading this research another question might arise; what will happen to these coral reef communities if coral abundance and diversity disappears before the fish do? The rate at which coral declines might start to outpace the rate at which corallivorous fish populations decline. There are already trends visible in which generalist species become much more abundant and the specialized species are beginning to disappear (Rice *et al.,* 2019; Clavel *et al.,* 2011). In case of the often highly specialised corallivorous fish species, this will mean the end of a taxa.

Graham *et al* (2011) was able to make predictions on which fish species are most sensitive to extinction due to global warming, concluding that the obligatory coral-feeders are under the biggest threat. Nonetheless, this is a prediction, which only considered the impacts of global warming. It did not include factors such as global- or local water pollution, intensification of the weather, overfishing or nutrification which are also important to fully chart the sensitivity of coral reefs. These other stressors can also have an effect on the coral algae competition, and disrupt the balance in the coral's protective microbes, which might expose corals to diseases and cause coral death (Zaneveld *et al., 2016).* Some studies, which do include such parameters, reveal that 62% of present fish species declined in abundance within 3 years of the disturbance and in most studies, these disturbances caused over 10% coral cover decline (Wilson *et al.,* 2006).

This literature review does not discuss in depth which other organisms depend on coral, and feed on it. For example, there are small organisms, the micro- and macro bores, which are collectively responsible for the production of 1.1 million school buses of white sand from coral. These organisms can also leave the coral weak and damaged (Tribollet & Payri, 2001). However, micro- and macro bores are key species, since they can influence the population sizes of larger invertebrates, like coral eating starfishes or urchins (Dulvy, Sadovy, & Reynold, 2003). Neither are any specifications made between corallivorous fish' lifecycle. Some of them have their diet focused on coral for their interior lives, but others only consume coral in a later, more grown stage. Follow up research must take such topics into consideration.

In the literature it was addressed multiple times how the herbivorous species are crucial to long term survival of coral reefs, since they clean the reefs and prevent algae from overgrowing (Glynn & Manzello, 2015; Home, 2018). Many of the corallivorous species however, are partially also herbivorous, and many herbivorous species are also corallivorous. Future species-specific research is recommended. It is important to learn about the exact roles that the different species play within the ecosystem. This is necessary not only to know which animals fulfil indispensably important jobs on the reef, but also to predict which species are vulnerable to the impending change. More knowledge about the species and their roles can also help in planning species-specific protection, population control, or to calculate the amount of permitted corallivory on coral reefs. However, this should be investigated with necessary caution, from local as well as global standpoints since issues and communities differ around the globe.

Of over the six thousand coral species that exists, only a small portion of it is predated on (National Geographic Society, 2019). This is probably due to the underrepresentation of some coral species in different oceans, implying that preferred coral prey are often the ones that are largely represented. This also indicates that many species of coral are never preyed upon by corallivores, meaning that these corals never experience any negative effects of them. It is interesting to further investigate whether these once untouched corals will become prey, now that preferred coral cover is often declining.

It also became clear that many species of corallivores only feed on the fast-growing coral species, managing their abundance and preventing overgrowth. The fact that they feed on these fast-growing corals might not be just to prevent overgrowth, but can be an example of the arms-race between prey and predators, resulting in this adaption by corals to keep up with predation pressure.

Literature used in this study should not be older than 20 years. It was not always easy to find literature that met these requirements, but after some additional searching, similar studies from more recent years were always found. For a subsequent study, the approach would not differ from that used for this literature review. However, in a follow-up study, the subject would be further limited to prevent unexpected extensions. This would make it easier to collect data and to steer the subject into a certain direction, which was challenging in some areas of this study. Nonetheless, an attempt has been made to answer all the sub- and main questions as clearly as possible, and in the best possible way, which is why the end-product stands for itself.

Now that multiple aspects of this research have been critically discussed, in the next sub-chapter, the sub- and main questions will be elaborated on.

4.2 Discussion on the main research question

The aim of this literature study was to answer the following main question; what are the consequences for coral reefs if corallivorous fish become extinct? The numerous sub-questions served as a guide to find the necessary information to do so. In this subchapter, per sub-question is explained how the information contributed to answering the main question.

The first sub question - what are the different corallivorous feeding strategies - contributed to this process by giving insight into what kinds of different methods are used to feed on coral. By doing this it became clear there are many different ways facultative and obligatory corallivores feed, all impacting coral differently. Also, without this information no clear answer can be given to the second sub-question, namely: how do the different feeding strategies impact coral? This question allowed further investigation into the negative and damaging aspects of these feeding modes, but also mentioned the more positive and functional properties of it for coral reefs. Considering these negative effects, which can be quite extensive, it might be best for the already declining coral reefs, if corallivorous fish would go extinct. This would mean no further damage will be implied by these fishes, in particular the excavators and scrapers, which cause the most structural damage. However, other research also sheds light on the more positive effects of corallivorous fish. By eating corals, these fish do not only keep dominant coral species' populations in check, they also help in cleaning the reefs and building new and more diverse habitat. Furthermore, fish species that are less obligatory, and have a more diverse diet also often keep competing algae growth down.

The third sub question - what function do corallivorous fish have, aside from their feeding-habits, in relation to the ecosystem – allows for a more detailed description on what function the fishes fulfil when looking at the bigger picture; the whole ecosystem. In the food web only humans and top predators, like sharks and barracudas, are above the corallivorous fishes. They fulfil a role in the ecosystem, simply by being prey species for these top predators. Also, the more facultative fishes themselves, sometimes feed on invertebrates and other reef organisms, balancing possibly harmful invasive species populations. Furthermore, more recent research also showed that the corallivorous fishes spread live symbionts over the reef that can be used by corals for their tissues and even assist in the healing process after bleaching. Especially now that coral bleaching has been going so quickly in recent years, the spreading of symbionts might be crucial for the preservation and possible recovery of coral reefs in the future. More research on the importance of symbiont spreading for coral reefs, is one of the most urgent next steps.

The last sub-question - are there other organisms that can take over the function of corallivorous fish, would they become extinct – proved that there are species which have similar feeding modes when compared to the corallivorous fish, but almost no species fulfil the exact same function. This is due to the fact that 40 percent of the reefs 'jobs' are fulfilled by one species only. Knowing this, it also becomes clear that the coral-eating fish cannot simply die out, expecting all tasks to be taken over by other organisms. There are no species that will function on the same scale for the ecosystem. The trophic lower species that will take over might me even more harmful to coral, without providing the same amount of beneficial counterbalancing positives. This proposes a large threat for remaining coral reefs in the future.

Ultimately this leads to the following main question: What are the consequences for coral reefs if corallivorous fish become extinct? Now, it can be concluded that if corallivorous fish would go extinct, not only will algae cultures take the upper hand so will some harmful trophic lower species. Furthermore, the positive consequences of coral-eating fish, such as the spreading of nutrients, symbionts or further necessary reef maintenance, will be lost. It is not yet decided in the literature whether corallivorous fish are predominantly net negative or positive. For a long time, they were viewed as damaging and thus negative, but most recent studies seem to argue otherwise saying that corallivorous fish play an important role in nutrient and algae distribution which corals need for growing, survival and even help in the recovery of bleaching. No matter the outcome on whether corallivorous fish are beneficial for coral health, the positive effects of the facultative corallivorous fish outweighs the negative effects of corallivorous behaviour. These dietary variated fish have an important cleaning and maintenance function on the reefs, which would cause large coral declines when no longer implemented. Whilst these fish do, to some extent, damage corals, the corals benefit largely from a clean reef, prevention of algae overgrowth and keeping dominant coral- and organism populations down to insure diversity.

Chapter 5. Conclusion

This research investigates the impact of corallivorous fish, and how their possible extinction would impact coral reefs and the communities. In this chapter the multiple sub-questions and main questions are answered.

5.1 What are the different corallivorous feeding strategies?

There are six different corallivorous strategies that fish can use, partially overlapping with the herbivorous methods. There are excavators, scrapers, browsers, grazers, mucus-feeders and bioeroders. All mechanism have their own specific impact on coral prey.

5.2 How do these different feeding strategies impact coral?

There are negative and positive effects present when coral is under corallivorous pressure. Often growth and reproduction are limited, and corallivorous fish can also deplete energy that is needed for wound healing, recovery from bleaching, or fighting diseases. Furthermore, corallivorous fish might transmit coral diseases due to direct oral contact with different corals.

There are also some positive effects visible that come out of corallivory. Some species only feed on very abundant, fast growing corals. This restricts their growth and allows for more coral diversity. Also, many facultative corallivores feed on algae, which prevents overgrowth and limits light and resource competition.

5.3 What function do corallivorous fish have, aside from their feeding-habits, in relation to the ecosystem?

Corallivorous fish fulfil many different functions. They form a large part of the food chain, and their excrement's serve as nutrient- and symbiont enrichment which is crucial for healthy coral reefs. The presence of some corallivores fish keeps overgrowing corals algae in check, maintaining the balance between them. Some facultative corallivorous species like the trigger- and pufferfishes also maintain a healthy number of generalist corallivorous invertebrates like starfish and urchins, preventing them from becoming dominant on the reef. Healthy coral reefs are also very important for mankind as a food source, providing one fifth of all available protein. Economically, colourful fish and reefs attract tourism which generates money and employs many workers. Often the reefs are also consulted when it comes to human diseases. Some species of fish, coral or other reef organism contain special chemicals or substances of which medicines can be manufactured.

5.4 Are there other organisms that can take over the function of corallivorous fish, would they become extinct?

There are other organism with similar feeding habits to corallivorous fish, like the Crown of Thorns, the urchin *Eucidaris thouarsiiin* or the Bearded fireworm, but none have the exact same function. Although there are other corallivorous species that eat corals, they do not shape habitat and spread nutrients like the fish do. The most likely consequence is an increase in reef generalist of lower trophic levels. This are either vertebrates, some crab species or annelids. These species will feed on a larger variety of corals, since they have no distinct coral prey preference. As described, some reef-niches are only managed by a few, if not only one, species. Meaning that if some of these unique species would go extinct, no other animal is able to replace it. The loss of these fishes would re-shape the whole community.

5.5 Main research question: What are the consequences for coral reefs if corallivorous fish become extinct?

Losing corallivorous fishes would mean the loss of the negative effects, but also of the positive effects of these animals. The positive effect of coral-maintenance outweighs the negative impact of corallivory. This leads to the conclusion that the loss of the facultative corallivores or more dietary variated fishes, will cause the most coral declines. Algae is expected to overgrow and dominant species would take over, decreasing diversity. Facultative corallivores are often the browsers and the grazers, but also the bioeroders. Most are either butterfly fishes, damselfishes, rabbitfishes, puffer- and triggerfishes or some species of parrotfish.

Increased knowledge on the different corallivorous feeding strategies and ecological functions seems to slowly take a turn from the thought that these animals are a net negative influence, to acknowledging that their presence on the reefs is most important to coral reefs and their trophic cascade for which further research is recommended.

Chapter 6. References

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