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# Corals as Food: What Factors Dictate Corallivore Foraging Behavior?

Ashley Hannigan
*Nova Southeastern University*

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# Thesis of
# Ashley Hannigan

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## Master of Science
## Marine Science

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Approved:
Thesis Committee

Committee Chair: Lauren Nadler, Ph.D

Committee Member: Rosanna Milligan, Ph.D

Committee Member: David Gilliam, Ph.D

NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF ARTS AND SCIENCES

# Corals As Food: What Factors Dictate Corallivore Foraging Behavior?

By

Ashley Hannigan

Submitted to the Faculty of
Halmos College of Arts and Sciences
in partial fulfillment of the requirements for
the degree of Master of Science with a specialty in:

Marine Science
Concentration in Marine Biology
Concentration in Coastal Zone Management

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## Abstract

Corallivory is a common foraging strategy used by many fishes (e.g., parrotfish, butterflyfish) and invertebrates (e.g., Gastropoda, Asteroidea) on coral reefs and can be defined as the act of consuming coral mucus, tissue, and/or skeleton. While studies often focus on corallivorous fishes, we still have a limited understanding of corallivore foraging preferences even in these more well-studied taxa. To date, broad conclusions on corallivore selective foraging have been limited, as most studies focus on particular corals or corallivores in specific geographic locations. Using a meta-analytical approach, this project aims to study coral-corallivore interactions to identify any preferred characteristics that promote selective foraging. Using generalized linear models examining data from the published literature, we examined coral predation by butterflyfish (through bite rate using data on in situ measurements of fish behavior) and parrotfish (using percent predation on coral colonies through grazing scars). These analyses showed that butterflyfish forage selectively based on coral morphology, with a particular preference for branching morphology. Parrotfish were selective for the interaction of the factors coral family and coral size, measured as surface area in centimeters-squared. These analyses indicate that within complex ecosystems like coral reefs, a variety of factors are likely to affect coral-corallivore interactions and future scientific studies should delve into more diverse factors (e.g., fish behavior and territories, depth, coral abundance, presence/absence of predators, predated coral species, and predation on both established and transplanted corals) to draw broader conclusions about corallivore predation.

**Keywords***: Parrotfish, Butterflyfish, Corallivore, Prey selectivity, Meta-analysis*

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## Introduction

On coral reefs, corallivory is a common foraging strategy, defined as the act of attacking coral mucus, tissue, and/or skeleton for its nutritional value (Rice et al., 2019). Many reef fishes (e.g., parrotfish, damselfish, butterflyfish, surgeonfish, triggerfish) and invertebrates (e.g., gastropods, asteroids) rely on corals for at least a portion of their diet (Bonaldo et al., 2012; Cole et al., 2008; Morton, Blackmore, & Kwok, 2002; Shaver et al., 2020; Smith et al., 2021). There are over 160 known corallivores from 11 families of fishes and five invertebrate phyla and corallivory has been documented in 28 genera of Scleractinian or hard coral (Cole et al., 2008; Rotjan & Lewis). Consuming corals by parrotfish and butterflyfish can be broadly divided into two categories: obligate and facultative. Obligate corallivores consist of species that rely on coral for greater than 80% of their diet (Bonaldo & Rotjan, 2018; Cole et al., 2008). Approximately a third of all corallivores are obligate, feeding nearly exclusively on a range of Scleractinian corals (Cole et al., 2008). Facultative corallivores vary in how much of their diet is composed of coral, ranging from just 1% to more than half of their diet (Cole et al., 2008).

Corallivores use predator-specific feeding strategies to gain nutrition from corals. Many gastropods insert a tube-like buccal mass into the coral polyp, allowing them to use their radula to consume the tissue and mucus (Figure 1; Kaullysing et al., 2019; Kohn, 1983). Invertebrates in the class Asteroidea, like the crown-of-thorns starfish (*Acanthaster planci*), feed by extruding their stomach over the surface of the coral and digesting coral polyps via enzymatic breakdown (Kamya et al., 2018). Butterflyfishes predominately remove individual coral polyps using notably short, strong jaws with a few rows of teeth that allow them to excavate, scrape, or bite off polyps using their forcep-like mouths (Konow & Ferry, 2014). Of all of the corallivores, parrotfishes generally create the most damage to a coral colony, through the removal of large areas of coral tissue and skeleton that leave behind visible grazing scars (Figure 2;Bonaldo et al., 2012) Parrotfish are both herbivores (Burkepile & Hay, 2010; Mumby, 2006) and corallivores (Bonaldo & Bellwood, 2010; Rotjan & Lewis, 2005), both are key components for maintaining a healthy equilibrium between live coral and algal growth within a shallow coral reef. Parrotfish coral foraging behavior has two common modes: scraping (removing a thin layer of skeleton while scraping live tissue from the coral's surface through spot biting in which bites are taken across different spots in the coral colony, Figure 2a) or excavating (removing pieces of skeleton and tissue through focused biting consumes substantial portions of the coral colony, Figure 2b) (Bonaldo et al., 2012; Burkepile, 2012; Rice et al., 2019).

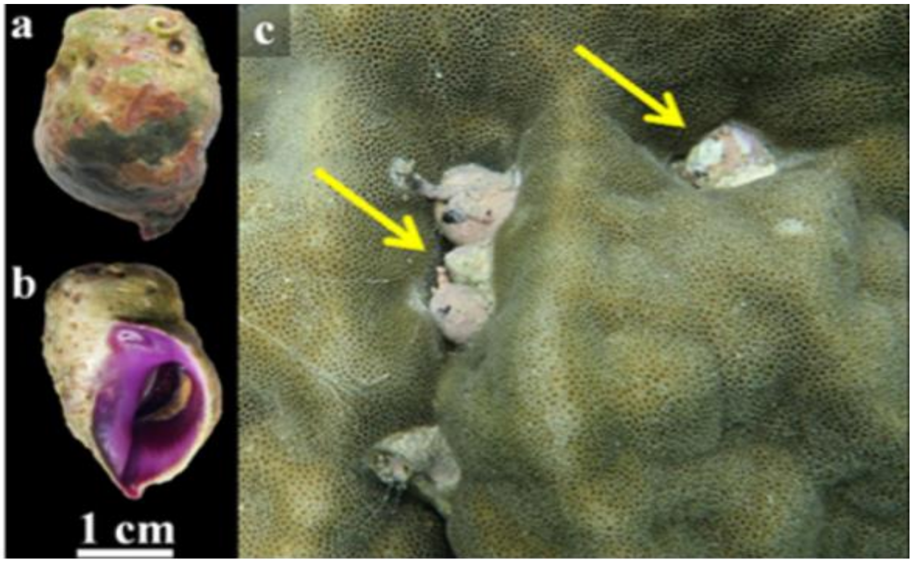


*Figure 1:* This sea snail species *Coralliophila* sp., a common corallivorous gastropod in the Western Atlantic and Caribbean. Here, the different sides of snails are depicted, including the **a)** dorsal and **b)** ventral side of the snail. In **c),** *Coralliophila* sp. is feeding on the coral *Porites lutea* using its radula. Figure from Kaullysing et al. (2019).

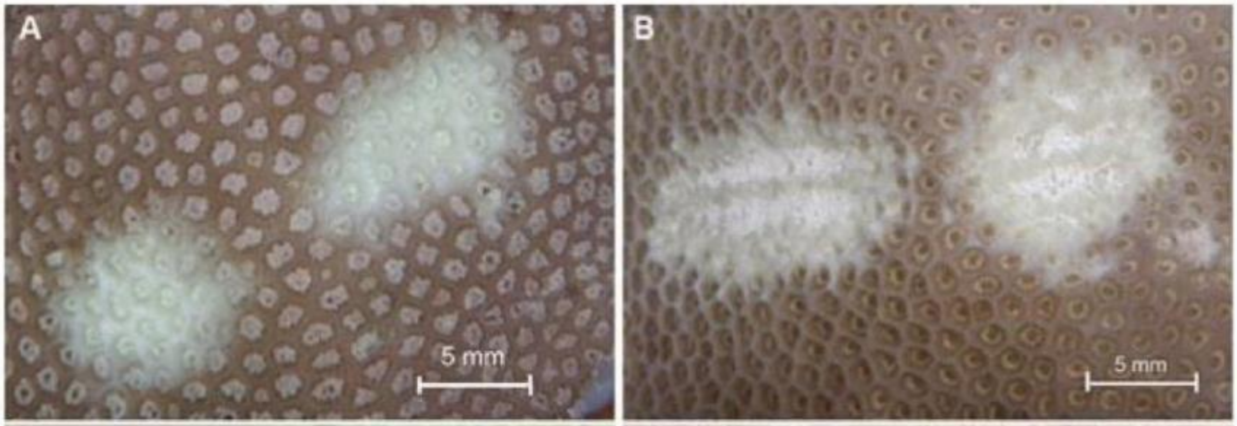


*Figure 2:* Photographs of the two common parrotfish feeding scars, including A) scraping scars and B) excavating scars. Figure from Bonaldo and Rotjan (2018).

Corallivores may target particular corals or coral tissues depending on their individual nutritional needs and the coral colony's accessibility, based on the coral's morphology, abundance, size, depth, or location. During foraging, corallivores may target mucus that is produced by corals to trap prey and for defense (Meikle et al., 1988). Mucus provides corallivores with a source of carbohydrates for energy (Wild et al., 2010). Conversely, coral polyp tissue is high in protein (Houlbrã¨Que & Ferrier-Pagã¨S, 2009) and lipids (Al-Lihaibi et al., 1998) that provide nutritional value to potential coral predators. The nutritional value and accessibility of coral prey can vary depending on the coral colonies' morphology, which is typically divided into seven categories (Figure 3): brain (characterized by broad ridges and valleys), branching (growing with a branch-like skeleton consisting of primary and secondary branches), massive (mound shaped), encrusting (adhering to a substrate), columnar (forming columns or pillars consisting of primary branches), laminar (growing in a leaf-like shape), and free-living (taking on a fleshy texture due to water absorbed by the underlying skeleton).

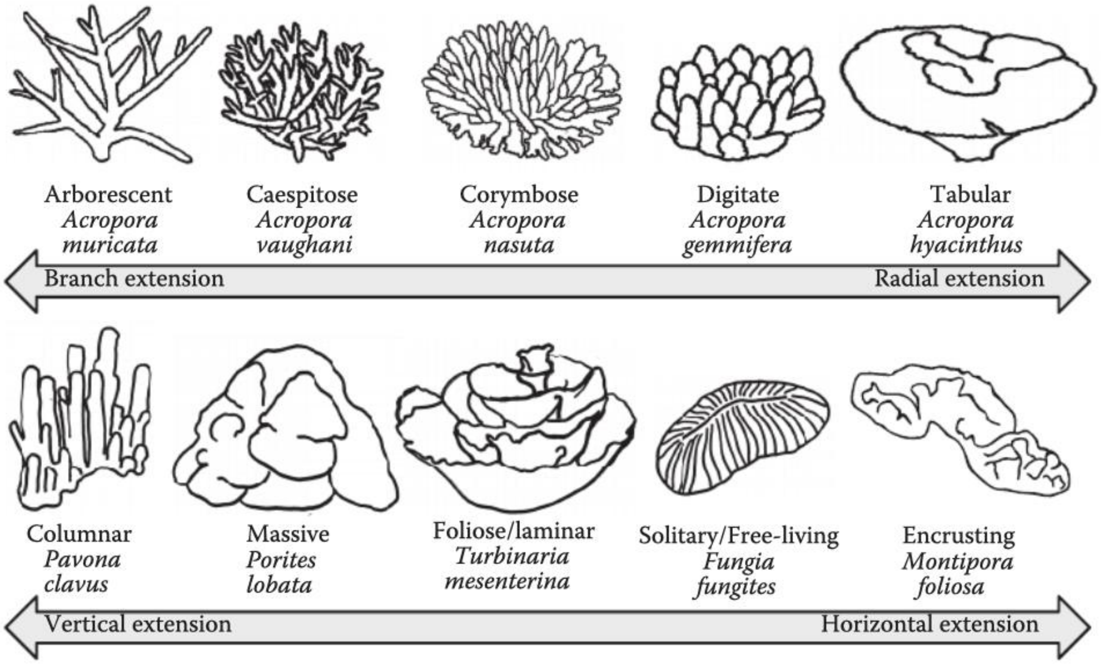


*Figure 3:* This figure illustrates the seven different growth form morphologies of scleractinian corals, arranged by their major growth axis. Arborescent, caespitose, corymbose, and digitate are examples of branching sub-morphologies and were thus considered branching within this study. The top portion of this figure depicts corals with the longest branch extension (arborescent but referred to as branching in this study) to the left and the largest radial extension (tabular, referred to as plate in this study) to the right. The bottom portion of this photo illustrates corals with the largest vertical extension (columnar) to the left, and the largest horizontal extension (encrusting) to the right. This picture was taken from Pratchett et al (2015).

Predatory corallivores with different feeding mechanisms may non-randomly target corals with particular morphologies or characteristics. Coral colony size likely plays a role. Studies indicate that smaller coral colonies may experience a greater density of corallivore scars, which can increase mortality rates by suffering relatively worse damage when compared to the same levels of predation on larger coral colonies (Huertas et al., 2021; Rivas et al., 2021). Corallivores may also detect the nutritional value of the coral colony and shift their foraging preferences accordingly, with coral genotypes associated with higher lipid and protein content exhibiting higher predation pressure and mortality than those with lower nutritional value (Rivas et al., 2021).

However, research on this topic remains limited. Thus, we know little about the factors driving intra- and interspecific differences in corallivory and whether these trends vary globally on shallow, tropical coral reefs.

## Historical Basis of The Research Field

The first known records of corallivory were made in 1845 by Charles Darwin, who documented corallivory as a foraging strategy by fishes on coral reefs, and further discovered that two species of parrotfishes fed exclusively on coral (Darwin, 1845). At this time, Darwin hypothesized that corallivory may negatively impact coral growth (Darwin, 1845). Parrotfishes were the only reef fishes thought to use this feeding strategy until the late 20th century, when direct observations of coral feeding by triggerfishes, pufferfishes, butterflyfishes, crown-of-thorns starfish, and wrasses were recorded (Neudecker, 1979; Randall, 1974). Robertson (1970) reported that several species of fish and invertebrates fed either facultatively or obligately on living Scleractinian coral tissues. However, at that time, little was known about the importance of coral predation on broader scale reef processes.

Specialized studies about corallivores and their foraging behavior were uncommon until around 20 years ago. When the first instance of coral mortality was recorded following repeated, methodical biting by the stoplight parrotfish, *Sparisoma viride* (Bruckner & Bruckner, 1998). As parrotfish leave behind recognizable predation scars following bites, corallivory by parrotfish could be documented with ease, even without direct observations of bites. However, other corallivores, like butterflyfishes (Family: Chaetodontidae) and gastropods (Family: Muricidae), do not cause such obvious scarring on coral tissue. Of all corallivores, butterflyfishes have the highest proportion of corallivorous species (over 50%), including both obligate and facultative corallivorous species as previously defined in the Introduction section of this paper (Cox, 2013; Hoeksema et al., 2013). *Coralliophila* spp. and *Drupella* spp. marine gastropods, in contrast, are exclusively obligate corallivores, and have been observed feeding on several live coral species (Ott, 1972). Unlike parrotfish and butterflyfish, these invertebrate corallivores are generally slow moving and exhibit a lower feeding rate (Ott, 1972). It is more difficult to analyze gastropod coral feeding behavior in situ on a reef than corallivorous fishes. By the early 2000s, studies on corallivory shifted focus away from localized impacts on individual corals to their functional role in coral reef community dynamics. Further, studies are beginning to focus on the mechanisms that drive corallivore foraging, and whether this is a random or selective process (Baums et al., 2003; Burkepile et al., 2019; Chandler et al., 2016; Graham et al., 2009; Rotjan & Lewis, 2008)

## Existing Evidence in the Research Field

Corallivores fill an important ecological niche within coral reef communities and maintain or influence algal dynamics and reef structure. Coral predation may have positive impacts on a reef system's health and function (Enochs & Glynn, 2017), aiding in recovery from bleaching (if bleached tissue and/or skeleton is consumed), enhancing coral reproduction (through exposing coral fragments to wave action that enhances coral larval dispersal), and forming a trophic pathway that supports diverse species (Enochs & Glynn, 2017). Alternatively, corallivory can have devastating impacts on coral reefs if corallivore populations grow unfettered, such as coral tissue damage and mortality, slow healing of grazing scars, and colony mortality (Enochs & Glynn, 2017; Rotjan & Lewis, 2008).

All corallivorous fishes are diurnal feeders, thus allowing for corallivory to be documented via direct observation of grazing or before-and-after photographs of corals  (Cole et al., 2008).

SCUBA divers or snorkelers can observe coral predation directly, a method commonly used for butterflyfish that leave behind minimal evidence of predation (Alwany et al., 2003; Brooker et al., 2013b; Johnston & Miller, 2007; Ott, 1972; Slattery & Gochfeld, 2016). For corallivore taxa like parrotfish that create visible scars, photographs can provide accurate and quantitative evidence of the coral that was preyed upon (Bonaldo & Bellwood, 2010; Huertas et al., 2021). Parrotfish corallivory exhibits much intra- and inter-specific variability, with feeding rates, bite area, and bite depth varying among parrotfish species, life phase, and body size (Bonaldo et al., 2014).

Compared to corallivorous fishes, few studies describing direct observations of gastropod corallivory have been published. This gap in the literature could be due to the nocturnal foraging behavior of corallivorous gastropods, which makes them difficult to detect for direct observations of grazing, and scars are typically minimal, so not visible through before-and-after photographs. The studies to date typically collect both the gastropod and live coral species so that foraging can be monitored and quantified using aquarium experiments (Morton, Blackmore, & Kwok, 2002). Butterflyfish predation can be recorded from direct observation, but because their jaws do not create visible scars like parrotfish, gut content analysis is another technique to identify coral consumption (Madduppa et al., 2014) and can aid in distinguishing the specific types of coral consumed by obligate corallivorous butterflyfishes in the absence of direct observations through molecular analyses (Nagelkerken et al., 2009). Using this type of analysis, Madduppa et al (2014) identified up to nine types of coral nematocysts (coral’s stinging cells) in the gut of the eight-banded butterflyfish (*Chaetodon octofasciatus*), suggesting corallivory on a wide range of coral species.

Corallivore predation foraging theories suggest that prey (i.e., coral colonies) selection by corallivores should occur based on factors like morphology, nutritional value, and availability to provide a maximal energy return (Brooker et al., 2013a). Coral morphology may be an influential factor in corallivore foraging behavior and morphological preferences may vary among corallivore taxa. For example, the butterflyfish *Chaetodon multicinctus* preferentially forages on the massive *Porites lobata* over the branching *P. compressa,* potentially because the flatter surface of the massive coral morphology is easier to access and bite (Tricas, 1989). Similarly, off Mauritius Island, while branching corals are the most abundant available morphotype, the gastropod genus *Coralliophila* preferred to prey on the less common massive *Porites* spp., by attaching itself firmly on the coral surface (Figure 1; Kaullysing et al., 2019). Corallivores may also target prey based on the coral colony's biochemical profile or nutrient availability (Brooker et al., 2013b; Rotjan & Lewis, 2005; Tricas, 1989). For example, butterflyfish foraging behavior was investigated using direct observations of the number of bites on coral colonies, and found a correlation between number of corallivore bites and coral colony caloric density, determined by microbomb calorimetry (Tricas, 1989). *Chaetodon multicinctus* (pebbled butterflyfish) foraged with the highest number of bites on *P. lobata*, the prey with the highest coral cover, second highest caloric density and energy gain, or calories per bite, over other species and morphologies (Tricas, 1989). Further, when morphology was masked by paired fragments placed in feeder tubes, pooled feeding data revealed the pebbled butterflyfish did not selectively feed in the expected proportions among *Porites compressa* and *Porites lobata* compared to when morphologies were not masked, but *Pocillopora meandrina* was still preferred over *Porites lobata* when morphologies were masked. Thus, hypothesizing that *Pocillopora meandrina* was preferred as it had the highest energy content with a mean caloric density 16% higher than *Porites* (Tricas, 1989). Macronutrient concentrations can also vary seasonally, potentially influencing corallivore foraging preferences. Massive *Porites* spp., for example, exhibit higher frequencies of parrotfish excavating and feeding scars in Orpheus

Island during the coral spawning season in Australia, November to January, but no seasonal variation of predation scars on Lizard Island (Bonaldo et al., 2012). Overall, excavating scars were more abundant in October than April, the two studied months, which may be related to higher nutritional quality of coral colonies in October (Bonaldo et al., 2012).

Corallivores may prey on corals in a range of conditions, from relatively healthy corals with no signs of prior corallivore lesions to corals exhibiting signs of disease and corallivore scars (Bruckner & Bruckner, 2016). Injured coral tissues release excess mucus to aid in healing that could act as a feedback loop, attracting more corallivore predation (Bright et al., 2015; Rivera-Ortega & Thomé, 2018). This type of corallivore feeding is particular common in corallivorous gastropods (including *Drupella* and *Coralliophila* spp.), and is termed "feeding-attractant activity" (Bright et al., 2015; Hay, 2009; Kita et al., 2005; Morton, Blackmore, & Kowk, 2002) could also be attracted to coral by auditory cues. For example, butterflyfish may use auditory cues from other corallivores' foraging, including foraging durations, frequencies, and intensities, as an indication of the coral resources' nutritional potential and location (Tricas & Webb, 2016).

As coral reefs globally are rapidly declining, recent studies on corallivory have shifted towards understanding how corallivory may change under projected future conditions and how corallivores impact restoration efforts on degraded reefs. Different anthropogenic stressors, such as overfishing, nutrient pollution, and sedimentation can cause an imbalance in the associated coral-fish community, such as increased macroalgal growth within coral colonies (Rice et al., 2019 2019). Coral transplantation, outplanting, and micro-fragmentation involves collecting and then sectioning live coral, with sections then mounted on ceramic plugs or discs and placed on a degraded reef to promote recovery (Koval et al., 2020; Page et al., 2018; Rivas et al., 2021). These corals are commonly targeted by corallivores before they can establish (Koval et al., 2020). This intense corallivore grazing often limits the success of these restoration efforts, removing many fragments entirely or causing high tissue mortality on remaining fragments (Koval et al., 2020). Predator-exclusion cages around outplanted corals have been unsuccessful, as intense corallivore pressure resumes shortly after the cage is removed (Rivas et al., 2021). A greater understanding of corallivore foraging preferences and the sensory cues driving selective predation would be invaluable to devise strategies to protect coral outplants until they are established within a coral reef habitat.

## Knowledge Gaps

While most studies historically have focused on evidence for corallivory, few studies have examined the mechanisms driving intra- and inter-specific variation in the foraging preferences of corallivores in tropical, shallow reefs. Parrotfishes, an important group that are found on coral reefs around the world, partake in both corallivorous and herbivorous feeding strategies that are species specific (Bonaldo & Rotjan, 2018). Herbivorous and corallivorous foraging have a delicate balance on a coral reef, but the factors that cause a shift towards detrimental corallivory rather than herbivory on coral reefs remains poorly understood (Kavousi et al., 2020; Mumby, 2009; Rotjan & Lewis, 2008). Furthermore, literature on corallivory is heavily biased towards butterflyfishes, another diverse group of corallivores with a global geographic distribution, accounting for about 75% of publications on corallivory (Cole et al., 2008). This bias could be due to, in part, to the fact that corallivory represents  a minor feeding mode (<5%) in most other families of corallivore (e.g., Tetraodontidae, Balisidae, Scaridae, Labridae) (Cole et al., 2008). The butterflyfish family, Chaetodontidae, is the only one in which corallivory is a major feeding mode, with over 50% of species diet including coral (Cole et al., 2008).

Patterns of parrotfish and butterflyfish selectivity varies by geographic region but generally seems to occur in spite of which coral species is most abundant. For example, Rotjan & Lewis (2006) provided the most comprehensive study to date on parrotfish grazing preferences across all reef habitats (backreef, lower spur, upper spur, lagoon, inner reef slope and outer ridge) with the highest selectivity for *Montastrea annularis* despite *Montastrea franksi* being the dominant species in the deeper habitats, such as the outer ridge, and *Porites astreoides* being the dominant species in the shallow backreef. Thus, Rotjan & Lewis (2006) concluded that parrotfish preferentially graze on *Montastrea annularis* species more than expected by chance given their relative abundance. Pratchett (2005) was the first to examine butterflyfish inter-specific variation in dietary composition within a single reef, finding that dietary composition varied within and among butterflyfish species. The most dominant and territorially aggressive species, *Chaetodon baronessa* and *C. trifascialis,* eating *Acropora hyacinthus* while subordinate *C. lunulatus* foraged less frequently on their preferred *Acropora* and instead fed on “other” hard corals (coral genus and species were not identified for this category). This work led Pratchett to hypothesize that dominance hierarchies may determine corallivore selectivity, as dominant aggressors may prevent other coral-feeding butterflyfishes to feed on coral within their territories (Berumen & Pratchett, 2005; Pratchett, 2005; Reese, 1979). Further, Pereira et al (2016) studied variation in bite rate through ontogeny in the Zelinda’s parrotfish *Scarus zelindae*, finding that terminal phase individuals fed on Scleractinian corals at higher rates than the juvenile or initial phase. Due to a dearth of studies that examine inter-specific variation in corallivore foraging, there is a striking knowledge gap in this field that makes it difficult to draw broader conclusions about corallivore foraging selectivity, patterns, similarities, and differences across the many corallivorous taxa.

## Aims and Objectives

### *Project synthesis*

My research used a meta-analytical approach to identify what coral traits (morphologies, availability, or size) promote selective foraging by corallivores and whether these preferences are maintained across tropical coral reef habitats in different geographic regions. Meta-analyses have become an important supplement to traditional methods of literature review (Hedges, 1982), helping to address challenges associated with synthesizing the literature and generating hypotheses about broad-scale ecological processes (Rosenthal & DiMatteo, 2001; Stone & Rosopa, 2017). This work can provide important knowledge on the ecological role of corallivory on global coral reefs. In addition, a challenge to restoration efforts via newly transplanted coral colonies is that they can experience intense corallivory pressure immediately following outplanting that limit their growth and survival (Burkepile, 2012; Rotjan & Lewis, 2006; Shaver et al., 2020). This project can therefore also provide an important knowledge base in the field of coral restoration by identifying what cues and traits should be masked to reduce predation pressure on outplanted corals. Through this project, I studied the following two questions related to corallivore foraging:

*1. Do butterflyfish preferentially target coral prey based off of growth form morphologies or reef location during foraging on coral reefs?*

Scleractinian corals exhibit a wide breadth of diversity in size, availability, coverage, and morphology both within and among species. Studies have shown butterflyfish to be highly selective in their feeding while disproportionately feeding on corals due to their availability (Pratchett, 2007; Slattery & Gochfeld, 2016; Wrathall et al., 1992; Zambre & Arthur, 2018). I hypothesize that butterflyfish do preferentially target a subset of available Scleractinian coral colonies' morphology during foraging based on these traits. Patterns of corallivory have been studied on coral reefs around the world (e.g., Australia, Puerto Rico, United States, Columbia, Maldives, Egypt, Saudi Arabia) (Alwany et al., 2003; Berumen et al., 2005; Bonaldo et al., 2012; Bruckner & Bruckner, 1998; Cole, 2011; Jayewardene et al., 2009; Madduppa et al., 2014). I hypothesize I will find that butterflyfish species will preferentially prey on corals with similar morphologies in different geographic locations.

### *2. Do parrotfish predation scars vary based on selectivity for coral families, and/or coral size, and/or locations?*

I hypothesize that predation scars and preferences for coral prey change depend on coral families. Studies have identified that parrotfish commonly graze upon the coral genera *Acropora, Montipora* (both in the Acroporidae family), *Pocillopora* (family: Pocilloporidae), *Montastraea* (family: Montastraeidae) and *Porites* (family: Poritidae) (Bruckner & Bruckner, 2016; Rotjan & Lewis, 2008). Patterns of foraging between specific corallivore and coral species have been established. However, broader scale preferences based on other coral traits (e.g. size, morphology, nutritional content, availability) that draw the corallivores to its prey remain unclear.

## Methods

### *Literature search*

For this meta-analysis, data was gathered from multiple authors that examined corallivory through either direct observation of corallivore bite rates or evidence of corallivory indirectly recorded through grazing scars on corals. Searches for relevant literature were completed on the database *Web of Science*. A systematic Boolean search included the following term combinations (see Table 1 for term definitions):

1) TOPIC: “corallivore” AND “foraging”, “corallivore” AND “feeding selectivity” OR “selective predation” OR “predation on coral”, “crown-of-thorns” AND “corallivore” OR “predation on coral”, “gastropod” AND “corallivore” OR “coral predation”, “butterflyfish” AND “corallivore” OR “coral predation”, “parrotfish” AND “corallivore” OR “predation on coral”, “finfish” AND “predation on coral” OR “corallivory”, “Chaetodontidae” AND “predation on coral” OR “corallivore”
2) ALL FIELDS: “gastropod” AND “corallivory”, “pufferfish” AND “corallivory”, “finfish” AND “corallivory”, “corallivore” AND “selective foraging”, “butterflyfish” AND “feeding mechanism” OR “selective predation” OR “coral foraging”, “parrotfish” AND “corallivory” OR “feeding mechanism” OR “selective predation” , “corallivory” AND “gastropod”, “corallivory” AND “acanthaster planci”, “wrasse” AND “selective foraging”, “damselfish” AND “corallivory”, “Chaetodontidae” AND “corallivore”, “Gastropoda” AND “corallivore”, “Labridae” AND “corallivore”
3) TITLE: “butterflyfish” AND ALL FIELDS: “corallivore”, TITLE: “parrotfish” AND ALL FIELDS “corallivore”

*Table 1:* The table below shows the individual terms searched, their corresponding definitions, and the reference for each definition.

| Search Term | Definition | Reference |
|---|---|---|
| Corallivore | Fishes or invertebrates that consume live coral, including coral mucus, tissue, and/or skeleton | (Rice et al., 2019; Rotjan & Lewis, 2008) |
| Foraging | Searching widely for food or provisions | Google dictionary |
| Foraging selectivity | Searching widely for the most suitable food or provisions | Oxford Dictionary |
| Selective predation | Relative frequencies of prey types in a predator's diet differ from the relative frequencies in the environment | (Chesson, 1978) |
| Chaetodontidae | A large family of percoid tropical marine fishes common about coral reefs that includes butterflyfishes | ("Chaetodontidae," 2022) |
| Scaridae | A family of marine percoid fishes closely resembling the Labridae but having the teeth of the jaws more or less coalescent and comprising the true parrot fishes | Merriam-Webster |
| Gastropod | A mollusk of the large class *Gastropoda* | Google dictionary |
| Butterflyfish | Any number of boldly marked or brightly colored fish of warm waters | Google dictionary |
| Parrotfish | A fish of the family Scaridae, usually brightly colored chiefly tropical marine fishes that have the teeth in each jaw fused into a cutting plate resembling a beak | Merriam-Webster |
| Finfish | All species of fishes and sharks; “true” fishes | ("Finfish Fisheries," 2013) |
| Damselfish | Any of numerous often brilliantly colored marine fishes living especially along coral reefs | ("Damselfish," 2022) |
| Labridae | A large and important family of percoid fishes having the palate toothless, the anterior teeth of the jaws separate and usually strong, and the lower pharyngeals completely united into one bone with conical or tubercular teeth | Merriam webster |

This search yielded 97 studies, which were then filtered using the following criteria:

1. The study must observe and record corallivory on scleractinian corals.
2. We attempted to compare the corallivory using comparable methodologies in both butterflyfish and parrotfish, but studies on these taxa used different methodologies for observing corallivory.
3. Papers on butterflyfish met the criteria if there were direct observations of the number of bites taken from coral within a recorded time.
4. Studies on parrotfish were selected if indirect evidence of corallivory was recorded through grazing scars observed by photographs, transects, or diver coral surveys (see Figure 2 in the introduction for photographs of stereotypical parrotfish grazing scars).
5. Studies that recorded data on other aspects of corallivore behaviors were excluded from this study (e.g., corallivore abundance and density on host corals). These traits are commonly quantified as proxies for gastropod corallivory, as direct coral predation by gastropods on coral reefs is rare in the literature. The few datasets that have completed direct observations of gastropod corallivory could not be obtained from those papers' corresponding authors (Hoeksema et al., 2013; Knowlton, 1990; Miller, 2001).

### *Data collection*

For papers that met all of the above criteria, papers were sorted by data availability. Those papers with data stored in public databases were downloaded (four total datasets were available publicly in data repositories, which are summarized in Table 1). For any studies in which the data was not publicly available, the papers' corresponding author was emailed with requests for the raw data sets (summarized in Table 2). In total, 24 corresponding authors were contacted for 29 unique raw data sets that met all relevant search criteria, of which 13 of these datasets were obtained. With the exception of Palacios et al. (2014), all collected data sets involved focused on butterflyfish and parrotfish. As a result, raw data sets obtained from the corresponding authors were assigned to one of two data sets, either direct observations of butterflyfish bite rates (which will be referred to as bite rate dataset hereafter) or observations of parrotfish predation through either diver surveys or photographs (which will from here on be referred to as predation dataset). Seven of the acquired datasets met the criteria for inclusion in bites rate dataset, while six of these datasets met all criteria for inclusion in the predation dataset. Three additional data sets were obtained but omitted from the meta-analysis: 1) Palacios et al. (2014) was omitted as it was the only data set obtained on pufferfish, so could not be directly compared to the other data sets; 2) Burkepile et al (2019) was omitted as it was the only study to observe parrotfish corallivory in terms of bite rate); and 3) Rempel et al (2020) was omitted as predation scars were assessed via healing rather than parrotfish grazing. For the predation dataset, papers recorded data as either percent of a coral colony preyed upon, number of bites on a coral species within a transect, or before-and-after photographs. To make the data in these papers comparison, these data were transformed into a binary response variable, in which predation was recorded as either present (1) or absent (0), and contained a total sample size of 6,773 observations (Table 6). The bite rate dataset included 109,974 observations (Table 3). All relevant metadata can be found as supplementary files under the data sheets “combinedBites[.xlsx]” (bite rate dataset) and “combinedPredation[.xlsx]” (predation dataset).

*Table 2.* Summary of datasets considered for inclusion in this meta-analysis, including if the data was publicly available, if the raw data was acquired, if the data was included in one of the two datasets, either direct observations of butterflyfish foraging (“bite rate”) or observations of parrotfish corallivory (“predation”). Partially **bolded** rows indicate that the paper did not have publicly available raw dataset(s) but was received through email correspondence for use in the statistical analysis. **Full bolded** rows indicate the paper was publicly available and was used in the statistical analysis.

| Authors Contacted | Public data? | Raw Data Acqu -ired? | Included in Meta-analysis ? | Corallivore Taxa | Location | Combined Dataset |
|---|---|---|---|---|---|---|
| Alwany et al 2003 | No | No | No | Butterflyfish | Gulf of Aqaba coast, Egypt | Bite rate |
| Berumen et al 2005 | No | No | No | Butterflyfish | Lizard Island Great Barrier Reef, Australia | Bite rate |
| Bonaldo & Bellwood 2010<br>Bonaldo et al 2012 | No<br>No | No<br>No | No<br>No | Parrotfish<br>Parrotfish | Lizard Island Great Barrier Reef, Australia<br>Pioneer Bay located at Orpheus Island Great Barrier Reef, Australia | Predation<br>Predation |
| Burkepile 2012<br>Burkepile et al 2019 | No<br>No | **Yes**<br>Yes | **Yes**<br>No | **Parrotfish**<br>Parrotfish | **Florida Keys National Marine Sanctuary Key Largo, FL, USA** | **Predation**<br>Bite rate |
| Cameron 2014 | No | No | No | Parrotfish | Moorea, Polynesia's Society Islands archipelago | Predation |
| Chandler et al 2016 | **Yes** | **Yes** | **Yes** | **Butterflyfish** | **Vavvaru Island, Maldives** | **Bite rate** |
| Cole et al 2011 | No | No | No | Butterflyfish | Kimbe Bay located at New Britain Island, Papua New Guinea | Bite rate |
| Graham 2007 | No | **Yes** | **Yes** | **Butterflyfish** | **Chagos Archipelagos at the Diego Atoll** | **Bite rate** |
| Gregson et al 2008 | No | **Yes** | **Yes** | **Butterflyfish** | **Lizard Island Great Barrier Reef, Australia** | **Bite rate** |
| Hoeksema et al 2013 | No | No | No | Gastropod | Koh Tao, Thailand | Predation |
| Huertas et al 2021 | **Yes** | **Yes** | **Yes** | **Parrotfish** | **Palfrey and South Island, Great Barrier Reef, Australia** | **Predation** |
| Jayewardene et al 2009 | No | No | No | Pufferfish and Filefish | Oahu and Hawaii Island | Predation |
| Johansson 2016 | No | No | No | Crown-of-thorns starfish | Corals collected from Davies Reef and Trunk Reef, Great Barrier Reef, Australia | Predation |
| Kavousi et al 2020 | No | **Yes** | **Yes** | **Parrotfish** | **Qeshm Island, Persian Gulf** | **Predation** |
| Knowlton et al 1990 | No | No | No | Gastropod and Damselfish | Jamaica | Predation |
| Koval et al 2020 | **Yes** | **Yes** | **Yes** | **Parrotfish** | **Miami, Florida, USA** | **Predation** |
| Madduppa et al 2014 | No | No | No | Butterflyfish | Petondan Timur Island, Thousand Islands Marine National Park, Indonesia | Predation |
| Miller 2001 | No | No | No | Gastropod | Florida Keys National Marine Sanctuary, FL, USA | Predation |
| Ong & Holland 2010 | No | No | No | Parrotfish | Hanauma Bay, Oahu, Hawaii | Predation |
| Palacios et al 2014 | No | Yes | No | Pufferfish | La Azufrada reef, located at Gorgona Island, Colombia | Bite rate |
| Pratchett 2007<br>Pratchett 2013 | No<br>No | **Yes**<br>**Yes** | **Yes**<br>**Yes** | **Butterflyfish**<br>**Butterflyfish** | **Lizard Island, Great Barrier Reef, Australia**<br>**Chagos Archipelagos located at the Great Chagos Bank, Peros Banhos, and Salaman Atoll** | **Bite rate**<br>**Bite rate** |
| Rivas et al 2021 | No | **Yes** | **Yes** | **Parrotfish** | **Miami, FL, USA** | **Predation** |
| Rempel et al 2020 | Yes | Yes | No | Parrotfish | St. Croix, US Virgin Islands | Predation |

| | | | | | | |
|---|---|---|---|---|---|---|
| Rotjan et al 2005 | No | No | No | Parrotfish | Carrie Bow Cay, Belize | Predation |
| Rotjan & Lewis 2006 | No | No | No | Parrotfish | | Predation |
| Saponari et al 2021 | No | No | No | Gastropod | Ari Atoll and Faafu Atoll, Maldives | Predation |
| Slattery & Gochfeld 2016 | No | **Yes** | **Yes** | **Butterflyfish** | **Piti Bomb Holes, Luminao Reef and Cocos Lagoon, Guam** | **Bite rate** |
| Smith et al 2018 | No | No | No | Parrotfish | **Florida Keys National Marine Sanctuary** | Predation |
| Smith et al 2021 | No | **Yes** | **Yes** | **Parrotfish** | | **Predation** |
| Zambre et al 2018 | No | **Yes** | **Yes** | **Butterflyfish** | **Lakshadweep archipelago, union territory of India** | **Bite rate** |

*Data extraction of bite rate data set*

Data from all acquired datasets in the bite rate model (focused on butterflyfish) were collated into a single spreadsheet. The datasets included bite rate observations from the following locations: Vavvaru Island, Maldives (Chandler et al., 2016); Chagos Archipelago at the Diego Atoll (Graham, 2007); Chagos Archipelago at the Great Chagos Bank, Peros Banhos, and Salaman Atoll (Pratchett, 2013); Guam (Slattery & Gochfeld, 2016); Lizard Island in the northern Great Barrier Reef, Australia (Gregson et al., 2008); other reefs across the Great Barrier Reef, Australia (Pratchett, 2007); and Lakshadweep archipelago, a union territory of India (Zambre & Arthur, 2018). The locations were compiled into the Indian Ocean (Chandler et al., 2016; Graham, 2007; Pratchett, 2013), Pacific Ocean (Slattery & Gochfeld, 2016), Coral Sea (Gregson et al., 2008; Pratchett, 2007), and Arabian Sea (Zambre & Arthur, 2018) based on their geographic locality to allow us to draw broader conclusions about how geography alters bite rate (Table 3).

*Table 3:* Summary of papers included in the meta-analysis dataset “bite rate.” Along with the sample size per citation, original location, and the recategorized location for the purpose of this dataset.

| **Citation for each paper in bite rate data** | **Sample size (number of observations)** | **Location from citation’s observed dataset** | **Transformed location for bites rate** |
|---|---|---|---|
| Chandler et al 2016 | 1,734 | Vavvaru Island, Maldives | Indian Ocean |
| Graham 2007 | 241 | Chagos Archipelagos at the Diego Atoll | Indian Ocean |
| Pratchett et al 2013 | 13,202 | Chagos Archipelagos at the Great Chagos Bank, Perro Banhos, and Salaman Atoll | Indian Ocean |
| Gregson et al 2008 | 1,272 | Lizard Island, Great Barrier Reef | Coral Sea |
| Pratchett 2007 | 90,312 | Great Barrier Reef | Coral Sea |
| Zambre et al 2018 | 33 | Lakshadweep | Arabian Sea |
| Slattery & Gochfeld 2016 | 3,180 | Guam | Pacific Ocean |

Coral species vary among geographic regions, thus, coral species is not a good indicator of global corallivory data. Further, each dataset identified corals at different levels of taxonomic specificity, such as to species, to genus, or more generally as Scleractinian coral. To account for this geographic and dataset-level variation, corals were identified in the bite rate dataset through coral morphology instead of coral species. Morphologies were determined using the *Coral Trait Database* (Aaron Harmer et al.; Veron J.E.N. et al., 2016), in which coral morphology of the typical morphology growth form for a particular species or genus is identified. Coral morphologies identified from the collated data were branching, columnar, encrusting, free-living, laminar, massive, polymorphic, and unknown. Morphological growth forms described in the *Coral Trait*

*Database* such as digitate, plate, corymbose, and sub-massive were re-categorized based on similar definitions to the selected categories (Table 4). The selected morphologies and their sample sizes can be found in Table 5. The category “unknown” was not analyzed further, as these corals were unable to be identified and could fit into any other category. Corals were categorized as “polymorphic” if the corals were only identified to family or genus in the dataset and those family and genus groups can take on multiple morphologies.

*Table 4:* This table outlines how coral taxonomy was transformed into coral morphology for categorization in further analyses, the citation(s) for which each group was observed, morphology and definitions as described under the typical growth form in the *Coral Trait Database*, and the transformed morphology for the purposes of the bite rate data set**.** Alternative definitions were also found from other sources to assist with comparability and accuracy of recategorizations. Alternative definitions are as follows: plate or table: grow outward in horizontal sheets (*Coral Growth Forms, 2016*); submassive: dense, irregular shape, massive: dense, spherical or hemispeherical, corymbose: "crazy" branching-like corals, laminar:thin plate-like corals that grow in horizontal sheets, digitate: small un-splitting branches which resemble "digits" or "fingers" with no secondary branches (*Coral Growth Forms*, 2016)

| **Coral species** | **Citation** | **Typical coral morphology growth form (as described in *Coral Trait Database)*** | **Morphology characterized in the bite rate data set** |
|---|---|---|---|
| *Acropora Cytherea (A. Cytherea), A. divaricate, A. hyacinthus* | Pratchett 2007 | Plate or Table (colony outline in the shape of a table) | Laminar (thin sheets often forming whorls) |
| *A. clathrate* | Pratchett et al 2013 | Plate | Laminar |
| *Porites rus* | Slattery & Gochfeld 2016 | Digitate (encrusting with irregular short upright branches) | Columnar (forming columns) |
| *A. digitifera, A. gemmifera* | Pratchett 2007 and Pratchett et al 2013 | Digitate | Columnar |
| *A. humilis* | Pratchett 2007 | Digitate | Columnar |
| *A. aculeus, A. cerealis, A. loripes, A. millepora, A. monticulosa, A. nastua, A. selago, A. tenuis, A. valida* | Pratchett 2007 | Corymbose (flat topped clumps) | Branching (branching open: branches of similar length given off at similar angles or branching closed: branches in clusters or tufts) |
| *Galaxea astreata, Hydnophora exesa* | Pratchett 2007 | Sub-massive (not quite massive) | Massive (solid with similar shape in all direction) |
| *A. elseyi* | Pratchett et al 2013 | Hispidose (open-branched with a second type of branch given off at regular intervals) | Branching |
| *Ctenella* | Pratchett et al 2013 | Sub-massive | Massive |

*Table 5:* Summary of morphology growth form categories, citations for which the morphology were observed, total sample size per morphology, and the sample size from each citation. It is important to note that Gregson et al (2008) was the only citation in which only "Unknown" corals were categorized, thus was not included in statistical analysis.

| **Morphology category**<br>Citation | **Total Sample size per morphology**<br>Sample size from each citation |
|---|---:|
| **Branching** | **38,567** |
| Pratchett 2007 | 28,930 |
| Pratchett et al 2013 | 8,160 |
| Slattery & Gochfeld 2016 | 1,060 |
| Chandler et al 2016 | 340 |
| Graham 2007 | 74 |
| Zambre et al 2018 | 3 |
| **Columnar** | **9,310** |
| Pratchett 2007 | 7,335 |
| Pratchett et al 2013 | 1,445 |
| Slattery & Gochfeld 2016 | 530 |
| **Encrusting** | **6,573** |
| Pratchett 2007 | 5,923 |
| Slattery & Gochfeld 2016 | 531 |
| Chandler et al 2016 | 90 |
| Pratchett et al 2013 | 26 |
| Zambre et al 2018 | 3 |
| **Laminar** | **5,088** |
| Pratchett 2007 | 5063 |
| Pratchett et al 2013 | 25 |
| **Massive** | **37,777** |
| Pratchett 2007 | 36,519 |
| Slattery & Gochfeld 2016 | 529 |
| Pratchett et al 2013 | 447 |
| Chandler et al 2016 | 250 |
| Graham 2007 | 20 |
| Zambre et al 2018 | 12 |
| **Plate** | **4,677** |
| Pratchett 2007 | 2,964 |
| Pratchett et al 2013 | 1,713 |
| **Polymorphic** | **6,155** |
| Pratchett 2007 | 4,829 |
| Slattery & Gochfeld 2016 | 530 |
| Chandler et al 2016 | 500 |
| Graham 2007 | 146 |
| Pratchett et al 2013 | 135 |
| Zambre et al 2018 | 15 |
| **Unknown** | **1,827** |
| Gregson et al 2008 | 1,272 |
| Chandler et al 2016 | 554 |
| Graham 2007 | 1 |

### *Data extraction of predation data set*

Data from all collected data sets involving parrotfish predation were collated into one spreadsheet. Predation data was identified through parrotfish grazing scars, which can be distinguished by a pair of opposing oval-shaped marks (created by the upper and lower jaws) on the coral surface (shape and depth of scar varies per parrotfish) (Huertas et al., 2021). In these datasets, the methodologies for quantifying parrotfish predation varied,  including counting coral colonies with parrotfish bites in 1m belt transects (Kavousi et al., 2020), recording percent of individual coral colony surface area that was preyed upon (Koval et al., 2020; Rivas et al., 2021; Smith et al., 2021), photographs of corals taken within a transect with visible scars recorded (Huertas et al., 2021), and determining percentage of coral colonies that were preyed upon in belt transect through predation scars per unit area (Burkepile, 2012). To make these diverse datasets comparable for the purpose of further analyses, predation in all datasets was transformed in a binary response variable, with predation either present (1) or absent (0). Data from Smith (2021) recorded finfish predation on coral transplants, but predation scars were assumed to be from parrotfish, through visual identification of stereotypical, visible grazing scars and in agreement with other literature observing parrotfish predation on recent coral outplants in Florida (Koval et al., 2020; Page et al., 2018). Thus, Smith (2021) was considered as having met criteria for the predation data set.

### *Predation location*

Location was used as an explanatory variable for the predation data set but was transformed into two categories: Florida and Other (Table 6). Burkepile (2012) and Smith et al (2021) were in the Florida Keys National Marine Sanctuary, USA; Koval et al (2020) and Rivas et al (2021) were from different reefs within Miami, FL, USA; Huertas et al (2021) included data were from Palfrey and South Islands, adjacent to Lizard Island on the Great Barrier Reef, Australia; and data from Kavousi et al (2020) was recorded in Qeshm Island, Persian Gulf, Iran. By transforming location into these broader categories, we Could make broader comparisons to examine comparisons in Florida versus elsewhere (Table 6).

*Table 6:* Summary of citations within the predation dataset, original location from the study, and the recategorized location for the purposes of this meta-analysis.

| **Citation** | **Original Location** | **Recategorized Location** |
|---|---|---|
| Burkepile 2012 | Florida Keys National Marine Sanctuary | Florida |
| Smith et al 2021 | Florida Keys National Marine Sanctuary | Florida |
| Koval et al 2020 | Miami, Florida | Florida |
| Rivas et al 2021 | Miami, Florida | Florida |
| Kavousi et al 2020 | Qeshm Island, Persian Gulf | Other |
| Huertas et al 2021 | Palfrey and South Island, Great Barrier Reef | Other |

*Predation coral families*

Coral families were used in the predation data set rather than coral morphologies, as all collected data, except Burkepile (2012), observed predation on only massive corals. Table 7 summarizes the coral families, citation, and sample size per family included in these analyses. Since only coral families were used in the predation data set, and not coral morphology or species, there was no suspected covariance.

*Table 7:* Summary of sample size data for the predation data set, explaining the identified coral families, associated citations, and number of observations (sample size) for each citation within the associated family.

| **Coral Family** | **Citation** | **Sample Size** |
|---|---|---|
| Merulinidae | Smith et al 2021 | 600 |
| | Rivas et al 2021 | 1416 |
| | Koval et al 2020 | 303 |
| Poritidae | Burkepile 2012 | 644 |
| | Huertas et al 2021 | 710 |
| | Kavousi et al 2020 | 30 |
| Montastraeidae | Burkepile 2012 | 112 |
| | Smith et al 2021 | 600 |
| | Koval et al 2020 | 141 |
| Mussidae | Burkepile 2012 | 38 |
| | Smith et al 2021 | 600 |
| | Koval et al 2020 | 213 |
| Agariciidae | Burkepile 2012 | 734 |
| Siderastreidae | Burkepile 2012 | 477 |
| Astrocoeniidae | Burkepile 2012 | 48 |
| Meandrinidae | Burkepile 2012 | 45 |
| Pocilloporidae | Burkepile 2012 | 32 |
| Acroporidae | Burkepile 2012 | 30 |

### *Statistical analysis for bite rate data*

In the bites rate dataset, statistical analysis focused on bites per unit time as the response variable. The explanatory variables in this model included coral morphology (seven categories:

branching, columnar, encrusting, free-living, laminar, massive, polymorphic) and location (four categories: Indian Ocean, Arabian Sea, Coral Sea, Pacific Ocean). Minutes recorded (i.e., the number of minutes that butterflyfish were observed in the respective dataset) was included as an offset term.  Citation (Graham 2007; Pratchett et al 2013; Zambre et al 2018; Pratchett 2007; and Slattery & Gochfeld 2016) was included as a random effect. Since only coral morphology was included in the model (not coral species or family), there was no suspected covariance. The data was fitted as a generalized linear mixed-effects model (GLMM) using the glmmTMB package (Brooks et al., 2017) in the R software (V4.1.2;Team, 2021). As the response variable was recorded as a count in terms of number of bites, the optimal distribution (Poisson or negative binomial) were determined using the Akaike information criterion (AIC) during the best-fit model selection process. AIC was also used to determine if a zero-inflation correction was needed. Missing values (e.g., some missing bites data from Pratchett et al 2013) were omitted from further analyses using the function "na.omit". Negative binomial (type 1) distribution with zero inflation correction was chosen as the best-fit model AIC (Table 8). Term selection was conducted by comparing the full model to the other possible term combinations, then choosing the best-fit through comparison of AIC scores (Table 9). Model assumptions were verified by plotting residuals versus fitted values (using the "DHARMa" package; Hartig, 2020). Pairwise comparisons of fitted factors were assessed using Tukey's post hoc analysis in the package "emmeans" (Lenth, 2022). Significance was determined by a p-value less than 0.05.

*Table 8:* Summary of each statistical distribution tested, the degrees of freedom (Ezzat et al., 2020) and associated AIC score. Table is ordered from lowest AIC (best-fit model) to highest AIC score. Families for each model tested in order as of AIC values are: negative binomial 1, negative binomial 1, negative binomial 2, negative binomial 2, Poisson, and Poisson. Zero inflated models tested are *italicized* and **bolded**.

| Model | df | AIC |
|---|---|---|
| ***coral_morphology+location + offset(log(minutes_recorded)) + (1\|citation)*** | 15 | 56,074.27 |
| coral_morphology+location + offset(log(minutes_recorded)) + (1\|citation) | 14 | 56,305.71 |
| ***coral_morphology+location + offset(log(minutes_recorded)) + (1\|citation)*** | 15 | 61,420.26 |
| coral_morphology+location + offset(log(minutes_recorded)) + (1\|citation) | 14 | 61,422.26 |
| ***coral_morphology+location + offset(log(minutes_recorded)) + (1\|citation)*** | 14 | 96,866.26 |
| coral_morphology+location + offset(log(minutes_recorded)) + (1\|citation) | 13 | 209,262.88 |

*Table 9:* Summary of statistical term selection tested, df, and the associated AIC score. Table is ordered from lowest AIC (best-fit model) to highest AIC score.

| Model | df | AIC |
|---|---|---|
| coral_morphology + offset(log(minutes_recorded)) + (1\|citation) | 11 | 56,068.29 |
| coral_morphology+location + offset(log(minutes_recorded)) + (1\|citation) | 15 | 56,074.27 |
| coral_morphology+location + offset(log(minutes_recorded)) | 14 | 58,674.54 |
| offset(log(minutes_recorded)) + (1\|citation) | 4 | 60,393.39 |
| location + offset(log(minutes_recorded)) + (1\|citation) | 8 | 60,398.87 |
| coral_morphology+offset(log(minutes_recorded)) | 10 | 61,573.93 |
| location + offset(log(minutes_recorded)) | 7 | 66,411.31 |
| offset(log(minutes_recorded)) | 3 | 70,449.83 |

### *Statistical analysis for predation data*

In the predation dataset, statistical analysis focused on presence (1) or absence (0) of corallivore predation as the response variable, and thus had a binomial distribution. The explanatory variables included coral family (10 categories: Acroporidae, Astrocoeniidae, Agariciidae, Meandrinidae, Merulinidae, Montastraeidae, Mussidae, Pocilloporidae, Poritidae, Siderastreidae ), location (2 categories: Florida and Other), and coral size (two categories; small: any coral size < 60cm$^2$, and large: any coral size > 60 cm$^2$). Coral size (cm$^2$) was decided to be split at the median, 60 cm$^2$. Citation (Burkepile 2012, Huertas et al 2021, Kavousi et al 2020, Koval et al 2020, Rivas et al 2021, Smith et al 2021) was included as a random effect (Table 10). Covariance was not expected among any of the variables. The data was fitted with a GLMM using the glmmTMB (Brooks et al., 2017) package in R software (V4.1.2;Team, 2021). To account for missing values(e.g., missing coral size from Kavousi et al 2020's original data), the function "na.omit" was used to create the "predation_omit" dataset without missing values. Term selection was evaluated using AIC scores. Model assumptions were verified by plotting residuals versus fitted values (using the "DHARMa" package; Hartig, 2020). Significant main effects ($p < 0.05$), were further explored using Tukey's post hoc analysis in the package "emmeans" (Lenth, 2022). Table 10 depicts the term selection process and the best-fit model chosen from AIC.

*Table 10:* Summary of term selection models tested, the associated degrees of freedom (Ezzat et al., 2020) and the Aikake Information Criterion (AIC) score used to determine the best-fit model. Table is ordered by lowest AIC value (best-fit model) to highest AIC score.

| **Model** | **df** | **AIC** |
|---|---|---|
| Coral family * coral size + location * coral size + (1\|citation) | 23 | 4,967.196 |
| Coral family * coral size + location | 21 | 5,065.957 |
| Coral family + location * coral size | 15 | 5,246.127 |
| Coral family + coral size + location | 12 | 5,275.803 |
| Coral family + location | 11 | 5,278.055 |
| Coral family + coral size | 12 | 5,315.816 |

## Results

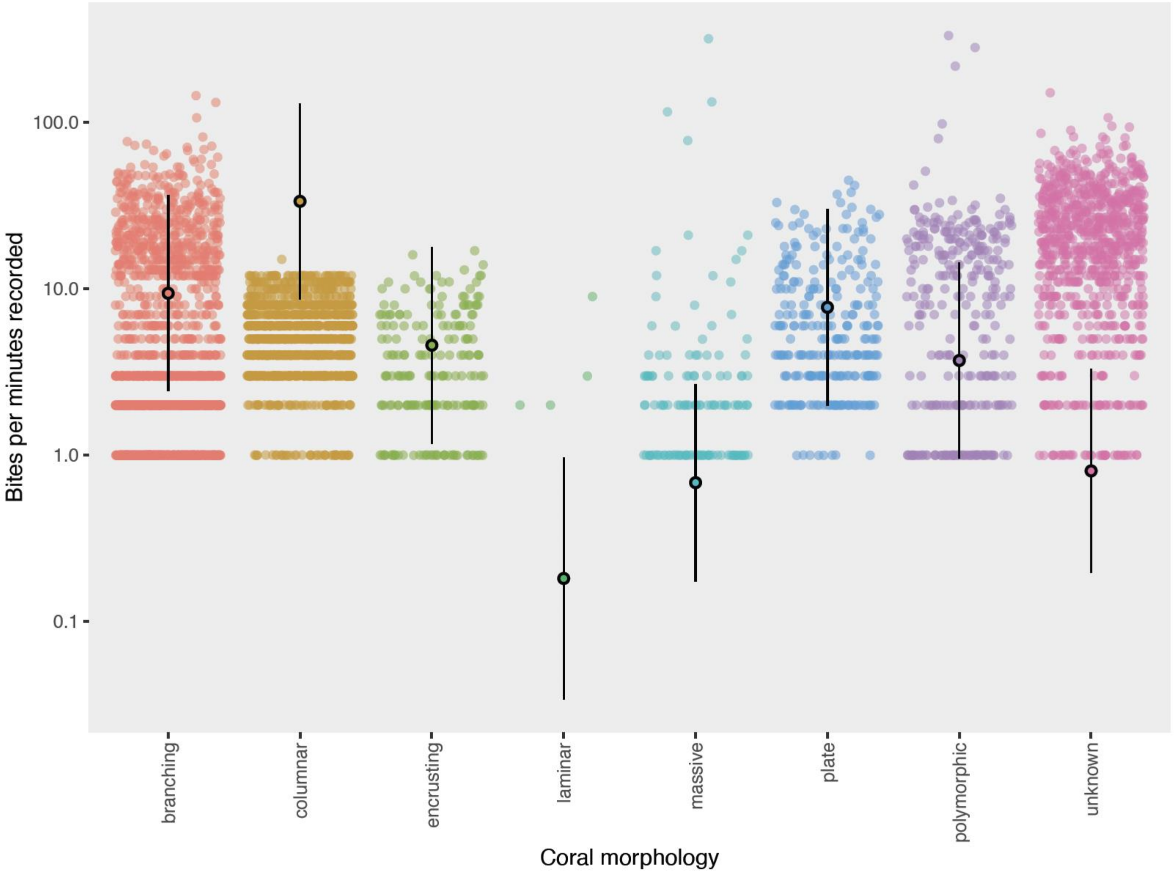
### *Bites rate*

The best-fit model ($R^2 = 0.2200$) included a correction for zero inflation, the citation random effect, the offset term (minutes recorded), and the explanatory variable coral morphology ($p < 0.0001$). Tukey's post hoc analysis showed 18 out of 21 pairwise comparisons were statistically significant ($p < 0.0001$; Table 11). Branching corals were preferred over all other morphologies, except for a few outliers in massive and polymorphic corals, but DHARMa residual diagnostics tested for outliers and proved them to be non-significant. Butterflyfish bite rates were lowest for laminar and massive morphologies, thus were the least preferred morphologies. Figure 4 illustrations butterflyfish bite rate data for each coral morphology category.

*Table 11:* Summary of Tukey's post hoc pairwise comparisons for the significant categorical variable, coral morphology.

| **Pairwise morphology** | **P-value** |
|---|---|
| *Branching / columnar* | < 0.0001 |
| *Branching/encrusting* | < 0.0001 |
| *Branching/laminar* | < 0.0001 |
| *Branching/massive* | < 0.0001 |
| *Branching/polymorphic* | < 0.0001 |
| *Columnar/encrusting* | < 0.0001 |
| *Columnar/laminar* | < 0.0001 |
| *Columnar/massive* | < 0.0001 |
| *Columnar/plate* | < 0.0001 |
| *Columnar/polymorphic* | < 0.0001 |
| *Encrusting/laminar* | < 0.0001 |
| *Encrusting/massive* | < 0.0001 |
| *Encrusting/plate* | < 0.0001 |
| *Laminar/plate* | < 0.0001 |
| *Laminar/polymorphic* | < 0.0001 |
| *Massive/plate* | < 0.0001 |
| *Massive/polymorphic* | < 0.0001 |
| *Plate/polymorphic* | < 0.0001 |
| *Branching/plate* | 0.1293 |
| *Encrusting/polymorphic* | 0.2988 |
| *Laminar/massive* | 0.1507 |

*Figure 4:* Illustration of summary statistics for butterflyfish bite rate data. The colored jitter points represent the bite rate data points. Bolded dots indicate the mean summary point and the black error bars illustrate the 95% confidence limits. Y axis is logged for illustration purposes.



*Predation*

AIC values showed the best-fit model to include all variables for this data set, coral family, coral size, location, and the offset term citation. An ANOVA (Table 12) determined the significant explanatory variables were coral family ($p < 0.0001$), coral size ($p < 0.0001$), and their interaction ($p < 0.0001$). A Tukey's post hoc analysis showed that 4 out of 45 pairwise comparisons of coral families were significant (Table 13). The coral family, Poritidae, was significantly preferred ($p < 0.0001$) over Agariciidae, Montastraeidae, and Siderastreidae (Figure 5). Siderastreidae had significantly higher levels of predation than Agariciidae ($p < 0.0001$, Figure 5). The predicted probability plot, Figure 5, illustrated that Poritidae had the highest levels of parrotfish predation. Levels of predicted predation for parrotfish were very low, presumably because most species in the taxa are strictly herbivores. The interaction of coral families and coral size were plotted in Figure 5 and show that parrotfish predation on Siderastreidae and Poritidae are size dependent. Smaller corals were preyed upon more heavily than larger in the family Siderastreidae, while the opposite interaction of predation occurred in the family Poritidae.

*Table 12:* Analysis of variance for the predation dataset’s best fit model, including the variables (arranged by significance), the chi-squared value, and p-value. A colon “:” indicates an interaction between variable terms.

| Variable | Chi-squared value | P-value |
|---|---|---|
| Coral family | 349.2505 | < 0.0001 |
| Coral size | 70.1203 | < 0.0001 |
| Location | 0.0083 | 0.9272 |
| Coral family:coral size | 57.9587 | < 0.0001 |
| Coral size:location | 0.0490 | 0.8248 |

*Table 13:* Summary of Tukey's post hoc pairwise comparisons for the significant categorical variable coral family in the predation data set. Significant coral families are at the top and the non-significant families are below.

| **Pairwise coral families** | **P-value** |
|---|---|
| Agariciidae / Poritidae | < 0.0001 |
| Agariciidae / Siderastreidae | < 0.0001 |
| Montastraeidae / Poritidae | < 0.0001 |
| Poritidae / Siderastreidae | < 0.0001 |
| Acroporidae / Agariciidae | 1.0000 |
| Acroporidae / Astrocoeniidae | 1.0000 |
| Acroporidae / Meandrinidae | 1.0000 |
| Acroporidae / Merulinidae | 1.0000 |
| Acroporidae / Montastraeidae | 1.0000 |
| Acroporidae / Mussidae | 1.0000 |
| Acroporidae / Pocilloporidae | 1.0000 |
| Acroporidae / Poritidae | 1.0000 |
| Acroporidae / Siderastreidae | 1.0000 |
| Agariciidae / Astrocoeniidae | 0.1034 |
| Agariciidae / Meandrinidae | 0.0895 |
| Agariciidae / Merulinidae | 0.0049 |
| Agariciidae / Montastraeidae | 0.1744 |
| Agariciidae / Mussidae | 0.0386 |
| Agariciidae / Pocilloporidae | 0.8133 |
| Astrocoeniidae / Meandrinidae | 1.0000 |
| Astrocoeniidae / Merulinidae | 1.0000 |
| Astrocoeniidae / Montastraeidae | 0.9998 |
| Astrocoeniidae / Mussidae | 1.0000 |
| Astrocoeniidae / Pocilloporidae | 0.9978 |
| Astrocoeniidae / Poritidae | 0.0027 |
| Astrocoeniidae / Siderastreidae | 0.9818 |
| Meandrinidae / Merulinidae | 1.0000 |
| Meandrinidae / Montastraeidae | 0.9969 |
| Meandrinidae / Mussidae | 1.0000 |
| Meandrinidae / Pocilloporidae | 0.9870 |
| Meandrinidae / Poritidae | 0.0542 |
| Meandrinidae / Siderastreidae | 0.9998 |
| Merulinidae / Montastraeidae | 0.8323 |
| Merulinidae / Mussidae | 0.9987 |
| Merulinidae / Pocilloporidae | 0.9681 |
| Merulinidae / Poritidae | 0.0006 |
| Merulinidae / Siderastreidae | 0.9969 |
| Montastraeidae / Mussidae | 0.9945 |
| Montastraeidae / Pocilloporidae | 1.0000 |
| Montastraeidae / Siderastreidae | 0.3359 |
| Mussidae / Pocilloporidae | 0.9969 |
| Mussidae / Poritidae | 0.0002 |
| Mussidae / Siderastreidae | 0.9450 |
| Pocilloporidae / Poritidae | 0.0001 |

| Pocilloporidae / Siderastreidae | 0.4829 |
|---|---|

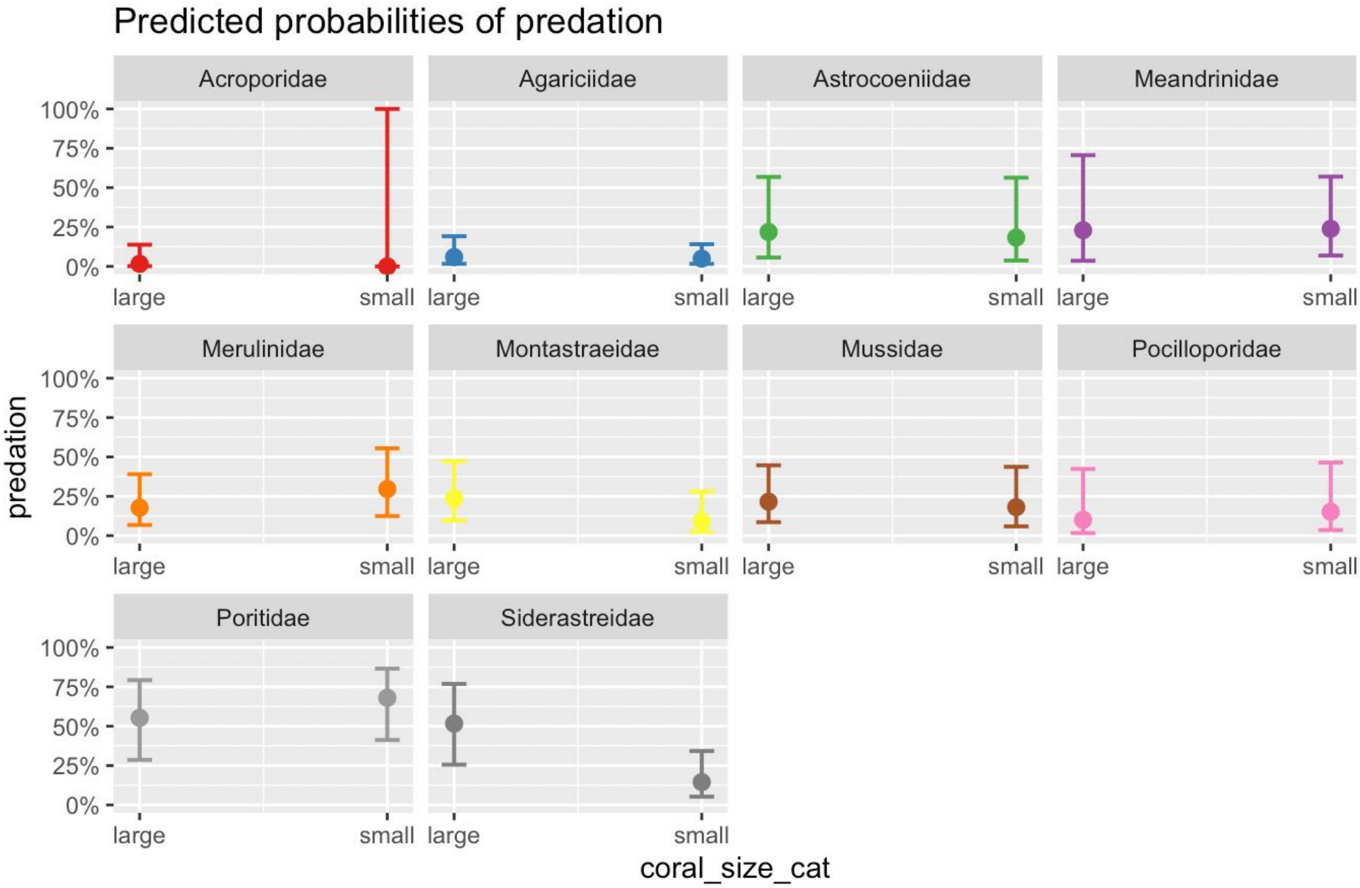


*Figure 5:* This plot summarizes the predicted probabilities of predation on the interaction of coral family and the coral size categories (large and small). Coral size categories (large and small) are on the x-axis and predicted predation (scale of 0 to 100%) is on the y-axis. Each grid represents a different coral families predation probability with the interaction of coral size.

## Discussion

This meta-analysis aimed to gain a broader understanding about the specific drivers that influence corallivorous fish (including butterfly and parrotfish) predation on Scleractinian corals. Documented drivers of corallivory have been coral morphology (Brooker et al., 2013b; Kaullysing et al., 2019; Neudecker, 1979; Randall, 1974; Tricas, 1989), coral species (Berumen et al., 2005; Cole & Pratchett, 2011; Gregson et al., 2008; Noble et al., 2014; Pratchett, 2005; Pratchett, 2007), location (Pratchett, 2007; Randall, 1974; Rotjan & Lewis, 2006), and nutritional content (Rotjan & Lewis, 2005; Tricas, 1989). Meta-analyses, like this one, can create a more integrated review of published literature, thus providing a stronger synthesis of our existing knowledge and generating future research questions (Rosenthal & DiMatteo, 2001; Stone & Rosopa, 2017). Here, we found that butterflyfish forage selectively based on coral morphology, with a significant preference for branching coral over other morphologies. Parrotfish exhibit selective foraging based on both coral family and coral size, with the preference for Poritidae and Siderastreidae depending on the coral size.

### *Bite rate*

In the bite rate dataset, butterflyfish showed selective foraging for the branching coral morphology, which was targeted with higher bite rates than other coral morphologies. Corallivores may be highly specialized, consuming a narrow range of available coral prey (Alwany et al., 2003; Berumen et al., 2005; Cole et al., 2008; Cox, 1986; Pratchett, 2005), particularly in butterflyfish (Chandler et al.; Pratchett, 2007). Branching corals, such as *Acropora* spp., are among the fastest growing corals, growing up to 10cm in growth per year, whereas massive and encrusting morphologies are among the slowest growing, up to 7.6mm per year (Anderson et al., 2017; Heemsoth, 2014; Wakeford et al., 2007). However, growth rates can vary geographically, with lower growth rates recorded at higher latitudes, especially in the genus *Acropora* (Anderson et al., 2017). Corals with a branching morphology may be targeted due to their fast growth rates. Fast growth rates allow for quicker recovery following stress, changing environmental conditions, or coral bleaching (Rice et al., 2019). Further, branching morphologies may be preferred as they could provide the corallivore species easier access to their food source. Cole et al (2008) suggest corallivores likely forage on more easily accessible morphologies, with branching corals generally exhibiting raised polyps that are easier to access by the butterflyfish. Coral abundance or availability was not controlled for in this study as previous research has already proven butterflyfish forage selectively but disproportionately to coral availability (Pratchett, 2007).

While this study aimed to bring together data on direct measurements of corallivory through bite rate, the study was limited in a number of ways, and interpretations of its results need to be viewed in the context of those limitations. First, we were unable to account for differences in corallivory among different corallivore taxa, as only data on butterflyfish bite rates could be attained. Research has shown there are differences across corallivore taxa in their foraging and dietary requirements (Berumen et al., 2005; Pratchett, 2005), and thus presents a short-coming of these analyses that we encourage researchers to focus on in future empirical studies. Further, while in the past considered the gold standard for coral ID, the book *Corals of the World* (Veron J.E.N. et al., 2016) is now considered an outdated source due to rapidly changing taxonomy with the advent of technology for genetic sequencing. Categorization for coral morphologies was instead derived from the typical growth forms as described in The *Coral Trait Database* (Aaron Harmer et al.). Despite these caveats, this analysis provides an important synthesis to aid in our understanding of the foraging of butterflyfish corallivores.

### *Percent predation*

Coral foraging documented through predation grazing scars of parrotfish showed significant variation by coral families, coral size, and a significant interaction of coral family and size. Two of the four most abundant stony coral families in Florida are Poritidae and Siderastraeidae (*What Are Corals*) the two coral families with the highest levels of predation in this data set. Predation on the Acroporidae family may be very low due to an extremely rapid decline of this family, specifically with the formerly abundant species *Acropora cervicornis* and *Acropora palmata.* Although Acroporidae are among the most common stony coral species in the Great Barrier Reef, there was only one study from this location considered in the "Other" location and abundance does not necessarily relate to amount of predation (*Great Barrier Reef Coral*).

The predation dataset incorporated data from both newly transplanted corals (Koval et al., 2020; Rivas et al., 2021; Smith et al., 2021) and grazing scars on an established coral reef (Kavousi et al., 2020). This form of preferential foraging on newly transplanted corals could occur due to several reasons. Size can be a factor influencing predation and mortality of transplanted corals; thus, it is recommended to rear juvenile corals to larger sizes, approximately 7-10 centimeters (Ligson et al., 2020; Seraphim et al., 2020). Preferential foraging on transplanted corals could be the result of a number of natural sources of variation with wild corals, such as calcification rates (Carlson, 1999), microbial communities (Kooperman et al., 2007), and symbiont associations (Hartle-Mougiou et al., 2011; Page et al., 2018). Results of the predation dataset could be affected by including both transplanted corals (typically small fragments ranging from 1 to 25 $cm^2$) and established coral reefs (typically larger coral sizes ranging from 1,000 to 3,000 $cm^2$) within the same analysis. Parrotfish predation probability plots showed higher expected levels of predation. Although parrotfish behavior with novel objects, such as transplanted corals, has not been studied, my results indicate that these smaller transplanted corals are preyed upon with higher intensity by corallivores than wild grown corals. It is important for future studies to separate predation on established coral colonies and transplanted corals to make comparisons of predation characteristics and develop a better understanding of corallivory among these diverse location and sizes of corals.

### *Overall Conclusions and Future Research*

This study used a meta-analytical approach to synthesize available data on corallivore selective foraging, an approach that comes with a variety of challenges. Meta-analyses may be limited by the selection of studies, heterogeneity of methods used in each individual study, small sample sizes, incomplete set of studies, and inclusion of studies that lack statistical conclusion validity (Stone & Rosopa, 2017). While a meta-analysis requires collecting data systematically from the published literature, this collection process was unexpectedly difficult. Of the studies that met the criteria for inclusion in this analysis, only three out of 35 studies had data stored publicly in a repository, meaning that 32 out of 35 studies required contacting the paper's corresponding author. During this process, email response times, out of date email addresses, and holidays/vacation made the data collection process extremely slow. Half of the authors did not reply, but out of the authors who eventually did reply, many no longer had the paper's raw data stored in their files. It was a common issue throughout this process for the data to be lost from either a corrupt hard drive, lack of a long-term storage plan for the data, or simply because the study was decades old. In recent years, many journals have begun to require that data be made publicly available as a condition of publication. As use of meta-analytical techniques becomes more common, the importance of making published data available in a usable format becomes ever more important. Another challenge to compiling the datasets was analyzing if the methodologies and variables were comparable in the various papers investigated, which led to 3 raw collected data sets being omitted from analysis.

While this study aimed to bring together data on corallivory, limitations were present within this meta-analysis. Comparisons among different corallivore taxa were not able to be made within the scopes of this data set, as only data on parrotfish and butterflyfish foraging data could be attained but were non-comparable due to varying methodologies. A short-coming of these analyses that we encourage researchers to focus on in future empirical studies is including differences across corallivore taxa in their feeding requirements. A complex factor to consider when discussing parrotfish predation is their ontogenetic changes in foraging activity (Bellwood, 1988; Pereira et al., 2016). The parrotfish family, Scaridae has 10 facultative corallivores that all have ontogenetic changes in foraging patterns. Life-stage was not a factor considered for parrotfish within the scope of this study due to insufficient data but should be considered for future studies. Despite these limitations, this meta-analysis provides beneficial insights into drivers of parrotfish coral foraging selectivity and generates hypotheses that can be tested by researchers in the future.

The literature search performed for this study illustrated that most studies often focus on the frequency and size of corallivore predation on the coral colony, rather than studying what traits of the corallivore modify its predation rate. The physical, behavioral, and physiological traits of both the coral prey and corallivore predator can alter foraging behavior and feeding rates (Gregson et al., 2008; Welsh & Bellwood, 2012; Zambre & Arthur, 2018). Corals have physically adapted methods to reduce predation incidents by corallivores, specifically the columnar coral *Porites compressa* responds to grazing from the pebbled butterflyfish by briefly withdrawing polyps into the skeleton and by increasing nemocyst, stinging cell, density as a long-term effect of grazing (Palacios 2014; Rotjan and Dimond 2010). A coral colony's response to predation has been minimally studied with only a few documented cases of either physical defense mechanisms (Palacios 2014; Rotjan and Dimon 2010), or phenotypic changes that can consequently result in irregular morphologies (Palacios, 2014; Jayewardene and Birkeland 2006). Schooling behavior of corallivores may also influence feeding rates, as studies of on herbivory in Scaridae parrotfish documented two to three-fold increases in bites on macroalgae in schooling fish compared to individuals (Bellwood & Welsh, 2012). However, the role of schooling behavior in corallivorous feeding rates are unknown, but is hypothesized to be different than in just individuals.

Depth is another extremely important variable for future corallivory studies to consider. Specifically, noting the depth of the reef and depth of the corals predated upon can provide a more definitive understanding of foraging behavior to better understand if corallivore foraging changes with depth. Depth can also be combined with factors such as butterflyfish territories to develop a better understanding if foraging changes or is affected by differing territories and depth (Chandler et al., 2016). Depth has shown to be a significant effect on the maximum linear coral skeletal growth, the carbon 13 isotope and the oxygen 18 isotope (Matthews et al., 2008). Deeper depths experience cooler temperatures; thus researchers have found decreases in calcium to cadmium ratios and carbon isotopes with depth as well as noting skeletal oxygen 18 isotope is directly affected by temperature (Matthews et al., 2008). Suggesting these factors may be influenced by light or temperature induced physiological effects. Through other research, scientists know that coral growth rates decrease with an increase in depth, but species diversity and coral feeding rates increase with depth (Huston, 1985; Palardy et al., 2005).

Corallivore predation may also change as coral reefs shift with current and projected future climate change. Within the past few decades, the frequency of coral bleaching events has increased and such events have proven to alter corallivore foraging preferences as well as lower the abundance of obligate corallivores (Pratchett et al., 2004). With the great decline of coral reefs worldwide, warming ocean temperatures, and higher acidification, establishing patterns of corallivory *in situ* for both established coral reefs and coral transplants will prove beneficial for coral restoration projects and conservation efforts.

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