CORALLIVORY ON HAWAIIAN REEFS

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By

Daniela Escontrela Dieguez

Disseration Committee:

Mark Hixon, Chairperon
Megan Donahue
Jake Ferguson
Tye Kindinger
Elizabeth Madin
John Casken

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DEDICATION

For my beloved family,
who led us to seek a better life outside of Venezuela,
who believed in my dreams even when they seemed unattainable, and
who walked every step of this journey with me,

and to my beloved husband...
who picked me up on the lowest of days,
who gave me confidence when I could not find it, and
who pushed me to follow my wildest dreams.

ABSTRACT

Corallivores, predators of coral, span a wide range of taxa on tropical reefs. Corallivores can affect coral fitness, leading to reduced growth and reproduction, and at high densities, can cause mass coral mortality. As human-made threats to corals escalate and compound the effects of corallivory, coral reef managers increasingly need monitoring tools to track changes in corallivory. Historically, corallivory has been monitored with *in situ* visual surveys or post-hoc estimates derived from photoquadrats, both methods of which have limitations. Structure from Motion (SfM) photogrammetry, an imagery-based methodology, has emerged as a potential alternative. I counted bite marks by reef fishes on colonies of 16 coral species in paired *in situ* visual and SfM surveys at sites around O‘ahu to evaluate the accuracy of SfM as corallivory monitoring tool. I found significant differences in bite counts between methods, with SfM detecting higher counts. This disparity was more pronounced at deep sites and locations with high coral cover, reflecting the limitations of SCUBA diving inherent during *in situ* surveys. However, despite differences in absolute counts, both methods were consistent in qualitative patterns across sites, indicating that SfM is a viable tool to quantify corallivory, with potential for enhanced accuracy. Given the success of this tool, I leveraged the same data to investigate patterns and drivers of corallivory. My analysis revealed consistent consumption of only six coral species by reef fishes. There was also a positive relationship between species-specific coral cover and predation intensity for the preferred coral species of each corallivore, shedding light on common predator-prey interactions. Considering the heightened vulnerability of recently outplanted corals to predation, this information can inform coral restoration methodologies, ultimately yielding more favorable outcomes. Lastly, I studied the feeding ecology of a common corallivore around O‘ahu, the cushion sea star (Culcita novaeguineae), which may be increasing in abundance at some sites, representing a potential local stressor. I tested prey choice by running pairwise comparisons of corals of opportunity from different species and tracking the order of consumption. I used three methods to construct a feeding hierarchy, and across all methods, stars overwhelmingly preferred *Pocillopora* spp. and rarely consumed *Porites* spp. These findings indicate which coral species may face increased predation as seastar populations increase, which has implications for local coral restoration efforts and coral community trajectory under future conditions.

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I always say, “It takes a village to raise a PhD student,” because we’re like children – we need education, nourishment, and emotional support. My village has been crucial to my success, from the academic guidance of my committee and advisor to the endless laughs during fieldwork, and the unwavering support from my family, husband, and friends. Without them, my dream of becoming a marine biologist with a PhD would not have been possible.

I must first thank my advisor, Dr. Mark Hixon, without whom this dissertation would not have been possible. When I began seriously considering graduate school as the next step in my professional journey, I was sitting in my small room in the Philippines, being devoured by mosquitos. After a few years away from school, I knew I wanted to study coral reef ecology. I emailed dozens of professors, many of whom did not respond, but I felt like I struck gold when I received a reply from Mark. I could not believe that this renowned coral reef fish ecologist had answered MY email. Ever since then, Mark has shown me unwavering support. The first glimpse of this was when he helped me conceive a project idea for my NSF GRFP proposal and subsequently helped me edit my statements. When I received the award email many graduate students dream of, I was unsure if I wanted to move to Hawai‘i. Nevertheless, Mark encouraged me to go to school, even if it meant not joining his lab. Five years later, it is obvious that I made the right move coming to Hawai‘i, as Mark’s mentorship helped me become a better writer, scientist, academic, and advocate for science and conservation.

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The support I received from my lab mates, Erik Brush, Ryan Jones, and Eric Dilley, was unparalleled. During our countless hours of fieldwork—many of them spent on the boat eagerly awaiting our next dive—we delved into life's greatest questions: What is the best pizza? (New York Style, not Chicago), What is “reggaeton”? (A type of music, not to be confused with the rigatoni pasta, as my lab mates did), and Who has the best shell collection? (Obviously me). Amidst our banter, they patiently fielded my endless questions, and we fostered a real camaraderie as we spent long days preparing for fieldwork, coordinated schedules, and repairing equipment. Beyond the lighthearted moments, each of them pursued remarkable research projects, offering me invaluable insights into new topics, methods, and skills. While I jokingly referred to them as my “workplace proximity associates,” I am thrilled to say they've evolved into lifelong friends.

Conducting fieldwork, especially underwater, is no small feat. It requires specialized training, gear, and a considerable amount of manpower. Needless to say, completing this PhD would not have been possible without the exceptional support of a dedicated group of individuals: Alexandra Barkman, Richard Chen, Hendrikje Jorissen, Chloé-Rose Colombero, Elena Turner, and Kylie Bebe. The latter three were also fabulous women whom I had the privilege to mentor, but truthfully, I learned just as much from them as they did from me. These three joined the lab during the latter half of my PhD, when my energy levels were waning, and motivation was sometimes hard to come by. However, their enthusiasm, curiosity, and eagerness to learn never failed to uplift our spirits, resulting in some of our best days on the water. In addition to this exceptional team, I extend my gratitude to the Dive Safety Office, who always prioritized our safety and ensured we were equipped with the latest safety and rescue protocols. I also owe a huge thank you to Austin Greene, who dedicated numerous hours to teaching me how to build, program, and deploy KiloCams and CoralCams, both of which were instrumental for my third chapter. Last but certainly not least, I extend a heartfelt thank you to Roger Pfeffer and Sarah Masciangelo, without whom I would not have been able to conduct fieldwork in Waikīkī and Kewalo.

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You might have thought I was close to wrapping up, but fortunately for you, there are more people to thank. I must extend a huge thank you to the many individuals at the University of Hawaiʻi who work tirelessly behind the scenes and often do not receive the recognition they deserve: Pia Dizon, Audrey Shintani, Carrie Caruso, Jenna Oʻ Neill, and Mark Nakamoto. Despite being frequently overworked, this remarkable group of individuals was always quick to respond to questions and adept at troubleshooting when issues arose, ensuring that all programs ran smoothly. A special shout-out goes to Jenna and Audrey, who patiently dealt with my many emails and inquiries as we navigated planning the Tester Symposium. From the graduate office, I offer heartfelt thanks to Kristen Connors, whose exceptional skills keep many of us students on track. Kristen not only helped me navigate the intricacies of my NSF GRFP award but also played a pivotal role in securing another funding award – the NSF INTERN – by providing invaluable feedback and tirelessly seeking answers to any uncertainties in the application process. I also extend a huge thank you to Jeff Kuwabara, who not only transported us to our field sites on multiple occasions but also taught the most memorable fish identification class. Jeff had ingenious tricks for learning intricate species names; I still remember "*Gomophosus varius"* thanks to his comical pronunciation, which I wish I could replicate on paper.

Conducting fieldwork with SCUBA demands not only significant manpower but also substantial financial resources, given the need for expensive, specialized equipment. The organizations that generously awarded me funding played a pivotal role in enabling me to complete my research. First and foremost, I extend a huge thank you to the National Science Foundation, which granted me a Graduate Research Fellowship and an INTERN fellowship. Equally deserving of gratitude is the funding I received from the NOAA Coral Reef Conservation Program. Both of these funding sources not only covered the costs associated with my research but also provided stipends, allowing me to reside in Hawaiʻi and dedicate my energy entirely to my research. In addition to these major funding sources, I am grateful for the scholarships and grants I received from Soroptimist International of the Americas, as well as various sources within the University of Hawaiʻi, including the Graduate Student Organization Grant and the Charles H. & Margaret B. Edmondson Research Fund Award.

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"Good company in a journey makes the way seem shorter." — Izaak Walton

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Chapter 1 – General Introduction

Daniela Escontrela Dieguez

Coral reefs are important undersea oases providing numerous goods and services to humanity (Moberg and Folke 1999). For example, coral reef tourism is a major revenue source in the United States (Spalding et al. 2017) and shoreline protection by reefs substantially reduces coastal erosion and flooding costs (Beck et al. 2018). As ecosystem engineers (Jones et al. 1994), corals are also ecologically important, offering habitat for a quarter of marine species (Knowlton et al. 2010), including fishes (Coker et al. 2014) and invertebrates (Stella et al. 2010).

Despite their importance, coral reefs have seen a 50% reduction in global cover since the 1950s due to increased human-induced stressors at both local and global levels (Eddy et al. 2021). Globally, rising ocean temperatures have made coral bleaching events more frequent and severe (Hughes et al. 2018), with predictions of annual occurrences as early as 2040 (Van Hooidonk et al. 2016). Locally, threats such as overfishing (Roberts 1995), sewage discharge (Sutherland et al. 2010), and sedimentation (Erftemeijer et al. 2012) add to coral reef stress. Given the numerous socioeconomic and ecological benefits coral reefs provide, their protection is imperative.

Addressing global stressors like coral bleaching will require time and international cooperation. In the meantime, evidence suggests that local management can help offset global changes or at least buy reefs time until carbon emissions are stabilized (Kennedy et al. 2013, Anthony 2016, Donovan et al. 2021). Effective local management will necessitate both passive (e.g., habitat protection) and active (e.g., restoration) interventions (Possingham et al. 2015), but the success of these approaches hinges on our understanding of coral reef ecology, particularly trophic interactions such as corallivory (predation on corals). Corallivores include a variety of taxa such as annelids, mollusks, crustaceans, echinoids, and fishes (Cole et al. 2008, Rotjan and Lewis 2008). These predators exhibit various feeding modes, consuming coral mucus, polyps, and/or tissue (Rice et al. 2019). As a natural and essential component of coral reefs, corallivores affect reefs at both the colony and reefscape scale.

The effects of corallivores on coral colonies are well documented (Cole et al. 2008, Rotjan and Lewis 2008, Rice et al. 2019). The most obvious consequence of corallivory is full colony mortality (Kopecky et al. 2021). But, because corals are limited by metabolic resources, predation can also reduce overall growth (Henry and Hart 2005, Lenihan and Edmunds 2010, Palacios et al. 2014), inhibit sexual reproduction (Henry and Hart 2005), and/or lead to morphological changes (Palacios et al. 2014) while materials and energy are directed to wound healing. Selective predation on coral polyps ripe with eggs has also been documented (Rotjan and Lewis 2008) and lesions caused by predators do not always heal, further debilitating corals and making them more susceptible to disease (Bak and Steward-Van Es 1980).

These colony-level effects often translate to changes at the reefscape level. Outbreaks of corallivores can lead to mass mortality events of corals. This phenomenon has been well documented on the Great Barrier Reef and in French Polynesia, where predation by the crown-of-thorns sea star (*Acanthaster planci*) was the leading source of coral mortality prior to recent bleaching events (De'ath et al. 2012, Kayal et al. 2012). Corallivores also help moderate coral-coral and coral-algae competition. For example, Cox (1986) found that selective predation of the faster-growing *Montipora capitata* by the corallivorous *Chaetodon unimaculatus* opened space for the slower-growing *Porites compressa*. Other animals, such as parrotfishes, which double as corallivores and herbivores depending on species and body size, can also moderate coral-algae competition (Miller and Hay 1998). Predation has also caused shifts in community composition towards predation-resistant coral species (McClanahan et al. 2005) and corallivores can hinder coral reef recovery after disturbance events (Mumby et al. 2016, Bruckner and Coward 2019).

The ecological importance of corallivores demands that we have better tools to accurately quantify predation on corals and understand its drivers. *In situ* visual surveys, where divers count bite marks underwater, have been the standard for corallivory assessments. However, these surveys are field-intensive and underwater time is limited, restricting the type and quantity of data divers can collect on a single dive. Alternatively, photoquadrats—post-hoc estimates of bite counts from individual photos of the reef—have been used. However, photoquadrats capture only small, non-continuous reef areas and may underestimate corallivory due to the challenge of studying a 3D environment through a single 2D image. Structure-from-motion (SfM) photogrammetry is increasingly being used by reef managers and can compile many reef metrics from a single model (Bryson et al. 2017, Ferrari et al. 2017, House et al. 2018, Lange and Perry 2020, Kornder et al. 2021). In the context of corallivory surveys, SfM has been used to study only parrotfish corallivory (Charendoff et al. 2023a, 2023b), but no studies have assessed its validity in quantifying corallivory more broadly.

Given the lack of studies investigating the use of SfM for accurate corallivory monitoring, the second chapter of this dissertation, “Whose Bite? Evaluating the use of structure-from-motion for monitoring corallivory,” compares *in situ* visual surveys with SfM surveys. The goals of this study were to (1) compare corallivory rates derived from SfM annotations with estimates from *in situ* surveys, (2) assess the strengths of SfM by evaluating how variables that could impose time limitations in the field—specifically depth and hard coral cover—influenced the recorded bite mark counts, and (3) evaluate how nuances specific to quantifying different types of predation on different coral species affected estimates from SfM.

With the growing need for passive and active management interventions, corallivores have emerged as a potential obstacle to the success of restoration activities. For example, recently outplanted corals experience high levels of predation (Koval et al. 2020, Smith et al. 2021), potentially undermining the efficacy of restoration efforts. Understanding trophic interactions such as corallivory could help inform more effective management strategies. Prey choice (Rotjan and Lewis 2008), the healing potential of bite scars (Cameron and Edmunds 2014), and the relationship between hard coral cover and the local distribution and abundance of corallivores (Bouchon-Navaro and Bouchon 1989, Jayewardene et al. 2009, Roff et al. 2011, Burkepile 2012) have been well documented. However, patterns have been equivocal and corallivory patterns show regional variation (Cox 1986, Pratchett 2005). Furthermore, the relationship between coral cover and corallivory is often not disaggregated by the availability of all coral species (Jayewardene et al. 2009), which is important given that corallivores use corals for both refuge (Cole et al. 2008) and as a source of food (Rotjan and Lewis 2008). Regional variance in corallivory patterns, combined with inconsistent results among studies at different localities, underscores the need for place-based knowledge to inform regional reef management.

Given the need for place-based knowledge, the third chapter of this dissertation, “Exploring corallivory patterns around O‘ahu, Hawai‘i to guide coral reef management,” used SfM data from chapter two to investigate patterns and drivers of corallivory around O‘ahu.

Based on previous studies and field observations, we hypothesized that only a select few coral species would be heavily consumed. Specifically, *Montipora* spp., *Pocillopora* spp., and *Porites* spp. were expected to be among the most eaten, with susceptibility varying by predator type. Since corallivores depend on coral for food and shelter, we also hypothesized that predation intensity would increase with resource availability (i.e., hard coral cover) and that there would be stronger positive relationships between predation and species-specific coral cover for the preferred coral species of each predator. Lastly, we hypothesized that the healing condition of observed corallivore bite marks would vary among coral species and predator types, with more healing bite marks observed on coral species with shallower tissue layers and on wounds of a more superficial nature.

Lastly, I delved into a native coral predator found around the island of O‘ahu, the cushion star (*Culcita novaeguineae*). Cushion stars are browsers that feed on coral polyps by everting their stomach over their prey (Birkeland 1989). Surveys conducted in the 1980s found densities of less than 21 individuals per hectare at my study site off Waikīkī, O‘ahu, whereas recent surveys I conducted in the same location had an average of 30 individuals per hectare (Glynn and Krupp, 1986, D. Escontrela Dieguez unpublished). Past studies have investigated the feeding preferences of the cushion seastar, but these studies lasted for short periods of time (e.g., approximately one day) (Glynn and Krupp 1986, Hawkins 2006, Bell 2008), tested only a few of the coral species common in Hawai‘i (Glynn and Krupp 1986), and were either conducted only in laboratory settings (Glynn and Krupp 1986, Hawkins 2006, Bell 2008) or were purely observational studies (Goreau et al. 1972, Thomassin 1976, Montalbetti et al. 2019).

Understanding which coral species are most susceptible to predation will be imperative for managers in the event of a cushion sea star outbreak.

Due to limitations in previous prey preference studies, chapter four, “Corallivory by the cushion seastar (*Culcita novaeguineae*) in Hawai‘i,” used manipulative *in situ* experiments to understand the feeding behavior and preferences of the cushion seastar. Drawing from previous studies, field observations, and known coral characteristics, we hypothesized that cushion seastars consume coral species in a nonrandom manner. Specifically, we predicted that, cushion seastars would exhibit the following hierarchy of prey choice, listed from most preferred to least preferred: *Pocillopora* spp., *Pavona varians*, *Pavona duerdeni*, *Montipora patula*, *Montipora capitata*, *Leptastrea* spp., *Lobactis scutaria*, and *Porites compressa* and mounding *Porites* tied at the bottom of the hierarchy.

The research presented in this dissertation employed observational and field studies to develop new tools for monitoring corallivores, investigate patterns and drivers of corallivory around the island of O‘ahu, and examine the feeding behavior of a prominent corallivore in the region.

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Chapter 2 – Whose bite? Evaluating the use of structure-from-motion for monitoring corallivory

Daniela Escontrela Dieguez, Roseanna M. Lee, Courtney S. Couch,
Jonathan A. Charendoff, and Tye L. Kindinger

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Abstract

Corallivory, or predation on corals, is a naturally occurring process which at high levels can impair coral growth, reproduction, and recovery. Traditionally, corallivory monitoring has been achieved through *in situ* visual surveys and 2D photoquadrats. However, 3D imaging techniques, such as structure-from-motion (SfM), provide a powerful tool to collect high resolution colony-level data with limited field effort. Here, we conducted corallivory surveys using a recently developed SfM method around the island of O‘ahu, Hawai‘i paired with *in situ* surveys to evaluate the accuracy of SfM as a corallivory monitoring tool. Our primary objectives were to test for differences in bite counts between methods and to understand how depth, hard coral cover, type of predator, and coral species further influenced that difference. Overall, bite counts varied significantly between methodologies, with higher counts recorded through SfM annotations, and an average difference between methods of 17.34 bite marks m^{-2}. These differences further varied among types of predators in combination with the coral species they consumed. Lastly, at deeper and higher coral cover sites, the difference in bite counts between methods was greater than those at shallower and lower cover sites. These differences likely reflect the inherent air and time limitations divers face that do not exist when annotating SfM models. Despite differences in absolute counts, both methods were consistent in the qualitative patterns of relative corallivory across sites, whereby methods aligned in the ranked order of sites from the least to most corallivory observed, and the estimated difference between methods was modest in relation to the range of observed bite mark densities. Overall, our results indicate SfM is a viable tool to quantify corallivory, with the added benefit of enhanced accuracy at sites where diver-based surveys are logistically limited.

Keywords: Corallivory, coral predation, coral reef, photogrammetry, structure-from-motion, benthic monitoring, Hawaiʻi

2.1 Introduction

Corallivores, or coral predators, encompass a diverse range of taxa (Rotjan and Lewis 2008) which confer many important benefits to coral reefs. For example, they can remove high sediment loads from corals (Stewart et al. 2013), mediate coral-coral (Cox 1986, Littler et al. 1989) and coral-algal competition (Miller and Hay 1998), and deter more voracious coral predators (Glynn 1976). However, corallivores can also negatively affect corals. At the colony level, corals have the ability to heal corallivory scars, but predation can hinder coral growth and reproduction as metabolic resources are diverted to wound healing (Henry and Hart 2005, Lenihan and Edmunds 2010, Palacios et al. 2014). Corallivores can also selectively feed on gravid polyps (Rotjan 2007), transfer diseases between coral colonies (Nicolet et al. 2018, Renzi et al. 2022), or cause complete colony mortality (Jayewardene et al. 2009). Moreover, corallivores are known to feed on coral recruits and/or juveniles which may impair or slow recovery following disturbance events (Mumby et al. 2016), and recently outplanted corals often experience high levels of predation, potentially threatening the efficacy of coral restoration efforts (Koval et al. 2020, Smith et al. 2021). At high densities, corallivores have also caused mass mortality of corals (De'ath et al. 2012). Aside from the negative effects of corallivory, coral reefs face many other threats at both global (e.g., ocean warming and acidification [(Hoegh-Guldberg and Bruno 2010, Hughes et al. 2018)]) and local scales (e.g., sedimentation [(Erftemeijer et al. 2012)], sewage discharge [(Sutherland et al. 2010)], etc.), which can further compound the effects of corallivory. For example, prolonged elevated temperatures can hinder wound healing from corallivores in *Acropora* spp. (Bonesso et al. 2017), overfishing can free invertebrate corallivores from top-down controls (McClanahan 1994), and nutrient enrichment can prolong wound repair in some coral species (Renegar et al. 2008). As threats to corals escalate and compound the effects of corallivory, coral reef managers increasingly need to implement monitoring strategies to track changes in corallivory.

The effect corallivores have on corals can be determined by their feeding mode, of which there are four modes: (1) mucus eaters (e.g., *Trapezia* crabs) consume only mucus and some coral tissue, (2) browsers (e.g., some seastars, snails, and blennies) remove only coral tissue, (3) scrapers (e.g., some pufferfishes, filefishes, and parrotfishes) remove living tissue and a superficial layer of skeleton, and (4) excavators (e.g., some pufferfishes, filefishes, and parrotfishes) remove substantial tissue and coral skeleton (Rotjan and Lewis 2008, Rice et al. 2019). Differentiating between these feeding modes is important because they can lead to varying coral healing rates (Rempel et al. 2020) that vary among coral species. For instance, scraper and browser bite marks heal more rapidly on *Pocillopora meandrina* than massive *Porites* species, whereas excavator lesions exhibit faster healing rates on massive *Porites* than *Pocillopora meandrina* (Cameron and Edmunds 2014). Therefore, monitoring tools must be able to distinguish between feeding modes as these can lead to distinct outcomes for coral colonies and coral reef communities.

Corallivory assessments have historically been completed using *in situ* surveys, where divers count bite marks while underwater, and from photoquadrats, which are post-hoc estimates of bite counts derived from assessments of individual photos. While *in situ* visual surveys are the current standard, they are field-intensive, have high long-term costs associated with field work, and validating observations would require multiple divers to survey the same area, further limiting the spatial extent of surveys as more resources are devoted to a single area. Alternately, photoquadrats offer a rapid way to gather corallivory data, but typically capture small, non-continuous reef areas and may underestimate corallivory due to the challenge of studying a 3D environment with a 2D image (Rice et al. 2020). Structure from Motion (SfM) photogrammetry is an imagery-based technique that is increasingly being used to monitor coral reefs (Remmers et al. 2024). SfM surveys capture hundreds to thousands of overlapping photographs of a coral reef, which are then assembled using computer software to construct 3D point clouds and 2D, top-down projections of the reef. Using SfM as a corallivory monitoring tool would enable researchers to survey continuous reef areas, thereby expanding coverage, and because imagery for multiple models can be captured in one dive, more surveys could be conducted per site. Furthermore, annotators could validate observations with each other without using up underwater time and estimates are likely more accurate than those derived from photoquadrats because surveyors have access to multiple images from different angles of the same reef area. Within the context of corallivory surveys, SfM has been used to study only parrotfish corallivory (Charendoff et al., 2023a, 2023b), with no studies conducted to assess its validity in quantifying corallivory more broadly.

Here, we conducted corallivory surveys using a recently developed SfM methodology paired with *in situ* visual surveys, hereafter *in situ* surveys, to evaluate the accuracy of SfM as corallivory monitoring tool. The goals of this study were to: (1) understand how corallivory rates derived from SfM annotations compared to estimates from *in situ* surveys, (2) assess the strengths of SfM by evaluating how variables that could impose time limitations in the field—specifically depth and hard coral cover—influenced the recorded bite mark counts, and (3) evaluate how nuances specific to quantifying different types of predation on different coral species affected estimates from SfM.

2.2 Materials and Methods

Sampling Design

Between June 2021 and October 2022, we surveyed two to six 20 m transects (sample size varied due to logistical constraints) at ten sites around Oʻahu, for a total of 39 transects (Figure 2.1). All sites were at least 3 km apart and transects within each site were separated by at least 20 m. Sites were selected to encompass a range in coral cover, rugosity, habitat type (as described in (Winston et al. 2020), and depth (Table S2.1). Transect placements within each site were haphazardly chosen along each depth contour.

In situ data collection

We surveyed all live coral tissue within seven 1 m × 1 m quadrats spaced 3 m apart along each 20 m transect. We recorded the number of bite marks on all live coral tissue, coral species, and identified the type of predation mark (hereafter 'bite mark category'; Table 2.1; Escontrela Dieguez et al. 2023). Although parrotfishes are considered scrapers and excavators, their bite marks received their own category in this study because they had a distinct bite shape that was easy to identify on most coral species. Note that parrotfish bites were not discernable on *Pocillopora* spp. and likely were lumped into the scraper and excavator category in those instances. We identified all corals to the species level except *Porites lobata* and *P. evermanni,* which were both categorized as “Massive *Porites*" and *Leptastrea bewickensis, L. purpurea,* and *L. transversa,* which were categorized as “*Leptastrea* species” due to difficulties in telling these species apart. Additionally, we documented invertebrate predation by *Drupella* snails and seastars, but ultimately excluded these predation types from the analysis due to infrequent occurrence (n= 24 out 273 quadrats). The placement of each quadrat was marked with a painted fishing weight to mark the boundary of the quadrat for post-hoc SfM analysis.

Structure-from-motion data collection

We collected SfM imagery covering the same transect area where we laid down quadrats to conduct corallivory surveys following techniques delineated in (Suka et al. 2019). Briefly, all imagery was captured using a Canon SL2 camera with an Ikelite housing and an 18 mm - 55 mm lens fixed at 18 mm. Imagery was inspected for issues with quality and uploaded to Agisoft Metashape to construct 3D dense point clouds (DPC) and 2D top-down orthomosaics, or geometrically accurate composite images based on the 3D structure of the DPC. Orthomosaics were exported from Agisoft Metashape (1 mm/pix resolution) and imported to ArcGIS Pro, where a geodatabase was added to each model and transect lines and quadrats were delineated, as described in Escontrela Dieguez et al. (2023). The fishing weights served as a guide for quadrat and transect placement in each ArcGIS Pro project and helped ensure the same reef areas were annotated as in the *in situ* surveys. We inspected the underlying imagery for all live coral tissue found within each quadrat using Viscore. When we found bite marks, we used the multipoint tool in ArcGIS Pro to annotate each bite mark and recorded the number of bite marks, coral species on which they were found, and bite mark category. Two annotators extracted corallivory data from all models: one annotator was involved in both *in situ* surveys and annotations, while the other focused solely on annotations. Before commencing the full annotation process, both individuals independently annotated the same six quadrats to calibrate with each other.

Hard coral cover data collection

To estimate percent cover of live coral per quadrat, we clipped images of each quadrat from high resolution orthomosaics (default resolution <1 mm/pix), hereafter orthoblocks, using the methods described in Escontrela Dieguez et al. (2023). Orthoblocks were imported to CoralNet, a software used for benthic image analysis, where we annotated 35 randomly selected points to the lowest taxonomic level of coral species. The percent hard coral cover for each quadrat was then calculated by dividing the number of points that were categorized as hard coral species by 35.

Data analysis

All data were analyzed using R v4.3.1. The number of bite marks, between-method count differences, hard coral cover, and depth were averaged across quadrats per transect. We used plots of residuals versus fitted values to test for homoscedasticity and q-q plots of residuals to test assumptions of normality.

To understand how corallivory rates derived from SfM annotations compared to estimates from *in situ* surveys, we employed a Wilcoxon Rank Test with and without outliers to test for differences in the total number of bite marks between methods. We defined outliers according to

(Baumann et al. 2022). To assess the strengths of SfM, we ran two analyses evaluating how variables that could impose time limitations in the field influenced recorded bite mark counts. First, we examined how bite mark counts varied between methods with depth by constructing a generalized linear mixed effects model (GLMM) using the Poisson distribution and site as a random effect. Second, we used a GLMM with a Poisson distribution to examine how bite mark counts varied between methods and bite mark categories with hard coral cover. Besides site, we also added depth, binned into 5 m increments, as a random effect to account for variability not explained in our fixed effects. Lastly, to evaluate nuances specific to quantifying corallivory with SfM, we examined how between-method differences varied between coral species with hard coral cover by building linear mixed effects models (LMMs) for each bite mark category with site and depth, binned into 5 m increments, as random effects. For these models, we removed all coral species in each bite mark category with less than four observations because their inclusion resulted in very wide confidence intervals from which we could not draw any conclusions.

The fixed effects in each model were evaluated for significance using likelihood ratio tests (LRT). Upon identifying significant interactions, we tested for differences between slopes using the ‘lstrends’ function in R (Lenth 2016). When interactions were not significant but individual predictors were, we tested for differences between levels using post-hoc Tukey’s test for pairwise comparisons.

2.3 Results

SfM vs. *in situ* surveys

Bite counts significantly differed between methods (Wilcoxon signed-rank test, z = -3.09, p = 0.002), even when outliers were excluded (z = -2.21, p = 0.03). We identified five outliers, three at Hanauma and two at Kewalo (Figure 2.2). The mean difference between methods (SfM counts minus *in situ* counts) was 17.34 bite marks m^{-2}, with SfM annotations recording 77.8% more bite marks than *in situ* surveys, which was more pronounced above 50 bites/m^{-2} (Figure 2.2).

SfM strengths

We found that the number of bite marks varied across depth depending on the method used (method × depth, LRT, $p < 0.0001$; Table S2.2). We detected higher corallivory rates through SfM surveys than *in situ* surveys, with greater differences between methods at deeper sites (Figure 2.3). Bite counts from SfM surveys increased with depth (slope = 0.04), particularly deeper than 8m, while counts from *in situ* surveys decreased with depth (slope = -0.05).

Bite mark counts varied with hard coral cover depending on method and bite mark category (method × hard coral cover × bite mark category, LRT, $p < 0.0001$; Table S2.2). Because the three-way interaction was significant, we built GLMMs for each bite mark category which further confirmed that for all predation types, bite mark counts varied with hard coral cover depending on the method used (method × hard coral cover, LRT, $p < 0.01$, Table S2.2). For all bite mark categories, the difference in bite counts between methods was greater at higher percent hard coral cover, with higher bite mark detection through SfM annotations. This interactive effect was particularly evident for blenny and parrotfish bites when coral cover was above 40% (Figure 2.4).

Considering the potential confusion between scraper and excavator bite marks, we also tested the three-way interaction with scraper and excavator bite marks combined. The three-way interaction as well as the subsequent method × coral cover GLMM for the combined category remained significant (Table S2.2 and S2.3).

SfM annotation nuances

Analysis of bite marks across coral species revealed the exclusive detection through SfM annotations (i.e., bite marks were not seen on these coral species *in situ*) of parrotfish bite marks on *Pavona duerdeni* and *Pocillopora meandrina*, excavator bite marks on *Pocillopora grandis*, and scraper bite marks on *Pavona duerdeni*.

Only for blenny bites marks, the difference between methods varied with coral cover depending on the coral species (hard coral cover × coral species, LRT, $p < 0.05$; Figure 2.5 and Table 2.2). However, pairwise comparisons of slopes between coral species did not yield significant results. Between-method differences remained close to zero irrespective of coral cover for *Porites compressa* and *Montipora patula.* However, for massive *Porites,* as hard coral cover increased, more bite marks were counted with SfM than *in situ* surveys.

For all other bite mark categories, the relationship between hard coral cover and differences between methods did not vary by coral species (hard coral cover × coral species, LRT, $p > 0.05$; Figure 2.5 and Table S2.2). For parrotfish, between-method differences varied with coral cover (hard coral cover, LRT, $p < 0.01$, Table S2.2). As hard coral cover increased, more bite marks were counted with SfM than *in situ* surveys for all coral species. For excavators and scrapers, the difference between methods varied across coral species (coral species, LRT, $p < 0.05$, Table S2.2). Excavator bite marks on massive *Porites* were more frequently observed in SfM surveys, in contrast to *Pocillopora meandrina* which had higher predation detection through *in situ* surveys (Figure 2.6). Similarly, scraper bite marks on massive *Porites* were more frequently detected through SfM surveys, while scraper bite marks on *Pocillopora meandrina* and *Porites compressa* were more frequently seen during *in situ* surveys (Figure 2.6).

The difference between methods for combined scraper and excavator bite marks did not vary with hard coral cover nor was there a significant interaction of hard coral cover × coral species (Table 2.2). However, similar to the individual bite mark categories, coral species had a significant effect on between-method differences for this combined category (Table S2.2). The trends in differences between methods across coral species were the same as when these bite marks were considered individually.

2.4 Discussion

Our SfM surveys captured high resolution imagery which allowed us to quantify predation rates and to differentiate between corallivory types. SfM estimates of corallivory differed from *in situ* counts, with more bite marks detected through SfM annotations. The mean difference, averaged across all transects, of 17.34 bite marks m^{-2} (or 55.82 bites m^{-2} of live coral tissue) was modest, especially given the broad range of bite marks we observed (0 to 419.58 bite marks m^{-2} of live coral tissue *in situ* and 15.36 to 567.93 bite marks m^{-2} of live coral tissue with

SfM annotations). These estimates roughly align with another *in situ* study conducted on O‘ahu, where bite marks on *Pocillopora meandrina* by the Barred Filefish (*Cantherhines dumerilii*) reached 117 bite marks m^{-2} of live coral tissue and on *Porites compressa* by the Spotted Pufferfish (*Arothron meleagris*) was noted at 69 bite marks m^{-2} of live coral tissue (Jayewardene et al. 2009). Despite variations between methods, trends in corallivory rates across sites were generally consistent between methods, indicating that SfM served as an accurate tool to quantify corallivory.

We detected higher corallivory rates through SfM surveys than *in situ surveys,* with greater differences between methods at deeper sites and those with high coral cover. This bias is likely the result of time and air limitations for SCUBA divers during *in situ* surveys. For example, a transect at 17.4 m deep in Hanauma Bay had abundant *Porites compressa* beds characterized by long, slender branches. While the surveyor had air and time constraints underwater, spending approximately 60 minutes conducting the survey and capturing SfM imagery, annotators dedicated approximately 50 hours to reviewing the underlying imagery, resulting in higher bite counts in SfM surveys (30.73 bite marks m^{-2} difference). Differences between methods were also more apparent for blenny and parrotfish bite marks which can be small and densely concentrated, usually with considerable overlap, which demands more survey time (Bruckner et al. 2000, Carlson 2012). The shared characteristics of these bite marks (i.e., small and densely concentrated), coupled with time constraints at deep sites and the additional time required to survey areas with extensive coral cover, resulted in more pronounced differences between methods for these two bite mark categories. For example, at the Kewalo site, overlapping blenny bite marks on *Montipora patula* and *Montipora capitata* formed long, white tracks on coral colonies. Underwater, surveyors estimated bite mark numbers based on size and shape, while annotators took their time to discern individual bite marks. These differences between methods when counting small features align with findings from (Charendoff et al. 2023), which indicated that SfM annotations led to increased counts of small, cryptic juvenile coral colonies compared to *in situ* surveys. Overall, SfM enabled us to surpass the air and time limitations inherent with *in situ* surveys, thereby granting us additional time to locate and distinguish individual bite marks.

Between method differences in blenny, scraper, and excavator bite mark counts varied with coral species, likely resulting from challenges in identifying bite marks on specific coral species through SfM annotations. For instance, *Pocillopora meandrina* often exhibited pale branch tips which could be mistaken for healing excavator or scraper bite marks. With SfM, identifying missing parts of the skeleton was challenging, as photographs tended to pixelate upon zooming in. Consequently, these pale branch tips were excluded from the tally of bite marks when the missing skeletal parts were not discernible. Conversely, during *in situ* surveys, divers could inspect coral branches very closely to identify whether parts of the skeleton were absent, potentially contributing to higher and more accurate counts. Scraper and excavator bite marks on *Porites compressa* can resemble broken branches and were not included in bite mark counts when broken colony branches were in the vicinity. Due to time constraints underwater, our ability to search for broken branches *in situ* was limited, sometimes leading to an overestimation of scraper bite marks during *in situ* assessments. Both methods for corallivory monitoring examined here involve inherent trade-offs, highlighted by the nuances related to specific coral species and types of predation.

Considerations for the utility of SfM for monitoring corallivory

Similar to other coral reef monitoring surveys, there is no definitive gold standard for monitoring corallivory (Couch et al. 2021). For researchers, the choice of methodology will depend on the specific questions asked, the available resources, and the urgency with which corallivory needs to be monitored. For example, due to time and air limitations during *in situ* surveys, SfM would be a better option for researchers wishing to obtain more precise estimates of corallivory. Repeated SfM surveys could also allow for tracking of corallivory scars through time to assess the effects of corallivory on colony health. Furthermore, given our ability to extract multiple reef metrics from one model, we could better investigate drivers of corallivory. Even though we only surveyed discrete quadrats in this study, SfM would also allow researchers to quantify corallivory across continuous stretches of reef.

Availability of resources will also be an important consideration. While SfM entails high initial costs, including expensive camera equipment, computers and software, *in situ* surveys have lower upfront expenses. However, because divers are limited to conducting one to a handful of surveys per dive, surveyors would need to revisit the same transect multiple times to collect data on various reef metrics, and this extra underwater time results in long-term expenses associated with the need for SCUBA gear, personnel costs, and extra boat time.

Moreover, the urgency with which data are needed is a crucial factor to consider. In situations where rapid estimates of corallivory are needed, *in situ* surveys might prove more suitable, given that the post-processing time for SfM models can span weeks to months. In this study, most *in situ* surveys took between 45 and 90 minutes, and divers walked out of the water with data in hand. Alternatively, a single model can take anywhere from four to 12 hours to build, depending on the quantity and quality of images, in addition to the time required to add features in ArcGIS Pro and to annotate each model, which in this study spanned between one and 50 hours. Ultimately, this study showed SfM serves as a valuable tool to quantify corallivory, but the decision of methodology will depend on various factors.

Utility and future directions

Our study details the use of SfM photogrammetry for quantifying corallivory rates on coral reefs. There is no gold standard for monitoring corallivory and the availability of diverse monitoring tools for corallivory is crucial in coral reef management. The SfM method holds promise as it can address a wide array of questions beyond the scope of this study. At smaller spatial scales, this method could enable the monitoring of individual colonies, proving especially beneficial for outplanted coral colonies which are highly vulnerable to corallivory (Knoester et al. 2023). Applied across a time series, SfM could be used to study the effects of corallivory on colony survival and growth. Lastly, given the capacity to extract numerous coral reef metrics from a single model (Burns et al. 2015, Bryson et al. 2017, Ferrari et al. 2017, House et al. 2018, Lange and Perry 2020, Couch et al. 2021, Kornder et al. 2021), SfM stands as a valuable tool for investigating the factors influencing corallivory such as rugosity, coral cover, and coral diversity.

While this study was a first step towards using SfM as a corallivory monitoring tool, these methods are not without improvement. For example, divers could take detailed site notes pre- and/or post-image collection, noting the presence of corallivorous species and giving annotators an idea of which bite mark categories they should expect to encounter. Because SfM imagery capture requires only one diver, a second diver could document and photograph regions exhibiting excess corallivory. Lastly, implementing trained image classifiers such as CoralNet could automate and expedite the annotation process. As threats to coral reefs continue to intensify, efficient monitoring tools capable of extracting diverse coral health metrics will become increasingly vital for timely management interventions. This study showed that SfM can be used as one of these tools which captures accurate counts of corallivory.

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Author Contributions

DED was the project lead and was responsible for all aspects of this study including data collection, model building and annotation, data analysis, data management, and writing. RML was responsible for image post processing, model building, model annotation, and manuscript review. TLK conceived the idea for the project, funding, assisted with data analysis, and reviewed the manuscript. CSC and JC reviewed the data analysis and manuscript. All authors contributed to method development, the writing of this article, and approved the submitted version.

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2.6 Tables

Table 2.1 Table displaying fish bite mark categories, the associated fish species causing each bite mark, descriptions of the categories, and accompanying close-up photographs. Note that parrotfishes are known to be scrapers and/or excavators. However, bite marks were categorized as parrotfish bite marks when they had the characteristic shape described below, but scrapers and excavators could include parrotfishes when there is no distinct shape.

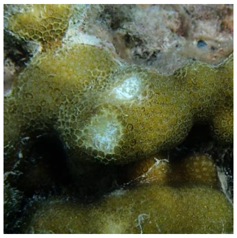
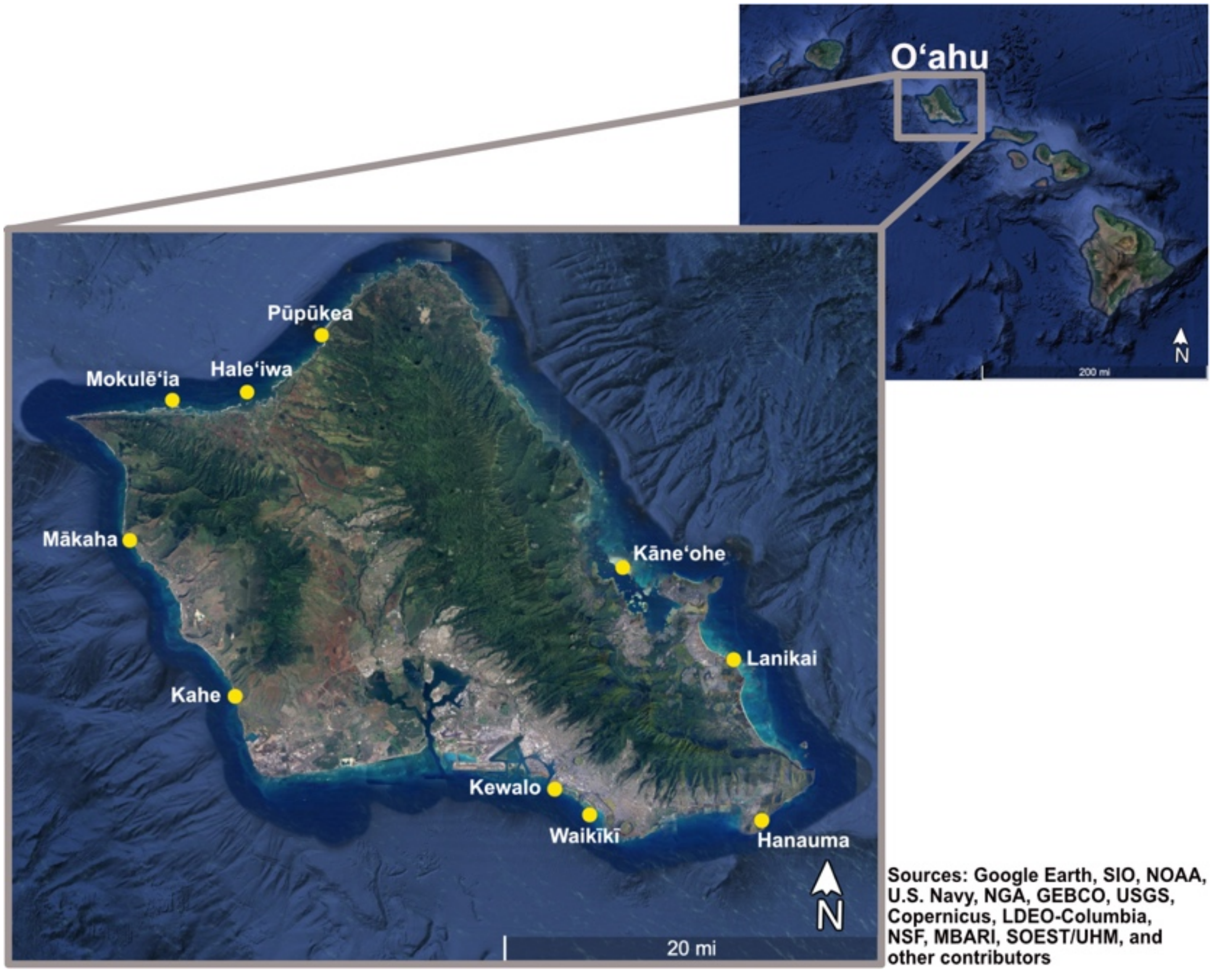
Bite Mark Category	**Blenny**	**Parrotfish**	**Scraper**	**Excavator**
Corallivore Species	*Exallias brevis*	Family Labridae, Subfamily Scarinae	- *Cantherhines dumerilii* - *Arothron meleagris* - Subfamily Scarinae	
Description	small circles with only tissue removal	paired, oval bite marks with superficial skeleton removal (gap between ovals not always evident)	shallow sections of skeleton removed (shallower than 3 mm)	large portions of skeleton removed (deeper than 3 mm)
Photograph				

Table 2.2 Comparison of SfM and *in situ* strengths and weaknesses

	SfM	***In situ* surveys**
Metrics collected per survey	Coral cover, rugosity, bleaching, coral disease, corallivory rate, etc.	Corallivory rate
Time limitations	None	Limited by depth and air
Area surveyed per unit time	Many transects over many reefs	Less transects over fewer reefs
Costs	High up-front costs	High long-term costs
Corallivory specific nuances	More likely to miss cryptic marks Harder to differentiate categories Harder to distinguish between pale branch tips & healed marks	Less likely to miss cryptic marks Easier to differentiate categories Easier to distinguish between pale branch tips & healed marks
Reviewing annotations	Can go back in time & can confer with other annotators	Cannot go back in time & difficult to confer with other surveyors
Time to data in hand	Weeks to months	Out of water with data in hand

2.7 Figures



Sources: Google Earth, SIO, NOAA, U.S. Navy, NGA, GEBCO, USGS, Copernicus, LDEO-Columbia, NSF, MBARI, SOEST/UHM, and other contributors

Figure 2.1 Location of 10 survey sites (yellow dots) around the island of O‘ahu, Hawai‘i.

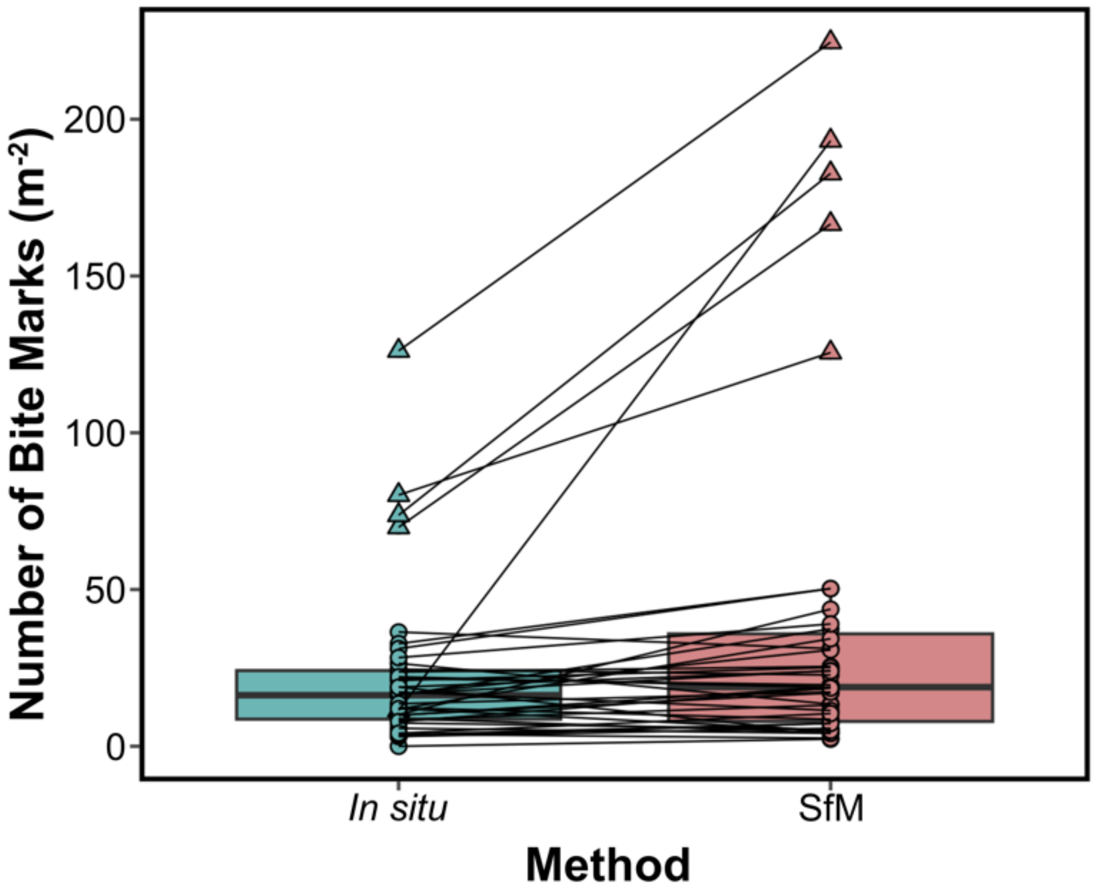


Figure 2.2 Boxplot illustrating transect-level corallivory density by method (Teal = *in situ*, Pink = SfM). Black lines connect the transect-level data between methods, while triangles denote outliers.

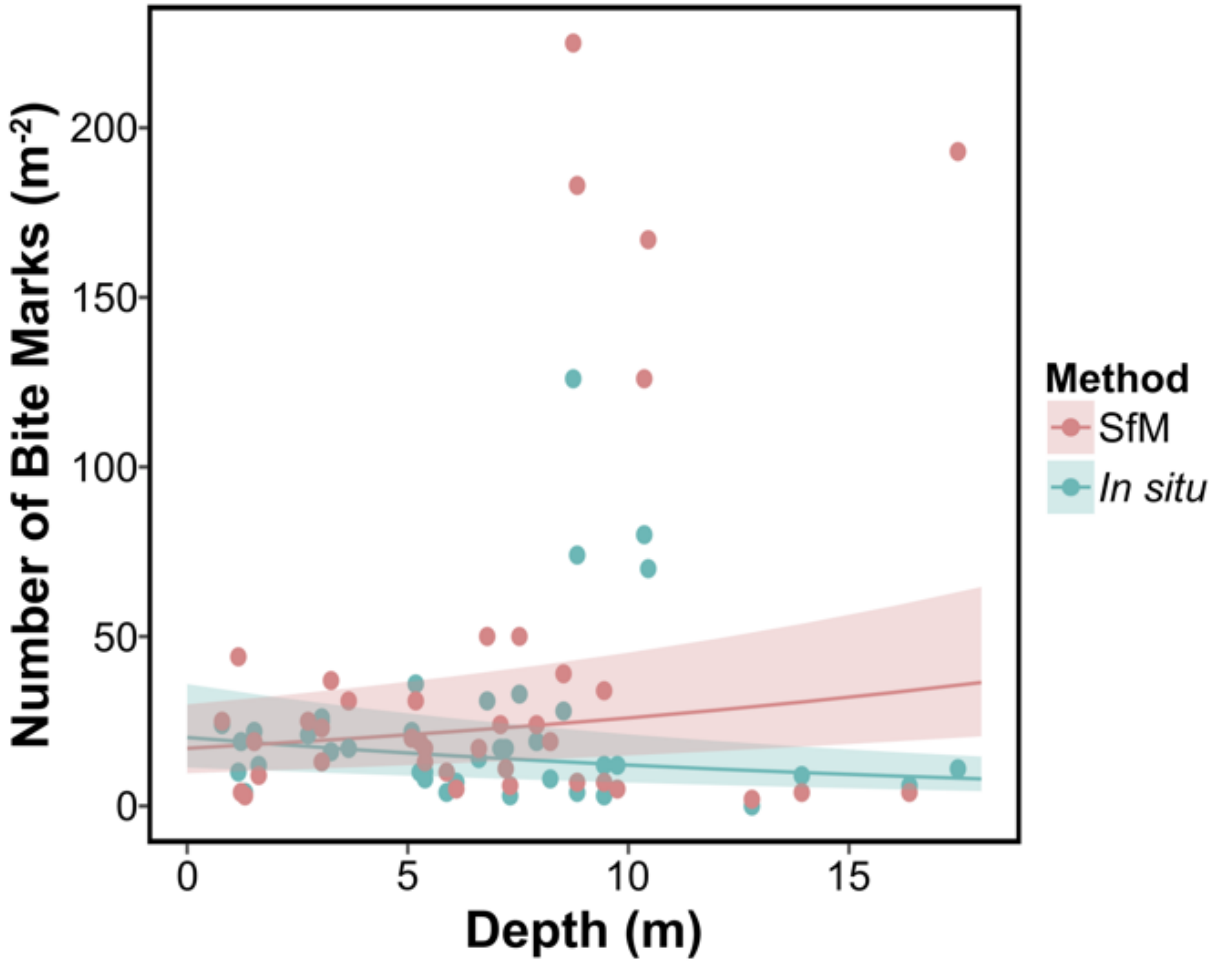


Figure 2.3 Marginal effects plot depicting corallivory density against depth and predicted values (lines) and 95% confidence intervals (shaded areas) from the GLMM by method (Teal = *in situ*, Pink = SfM).

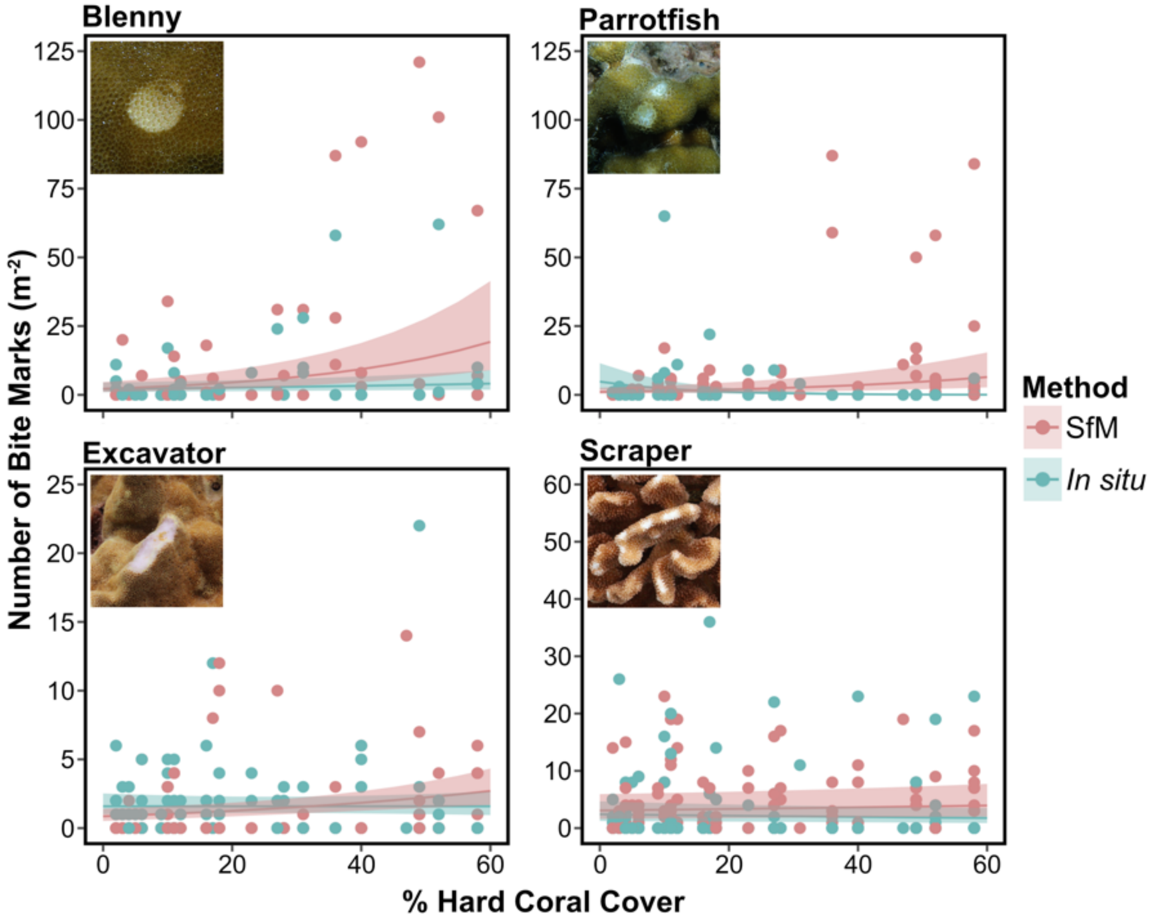


Figure 2.4 Marginal effects plot depicting corallivory density against hard coral cover for (A) blenny, (B) parrotfish, (C) excavator, and (D) scraper bite mark categories. Plots present predicted values (lines) and 95% confidence intervals (shaded areas) from GLMMs by method (Teal = *in situ*, Pink = SfM).

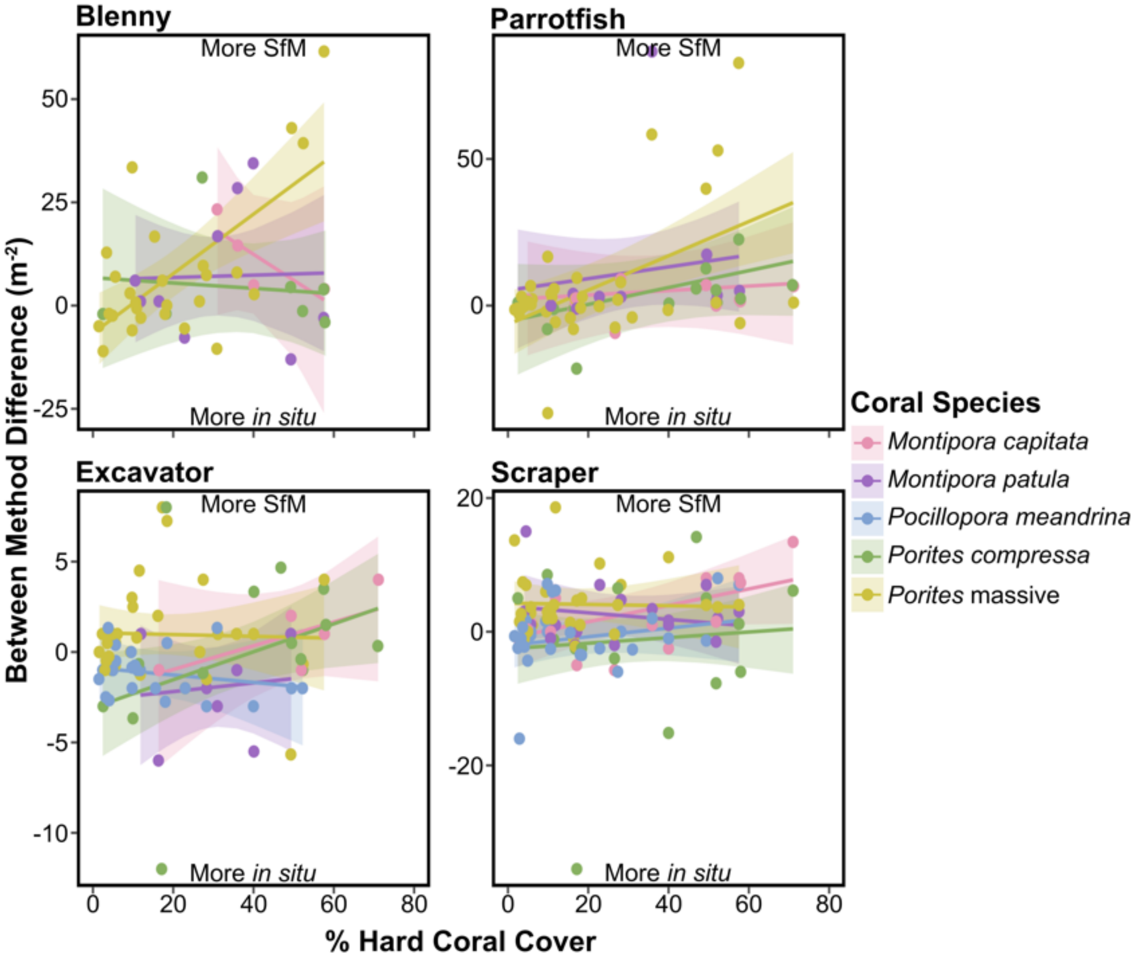


Figure 2.5 Marginal effects plot showcasing between-method differences in number of bite marks by percent hard coral cover for (A) blenny, (B) parrotfish, (C) excavator, and (D) scraper bite mark categories. Plots display predicted values (lines) and 95% confidence intervals (shaded areas) from LMMs categorized by coral species (Pink = *Montipora capitata*, Purple = *Montipora patula*, Blue = *Pocillopora meandrina*, Green = *Porites compressa*, Yellow = massive *Porites*). Coral species with fewer than four observations in each bite mark category were excluded. Positive values indicate more SfM bite mark counts while negative values indicate more *in situ* bite mark counts.

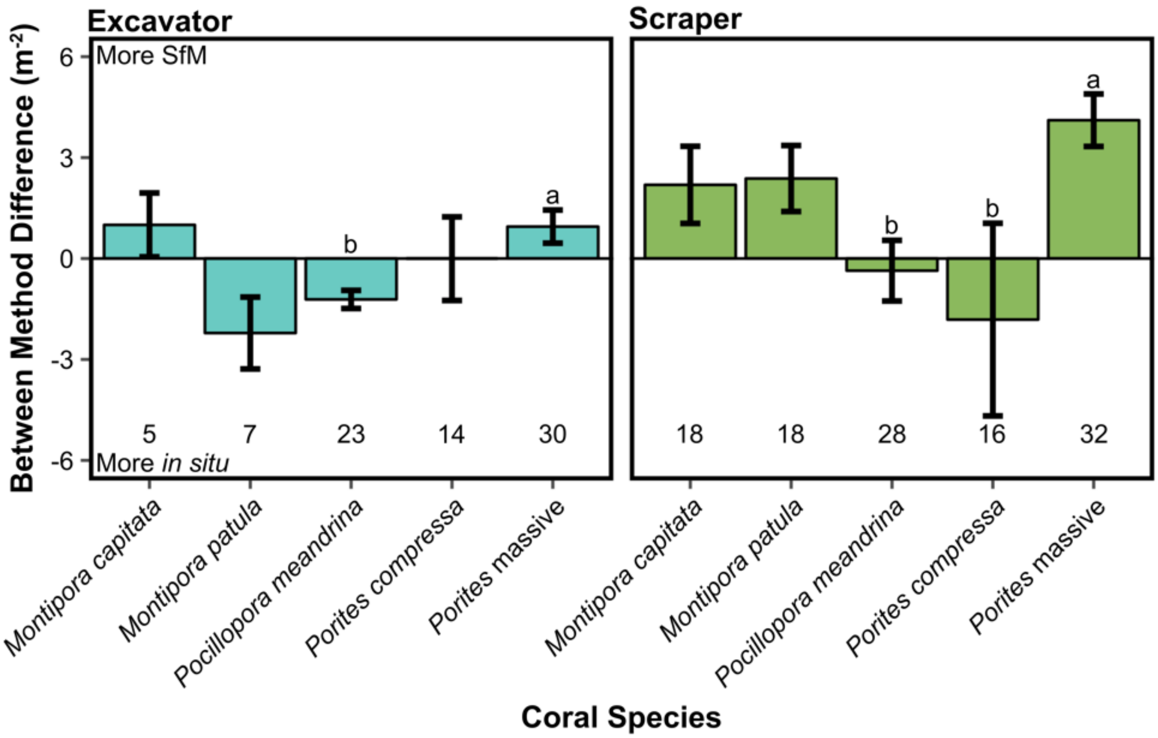


Figure 2.6 Bar graphs illustrating between-method differences in number of (A) excavator and (B) scraper bite mark categories by coral species ($\bar{x}$ ± SE). Positive values indicate more SfM bite mark counts while negative values indicate more *in situ* bite mark counts. The numbers below the bars denote the sample size for each coral species. Different letters (a, b) atop the bars indicate a significant difference between groups (post-hoc Tukey's test for pairwise comparisons, $P < 0.05$).

Chapter 3 – Exploring corallivory patterns around O‘ahu, Hawai‘i to guide coral reef management

Daniela Escontrela Dieguez, Roseanna M. Lee,
Courtney S. Couch, and Tye L. Kindinger

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Abstract

Coral reefs are in decline worldwide, requiring both passive and active management interventions to prevent collapse. The success of these interventions requires an understanding of the stressors that affect reef ecology, including trophic interactions such as corallivory. Corallivory, or predation on corals, is a naturally occurring process which, at high levels, can impair coral growth, reproduction, and survival. Regional variance in patterns of corallivory and inconsistent results among studies means place-based knowledge is vital to inform local reef management. We conducted photogrammetry surveys at ten sites around O‘ahu, Hawai’i, to quantify corallivory by reef fishes. We assessed coral species susceptibility to predation, the healing potential of bite marks, and because coral is both a food source and place of refuge for corallivores, we also tested the relationship between coral cover and predation. Of the 16 coral species we encountered, only six were widely consumed, and susceptibility varied by predator type. There was a positive correlation between hard coral cover and predation, but the strength of this relationship varied depending on predator type. We also found more positive relationships between coral cover and predation for the preferred coral species of each corallivore, further suggesting that the availability of specific coral species may affect corallivore abundance. Finally, the type of predator was more important than coral species in determining healing status, with excavators and scrapers (especially pufferfish and filefish) exhibiting the lowest proportion of healed marks. Regardless, we found a high proportion of healing bite marks across most coral species and types of predation. Given our results, we suggest managers carefully consider corallivore abundance when selecting sites for restoration. Furthermore, managers should consider conducting corallivore surveys prior to and after restoration activities to better track and

manage for potential changes in the abundance and composition of corallivorous species. Managers might also try to grow coral species vulnerable to predation to larger size classes before outplanting to overcome early life stage bottlenecks and employ a restoration design that prioritizes enhancing coral diversity to distribute corallivory across multiple taxa.

Keywords: Corallivory, coral predation, coral reef, photogrammetry, structure-from-motion, Hawaiʻi, coral restoration, trophic interactions

3.1 Introduction

Corals play a crucial role as ecosystem engineers (Jones et al. 1994), providing habitat that harbors a multitude of species and collectively form one of the most biodiverse ecosystems on earth (Knowlton et al. 2010). Despite their ecological importance, coral reefs around the world are in decline due to many local and global threats (Riegl et al. 2009, Birkeland 2019). Ensuring the long-term survival of coral reefs will necessitate both passive (e.g., habitat protection) and active (e.g., restoration) management interventions (Possingham et al. 2015). The success of these interventions hinges on understanding coral reef ecology, particularly trophic interactions such as corallivory (predation on corals).

Corallivores are a natural and essential part of coral reef ecosystems helping moderate coral-coral (Wellington 1982, Cox 1986) and coral-algae competition (Miller and Hay 1998), remove excessive sediment from corals (Stewart et al. 2013), and deter more voracious coral predators (Glynn 1976). But corallivores can also have negative consequences on corals and coral reefs as predation can impair coral fitness and further contribute to coral decline (De'ath et al. 2012). Even though bite marks often heal, predation can result in reduced growth and diminished reproductive output as corals allocate limited metabolic resources to wound healing (Henry and Hart 2005, Shaver et al. 2017). In more severe cases, corallivory can lead to shifts in community composition towards coral species that are resistant to predation (McClanahan et al. 2005), substantial energetic costs related to colony defense (Gochfeld 2004), and/or extensive removal of coral material (Hoey and Bellwood 2008, Palacios et al. 2014). Given the many effects of corallivores on reef ecosystems, management efforts aimed at enhancing coral reef persistence and resilience need to account for the role of coral predation.

Understanding coral species vulnerability to predation, the healing capacity of bite marks, and how live coral cover either concentrates or dilutes predation will be crucial to inform coral reef management. Numerous studies have documented the prey choice of corallivores, revealing that, globally, predators consume only a small subset of coral genera (Rotjan and Lewis 2008). The healing potential of bite scars has also been documented and varies depending on the coral species and type of predation (Cameron and Edmunds 2014). Differences in predation susceptibility and healing potential are partly attributed to coral characteristics such as morphology (Tricas 1989, Hall 1997) and tissue depth (Glynn and Krupp 1986, Henry and Hart 2005), which show geographical variance (Barnes and Lough 1992, Miller 1994) and likely contribute to observed regional differences in corallivory patterns (Cox 1986, Pratchett 2005). The relationship between hard coral cover and the local distribution and abundance of corallivores has also been documented, though results have been inconsistent (Bouchon-Navaro and Bouchon 1989, Jayewardene et al. 2009, Roff et al. 2011, Burkepile 2012). Furthermore, these relationships are often not disaggregated by availability of all coral species (Jayewardene et al. 2009), which is important given that corallivores use corals for both refuge (Cole et al. 2008) and as a source of food (Rotjan and Lewis 2008). Parsing-out these relationships based on coral species could provide insight into whether prey availability or refuge space plays a more important role affecting corallivore populations. For example, if predation increases with the abundance of some coral species but not others, this might be an indicator that availability of prey is more important than availability of refuge space in regulating corallivore abundance. However, this relationship assumes that the relationship between a species of coral as food versus shelter is known. Regional variance in patterns of corallivory, combined with inconsistent results among studies at different localities, underscores the need for place-based knowledge to inform local reef management.

Gaining a deeper understanding of the local patterns and drivers of corallivory will reveal considerations managers may want to incorporate into regional reef-management decisions. Corallivory studies in Hawaiʻi considered only a few coral predators at a time in some cases (Carlson 1992, Jayewardene et al. 2009), and relationships between coral cover and predation were considered only for a few coral species in other cases (Jayewardene et al. 2009). We conducted photogrammetry surveys to quantify corallivory across various predator types and on all coral species at multiple sites around the island of Oʻahu. Based on previous studies and field observations, we hypothesized that only a select few coral species would be consumed by predators. Specifically, *Montipora* spp., *Pocillopora* spp., and *Porites* spp. would be amongst the most consumed and susceptibility would vary by type of predator. Because corallivores depend on coral for food and shelter, we also hypothesized that predation intensity would increase with resource availability (i.e., hard coral cover), and that there would be more positive relationships between predation and species-specific coral cover for the preferred coral species of each predator. Lastly, we hypothesized that the healing condition of observed corallivore bite marks would vary among coral species and predator types, with more observations of healing bite marks on coral species with shallower tissue layers and on wounds of a more superficial nature.

3.2 Materials and Methods

Sampling design

We surveyed between two and six 20 m transects (sample size varied due to logistical constraints) at ten sites around O‘ahu, for a total of 39 transects (Figure 3.1). To capture a comprehensive range of corallivory patterns across various settings, we chose sites to cover a range in coral cover, reef rugosity, habitat type, and depth. We haphazardly placed transects at each site along each depth contour and ensured that transects were at least 20 m apart. All surveys were conducted between June 2021 and October 2022.

Corallivory data collection

We collected SfM imagery along each transect following the methods described in Suka et al. (2019). All imagery was captured using a Canon SL2 camera with an Ikelite housing and an 18 mm – 55 mm lens fixed at 18 mm. We imported images into Agisoft Metashape where we generated 3D dense point clouds (DPC) and 2D top-down orthomosaics, or geometrically accurate composite images based on the 3D structure of the DPC, which we exported at 1 mm/pix resolution (Suka et al. 2019). We imported orthomosaics into ArcGIS Pro where we added a geodatabase and delineated a transect line and seven 1 m x 1 m quadrats, spaced 3 m apart. We inspected the underlying imagery for all live coral within each quadrat for signs of predation using the software, Viscore, which allows users to visualize 3D models and the underlying imagery. We recorded the number of bite scars, coral species on which they were found, type of predator, and bite condition (Table 3.1; Escontrela Dieguez et al. 2023). Parrotfishes, despite being scrapers and excavators, were allocated a distinct predator type because we could readily identify their bite marks on all coral species except *Pocillopora* spp. Parrotfish bites, which were composed of two marks, were identifiable even when they were old because they were usually covered with a film of turf algae, which allowed us to detect both marks. All corals were identified to the species level except *Leptastrea* spp. and *Porites lobata* and *P. evermanni*, which we categorized as "massive *Porites*" due to challenges of species-level identification. Models were annotated by two individuals who calibrated with each other by both annotating the same six quadrats, at which point all data extracted were consistent between individuals.

Coral cover data collection

Using the methods described in Escontrela Dieguez et al. (2023), we extracted images of each 1 m x 1 m quadrat from high resolution orthomosaics (default resolution <1 mm/pix), hereafter orthoblocks. We loaded these orthoblocks into the web-based image annotation tool, CoralNet, where we annotated 35 randomly selected points per image to the lowest taxonomic level possible. Percent coral cover was calculated from a total of 35 points per image.

Data analysis

All data were analyzed using the statistical software, R (v4.3.1; R Core Team 2023). Bite mark densities, proportion of healed bite marks, hard coral cover, and depth were summarized at the transect level. We excluded from analysis coral species that did not experience any predation and those that were consumed in fewer than four transects (out of a total of 39 transects) because their inclusion resulted in wide confidence intervals from which we could not draw conclusions.

To determine whether specific coral species exhibited differential susceptibility to corallivory by predator type, we used a distance-based permutational multivariate analysis of variance (PERMANOVA) on a Bray-Curtis similarity matrix encompassing all consumed coral species to test for differences in consumption between predators. Data were square root transformed and the PERMANOVA assumption of multivariate homogeneity of dispersion among predator types was evaluated and confirmed for each model (PERMDISP2 procedure; Anderson 2006). We also performed a similarity percentage analysis (SIMPER) to determine the contribution of each coral species to similarities. Lastly, we explored data visually using a non-metric multidimensional scaling (NMDS) scatter plot with Bray-Curtis distance.

To investigate whether predation increased with resource availability, we conducted two analyses with bite density as the response variable. First, to assess how predation varied among predator types relative to hard coral cover, we constructed a generalized linear mixed effects model (GLMM) using predator type × hard coral cover as fixed effects. To then examine how predation varied across coral species and across coral abundance, we constructed separate GLMMs for each predator type and used coral species × the corresponding species-specific coral cover as fixed effects. In both models, we used the Poisson distribution and site and depth (binned into 5 m increments) as random effects.

Lastly, to examine the variation in healing status across coral species and predator types, we first excluded all bite marks categorized as “new” and those coral species exclusively associated with “new” bite marks (i.e., no old or healing bite marks were detected on those coral species), as we were aiming to assess the likelihood of healing. We calculated the proportion of healed bite marks out of pooled healed and old bites and subsequently applied a logit transformation to this proportion. To determine whether the proportion of healing bite marks differed by predator type and coral species, we constructed a GLMM using coral species and predator type as the fixed effects. Then, to discern whether the proportion of healed bite marks varied by coral species for each predator type, we developed separate GLMMs for each type of predator, using coral species as the fixed effect. For these models, we adopted the normal distribution, with site and depth (binned into 5 m increments) as random effects.

For all GLMMs, we used q-q plots of residuals to test for normality of the residuals and plots of residuals versus fitted values to test for homoscedasticity. Fixed effects in models were evaluated for significance using likelihood ratio tests (LRTs). We also performed sensitivity analyses by comparing results between models with versus without influential points defined according to Cook’s distance. When we identified significant interaction terms in a model, we tested for pairwise differences between slopes using the ‘lstrends’ function in the R package ‘lsmeans’ (v2.30.0; Lenth 2016). When individual categorical predictors were significant, we conducted post-hoc Tukey’s tests for pairwise comparisons.

3.3 Results

Coral susceptibility

Coral species varied in their level of susceptibility to predation, with massive *Porites, Montipora capitata, Montipora patula, Pocillopora meandrina,* and *Porites compressa* being the most vulnerable to predation. Susceptibility of the coral community varied significantly between coral predators (PERMANOVA, df = 3, F = 6.22, p = 0.001; Figure 3.2). Pairwise comparisons revealed significant differences between predators, except for blennies and parrotfishes which exhibited considerable overlap in the coral species they consumed (Figure 3.2, Table S3.1). Both Massive *Porites* and *Montipora patula* were most susceptible to blennies (massive *Porites:* 48.6% of bites, *Montipora patula*: 73.1% of bites) and to a lesser extent parrotfishes (massive *Porites:* 35.7% of bites, *Montipora patula*: 19.7% of bites). *Pocillopora meandrina* was mostly susceptible to scrapers (90.9% of bites), however it is worth noting that parrotfish bite marks could not be identified on this coral species, therefore some of this predation may have been inflicted by parrotfishes. *Montipora capitata* showed the highest susceptibility to blennies (42.7% of bites) and scrapers (35.6% of bites). Lastly, *Porites compressa* showed susceptibility to predation by scrapers (44.4% of bites) and parrotfishes (32.2 % of bites), and to a lesser extent excavators (18.9 % of bites) (Figure 3.2). The SIMPER analysis identified *Pocillopora meandrina*, *Montipora patula*, and massive *Porites* as key contributors to the differences observed between predators (Table S3.2). While we observed other coral species during surveys (i.e., *Cyphastrea ocellina*, *Leptastrea* spp., *Lobactis scutaria*, *Pavona duerdeni, Pavona varians*, *Pocillopora damicornis*, *Pocillopora grandis*, and *Pocillopora ligulata*), they experienced minimal (i.e., consumption observed in fewer than four transects) to no fish predation.

Bite mark density with coral abundance

Bite mark density (number of bite marks per m^2) was positively correlated with hard coral cover, yet the relationship also varied by predator type (type of predator × hard coral cover, df = 7, LRT = 171.4, $p < 0.0001$), even without outliers (df = 7, LRT = 222.77, $p < 0.0001$; Figure 3.3). There were significant differences in pairwise comparisons of slopes between all predators except parrotfish and blennies. However, similarities between these two predators seemed to be driven by outlier sites with high levels of parrotfish and low levels of blenny predation (see Table S3.3). After removing these outliers, parrotfish and blenny slopes were no longer similar and instead, parrotfish and excavator slopes became similar, likely due to the exclusion of a site with high parrotfish predation (see Table S3.3). As hard coral cover increased, the density of bite marks increased rapidly for blennies (slope without outliers = 7.01) and parrotfishes (slope without outliers = 5.71), particularly above 40% coral cover (Figure 3.3). Alternatively, scraper (slope without outliers = 1.14) and excavator (slope without outliers = 4.19) bite density remained stable as coral cover increased.

For all predator types, there was a positive relationship between predation density and coral cover in ways that varied depending on the coral species (Table 3.2, Figure 3.4, Table S3.4). Pairwise comparisons between slopes of predators were consistent when analyzing data with and without outliers except for one discrepancy with blennies (Table S3.4). Dissimilarities in the blenny slopes for *Montipora capitata* and *Montipora patula* with outliers were likely driven by a site with low blenny predation on *Montipora capitata.*

Species within the same genus did not always show the same relationship between predation and coral cover. For example, the density of blenny and parrotfish bite marks on massive *Porites* increased more rapidly with coral cover than for *Porites compressa* (Figures 3.4a, b), while the opposite was true for scrapers and excavators (Figures 3.4c, d). In some instances, species within the same genus did show similar relationships, for example with scraper bite marks on *Montipora patula* and *Montipora capitata* (Figure 3.4d). Of note is the exponential relationship between predation and coral cover for scraper bite marks on *Pocillopora meandrina,* even at very low coral cover (Figure 3.4a), although it is important to note that some of these bite marks might have been inflicted by parrotfishes. Blenny predation was not detected on *Pocillopora meandrina* (Figure 3.4a).

Healing status

Overall, we observed a high proportion of healing bite marks (>75%) across most coral species. The type of predator (LRT, df = 3, LRT = 69.96, $p < 0.0001$) was a more important factor in determining healing status than coral species (LRT, df = 4, LRT = 17.19, $p = 0.002$). Massive *Porites* had a significantly lower proportion of healing bite marks than *Pocillopora meandrina* (Figure 3.5, Table S3.5). Conversely, healing status varied significantly among all coral predators except for blennies and parrotfishes (Figure 3.5, Table S3.6). Blennies and parrotfishes exhibited the highest proportion of healing bite marks, followed by scrapers and excavators. Analysis without outliers yielded the same results.

Within each type of predator, the proportion of healing bite marks was similar across all coral species (Figure 3.6). When outliers were included, coral species was not a significant predictor of healing status for any type of predator. However, when we removed outliers, coral species became a significant predictor for scraper and excavator bite marks (Table 3.3). For scrapers, differences in results were likely due to the removal of outlier sites which had very low healing rates for *Montipora capitata* and *M. patula*. The two identified outliers for excavators were on *Montipora capitata*, which originally had a sample size of three, and exclusion of these outliers led to discrepancies in results. Nevertheless, post-hoc tests for pairwise comparisons between coral species for scrapes and excavators, excluding outliers, revealed no significant differences between pairs (Figure 3.6; Table S3.7). Overall, the proportion of healing blenny and parrotfish bite marks was high (>80%) with little variability between species. The proportion of healing excavator and scraper bite marks was lower (50%-80%) and there was more variability between coral species. Figure S3.1 illustrates a breakdown of the proportion of healing, new, and old bite marks by coral species and type of predator.

3.4 Discussion

Corallivory, a natural phenomenon on coral reefs, poses a challenge to the success of coral reef management strategies. While corallivores can be beneficial to reefs, for example moderating coral-coral (Wellington 1982) and algal-coral competition (Miller and Hay 1998), they can also affect coral fitness (Henry and Hart 2005), can remove high amounts of coral material (Hoey and Bellwood 2008), and can cause substantial coral mortality (De'ath et al. 2012). Understanding the identity of coral predators and the manner in which they consume coral is therefore crucial to inform local management decisions.

Corallivory is widespread across O'ahu reefs (Jayewardene et al. 2009, Carlson 2012), but our results suggest that it is largely restricted to a small subset of coral species. The three genera identified here, *Pocillopora* spp., *Porites* spp., and *Montipora* spp., have globally been identified as some of the most commonly consumed by corallivorous fishes (Rotjan and Lewis 2008). Susceptibility to predation also varied by predator and the results of this study coincide with previous findings. For example, blennies preferentially consumed massive *Porites* (Carlson 2012) and the Barred Filefish and Spotted Pufferfish, both scrapers and excavators, mostly consumed *Pocillopora meandrina* and *Porites compressa* (DiSalvo et al. 2007, Jayewardene et al. 2009, Palacios et al. 2014). While the coral feeding habits of parrotfishes have received little attention in Hawai‘i, parrotfish in other regions have also been known to selective feed on *Porites* spp. (Burkepile 2012). It is important to note that while parrotfishes can be corallivorous, they seldom bite live corals compared to turf and crustose algae (Ong and Holland 2010), continuing to fulfill crucial roles as herbivores and bioeroders on Hawaiian reefs (Hixon and Brostoff 1996, Ong and Holland 2010). Corallivores exhibit strong and consistent patterns of feeding selectivity which have been tied back to factors such as caloric content (Tricas 1989), nematocyst size and quantity (Gochfeld 2004), macroborer and symbiont presence (Rotjan and Lewis 2005), coral morphology (Tricas 1989), and tissue depth (Glynn and Krupp 1986). However, when these attributes have been matched to hierarchies of coral prey choice, the results have been equivocal, and it is likely that a combination of factors, rather than a single one, determine feeding preferences (Cole et al. 2008). Dietary composition can also vary among geographic locations and habitats in response to prey availability (Berumen et al. 2005, Burkepile 2012). For instance, blennies primarily consumed *Porites* spp., which was abundant relative to other coral genera at most sites, but at Kewalo, where *Montipora* spp. was the dominant coral genus, blennies consumed more of this genus. Because corallivores have the potential to moderate coral-coral competitive interactions, for example by preferentially consuming faster growing coral species (Cox 1986), understanding which species corallivores preferentially consume could help inform management decisions.

Corallivory generally increased with hard coral cover, although the intensity of predation and form of this relationship varied depending on the type of predator and coral species. The relationship between hard coral cover and predation intensity/corallivore abundance has been investigated previously, but findings have been equivocal, with many studies focusing on butterflyfishes (e.g., positive relationship [Bell and Galzin 1984, Bell et al. 1985, Zekeria and Videler 2000], no relationship [Guzman and Robertson 1989, Khalaf and Crosby 2005], negative relationship [Pratchett et al. 2008, Jayewardene et al. 2009]). Coral serves a dual role for corallivores, acting as both a food source (Rotjan and Lewis 2008) and a place of refuge (Cole et al. 2008), suggesting that coral availability may affect corallivore populations as a dual resource. The positive relationship observed in this study between hard coral cover and predation intensity supports this interpretation. Furthermore, the role of coral as a food source, rather than shelter, may be more important for corallivores, as more positive relationships were detected for the preferred coral species of each coral predator. However, because we documented bite marks rather than corallivore populations themselves, we cannot definitively say that higher predation rates were associated with larger corallivore assemblages. This relationship between bite scar density and corallivore abundance has been studied for other corallivores, but results have been equivocal (Rotjan and Lewis 2006, Roff et al. 2011). An alternate explanation is that higher coral availability may result in higher feeding rates per individual (Roff et al. 2011).

Differences in predation intensity among predator types can likely be attributed to different life histories. The Shortbodied Blenny establishes small territories (from 2.7 m^2 to 12 m^2

depending on sex and reproductive state; Carlson 1992) and is an obligate corallivore (Carlson 2012). Parrotfish also form territories, albeit larger (from 382m^2 to 2279m^2 depending on sex, phase, and species; Bellwood 1985, Howard et al. 2013) and often form schools that collectively descend upon the benthos and feed (pers. obs., Randall 2010). Combined, these life histories result in localized areas of concentrated predation. Alternately, Barred Filefish are either solitary or found in pairs and Spotted Pufferfish are solitary (pers. obs., Randall 2010), and neither form territories (Randall 2010), leading to lower levels of predation per reef area. Understanding how availability of coral either dilutes or concentrates predation is crucial for effective coral reef management, particularly in restoration sites where the objective is to enhance coral cover.

Finally, our research revealed that predator type played a larger role than coral species in determining the healing status of bite marks. Parrotfish bite marks were usually small with superficial skeleton removal and circular blenny bites involved only tissue removal. In contrast, scraper and excavator bites often led to more extensive skeleton removal. Prior studies have shown that deep wounds accompanied by skeletal damage require longer to heal and are more likely to heal incompletely compared to smaller lesions with only tissue removal (Carlson 1992, Jayewardene and Birkeland 2006, Cameron and Edmunds 2014). The prolonged healing time needed for excavator and scraper bite marks renders them more vulnerable to colonization by algae before they have had a chance to fully recover. Additionally, the larger areas created by scraper and excavator bites offer more opportunities for opportunistic algae to colonize (Rice et al. 2019). Although algal colonization itself does not impede full recovery, unless regeneration occurs rapidly, the probability of successful re-growth is diminished (Bak and Steward-Van Es 1980). The high healing capacity of parrotfish bite marks further highlights that the positive consequences of herbivory likely outweigh their negative role as corallivores. Massive *Porites* had the lowest proportion of healed bite marks compared to other coral species. Skeletal structure provides one plausible explanation for differences in healing status between species. For example, *Porites* spp. have perforate skeletons with deep tissue layers. While perforate skeletons allow for translocation of metabolic resources across the colony to wounds (Edmunds 2008), the deeper nature of the tissue layers might require more metabolic resources and time to regenerate (Cameron and Edmunds 2014), rendering wounds more susceptible to algae colonization. Overall, healing rates were high (between 50% and 75% depending on the predation type and coral species) and were comparable to other studies which tracked bite marks over time (Jayewardene et al. 2009, Palacios et al. 2014, Counsell et al. 2019, Charendoff et al. 2023). The high proportion of healing bite marks observed in this study, even with more severe wounds, is a positive sign for O‘ahu reefs and has broader implications for understanding recovery from other small-scale disturbances.

Corallivory, a natural phenomenon on coral reefs, may pose a challenge to the success of coral reef management strategies. For example, recently outplanted corals, especially small colonies, are particularly vulnerable to predation (Edwards and Gomez 2007, Jayewardene et al. 2009). Given our results, managers should consider corallivore abundance when selecting restoration sites to maximize the benefits of coral restoration efforts. Because restoration efforts are likely to increase coral cover, which could lead to an increase in corallivores (Cabaitan et al. 2008), it is advisable that managers conduct corallivory assessments both before and after restoration activities to better track and manage potential increases in corallivorous species. Furthermore, restoration practitioners should consider growing coral species susceptible to predation to larger size classes before outplanting to overcome the early life stage bottleneck observed in previous studies (Penin et al. 2010, Rivas et al. 2021). Lastly, recognizing the significance of the top three genera as reef builders in Hawaiʻi, rather than avoiding outplanting these corals, managers should instead consider employing a restoration design that prioritizes enhancing coral diversity to distribute corallivory across multiple taxa. By gaining a deeper understanding of these trophic interactions, we can implement preventative and mitigative measures to enhance the effectiveness of management interventions. This, in turn, will lead to improved conservation outcomes and reduced costs associated with conservation activities.

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Author Contributions

DED was the project lead and was responsible for all aspects of this study including data collection, model building and annotation, data analysis, data management, and writing. RML was responsible for image post processing, model building, model annotation, and manuscript review. TLK conceived the idea for the project, funding, assisted with data analysis, and reviewed the manuscript. CSC reviewed the data analysis and manuscript. All authors contributed to method development, the writing of this article, and approved the submitted version.

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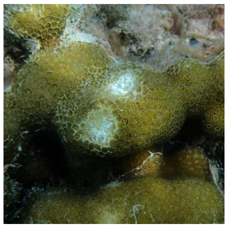
3.6 Tables

Table 3.1 Descriptions of fish corallivore types and bite characteristics.

<table>
<tr><th colspan="5">Type of Predator</th></tr>
<tr><td>Type of Predator</td><td>Blenny</td><td>Parrotfish</td><td>Scraper</td><td>Excavator</td></tr>
<tr><td>Corallivore Species</td><td><i>Exallias brevis</i> (Shortbodied Blenny)</td><td>Family Labridae, Subfamily Scarinae</td><td colspan="2">- <i>Cantherhines dumerilii</i> (Barred Filefish)
- <i>Arothron meleagris</i> (Spotted Pufferfish)
- Family Labridae, Subfamily Scarinae</td></tr>
<tr><td>Description</td><td>small circles with only tissue removal</td><td>paired, oval bite marks with superficial skeleton removal (gap between ovals not always evident)</td><td>shallow sections of skeleton removed (shallower than 3 mm)</td><td>large portions of skeleton removed (deeper than 3 mm)</td></tr>
<tr><td>Photograph</td><td></td><td></td><td></td><td></td></tr>
</table>

<table>
<tr><th colspan="4">Bite Mark Characteristics</th></tr>
<tr><td>Condition</td><td>New</td><td>Healing</td><td>Old</td></tr>
<tr><td>Description</td><td>the skeleton is exposed and bright white, no polyps or algae growth is visible, and, for bites with skeleton removal, the scar edges are sharp</td><td>area is pale compared to the rest of colony, some polyps might be visible, albeit usually transparent, and, for bites with skeleton removal, parts of the skeleton are still missing, and the edges of the bite marks appear dull</td><td>scar looks similar to a new or healed bite mark and the identity of the scar is still recognizable, but the area is covered with turf algae, or in some cases little “tufts” of cyanobacteria</td></tr>
<tr><td>Photograph</td><td></td><td></td><td></td></tr>
</table>

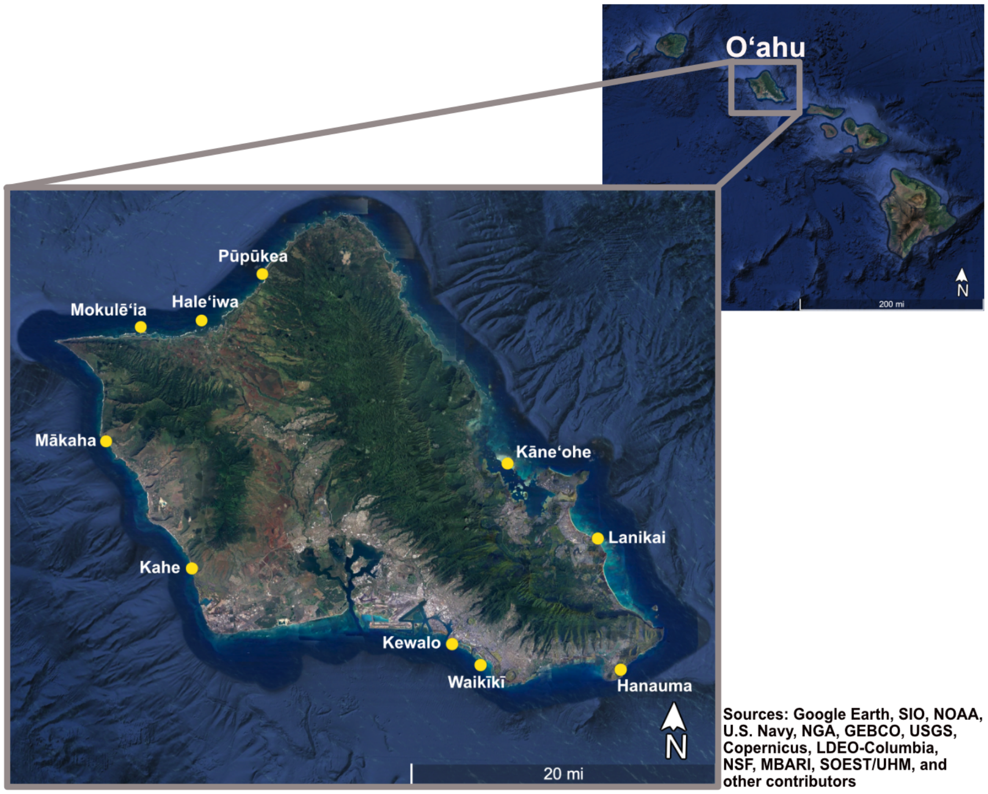
Table 3.2 Likelihood ratio test results for generalized linear mixed effects models for each type of predator. Significant fixed effects are bolded ($p < 0.05$). Excavators did not have outliers.

Response variable	Fixed effects	Type of Predator	With outliers		Without outliers	
			LRT	*p*	LRT	*p*
Bite mark density	Species-specific coral cover × coral species	Blenny	**273.43**	**<0.0001**	**277.12**	**<0.0001**
		Parrotfish	**63.85**	**<0.0001**	**64.88**	**<0.0001**
		Scraper	**73.32**	**<0.0001**	**55.31**	**<0.0001**
		Excavator	**20.81**	**0.0003**	NA	NA

Table 3.3 Likelihood ratio test results for generalized linear mixed effects models for each type of predator. Significant fixed effects are bolded ($p < 0.05$). The parrotfish and blenny bite mark categories did not have outliers.

Response variable	Fixed effect	Type of predator	With outliers		Without outliers	
			LRT	*p*	LRT	*p*
Proportion of healed bite marks	Coral species	Blenny	2.77	0.43	NA	NA
		Parrotfish	6.27	0.18	NA	NA
		Scraper	9.09	0.06	**11.51**	**0.02**
		Excavator	9.15	0.06	**9.41**	**0.05**

3.7 Figures



Sources: Google Earth, SIO, NOAA, U.S. Navy, NGA, GEBCO, USGS, Copernicus, LDEO-Columbia, NSF, MBARI, SOEST/UHM, and other contributors

Figure 3.1 Location of 10 survey sites (yellow dots) around the island of O‘ahu, Hawai‘i.

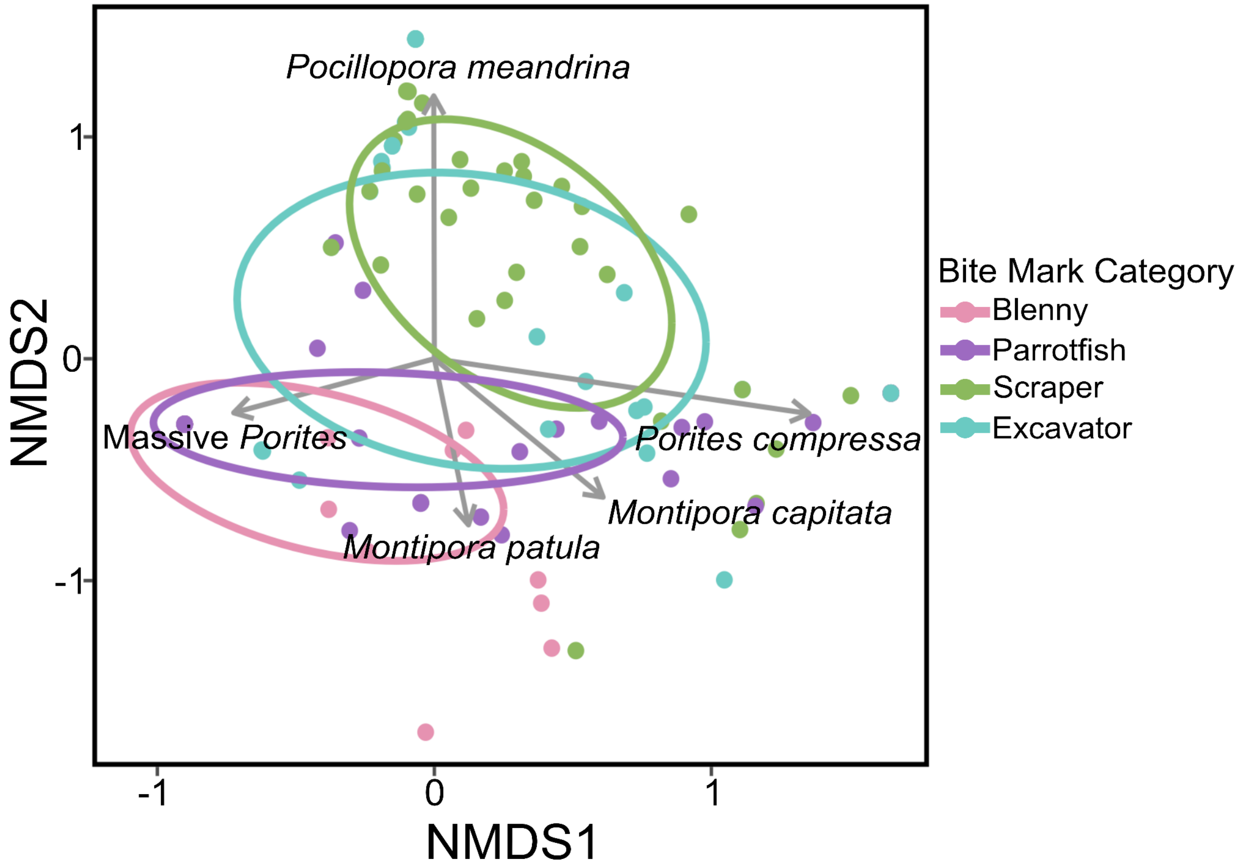


Figure 3.2 Nonmetric multidimensional scaling plot of coral consumption clustered by the type of coral predator (stress = 0.12).

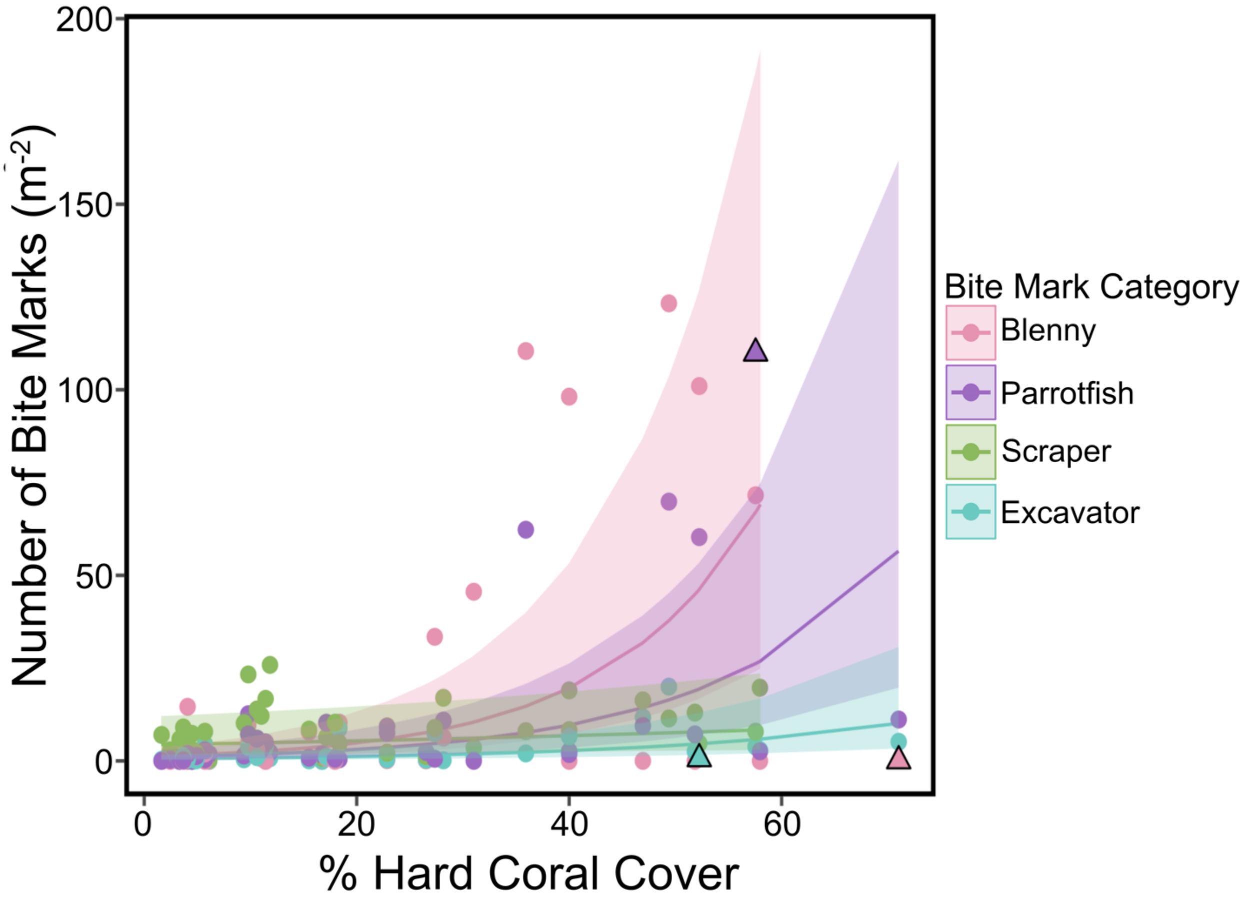


Figure 3.3 Marginal effects plot depicting number of bite marks (per m^2) against hard coral cover. Plots present predicted values (lines) and 95% confidence intervals (shaded areas) from GLMMs without outliers by type of predator (Pink = blenny, Purple = parrotfish, Green = scraper, Blue = excavator). Triangles outlined in black denote outliers.

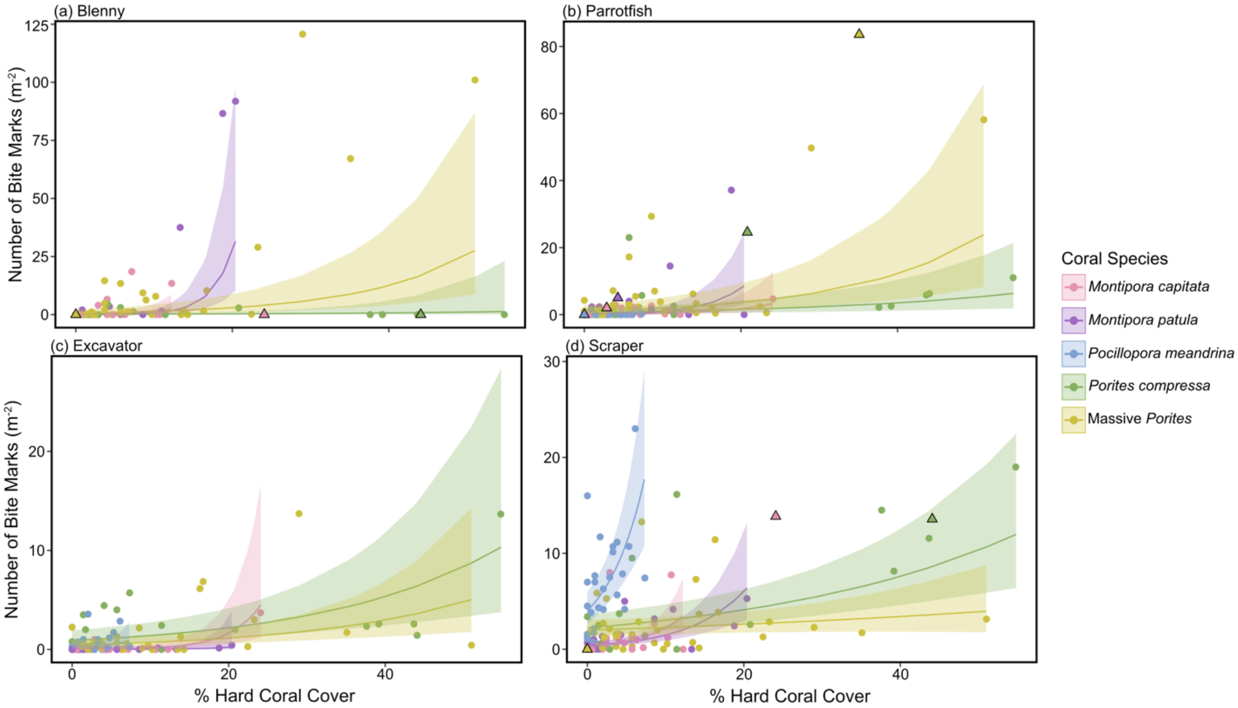


Figure 3.4 Marginal effects plot depicting number of bite marks (per m^2) against species-specific hard coral cover for (a) blenny, (b) parrotfish, (c) excavator, and (d) scraper bite mark categories. Plots display predicted values (lines) and 95% confidence intervals (shaded areas) from GLMMs without outliers by coral species (Pink = *Montipora capitata*, Purple = *Montipora patula*, Green = *Porites compressa*, Yellow = massive *Porites*, Blue = *Pocillopora meandrina*). Coral species with fewer than four observations for each predator type were excluded. Triangles outlined in black denote outliers.

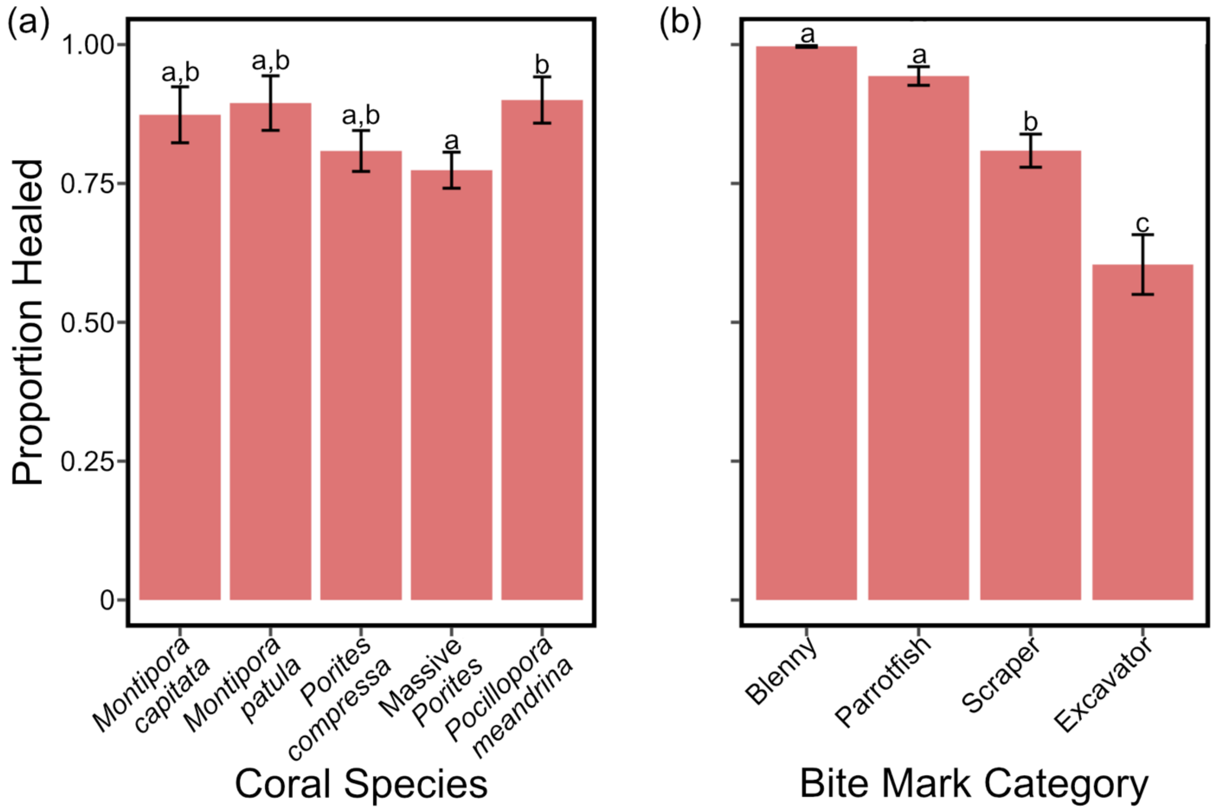


Figure 3.5 Bar graphs illustrating proportion of healed bite marks, including outliers, by (a) coral species and (b) type of predator ($\overline{x} \pm$ SE). Different letters (a, b, c) atop the bars indicate a significant difference between groups (post-hoc Tukey's test for pairwise comparisons, $p < 0.05$).

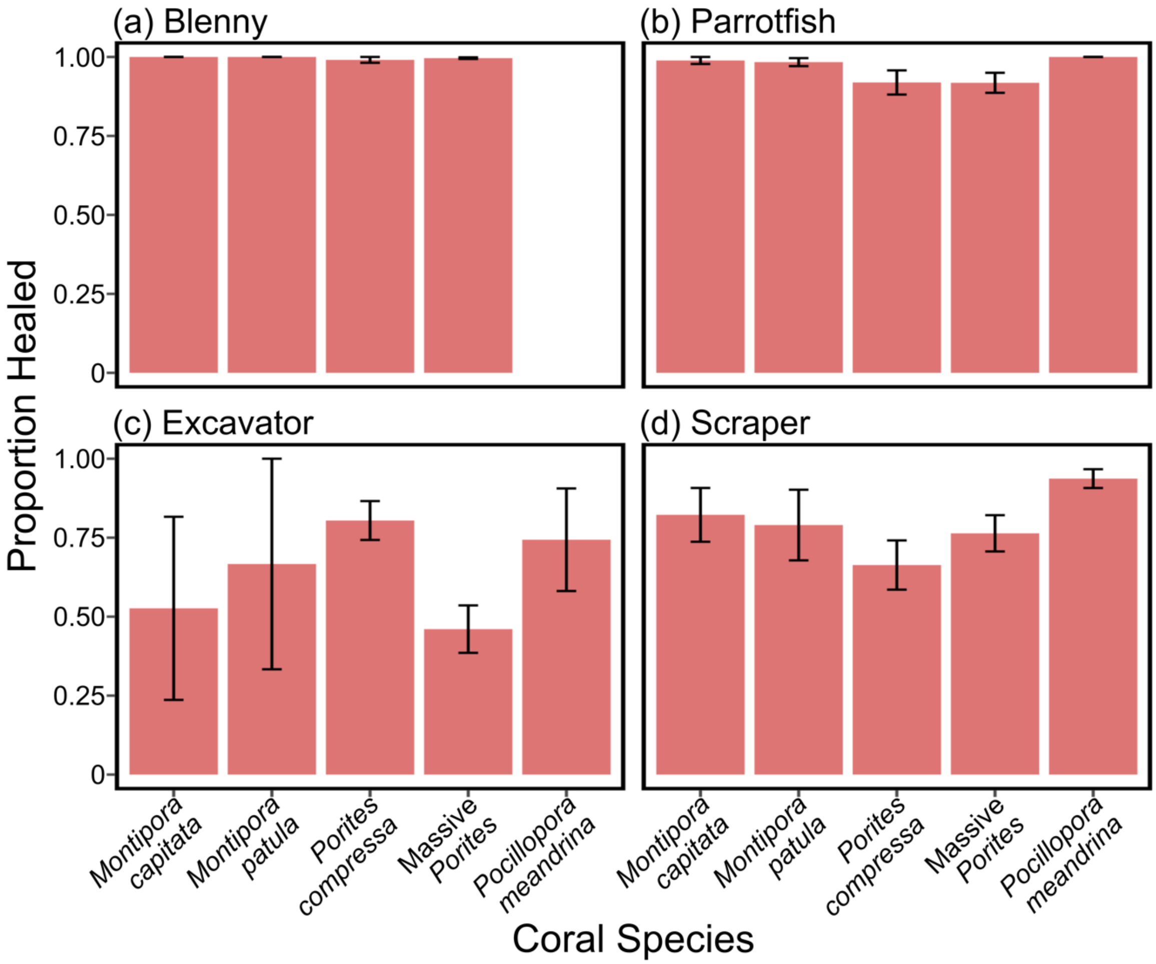


Figure 3.6 Bar graphs illustrating proportion of healed bite marks, including outliers, by coral species for (a) blennies, (b) parrotfishes, (c) excavators, and (d) scrapers ($\overline{x} \pm$ SE).

Chapter 4 – Corallivory by the cushion seastar (*Culcita novaeguineae*) in Hawai‘i

Daniela Escontrela Dieguez & Erik G. Brush

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in revision

Abstract

As global threats to coral reefs grow, it is imperative to manage local stressors such as outbreaks of coral predators, or corallivores. The corallivorous cushion seastar (*Culcita novaeguineae*) has increased in abundance around O‘ahu, Hawai‘i, since the 1980s. We studied the feeding preferences of this species experimentally *in situ* and determined whether or not coral species consumption was random. We deployed cages adjacent to a reef offshore of Waikīkī Beach and tested prey choice by running pairwise comparisons of corals of opportunity of different species and tracking the order of consumption. Consumption of coral species was nonrandom for all but two coral species. We used three methods to construct a feeding hierarchy, and across all methods, stars overwhelmingly preferred *Pocillopora* spp. and avoided *Porites* spp. Although there was variability in the remainder of the hierarchy depending on ranking method, *Pavona* spp. and *Montipora* spp. were usually the next most preferred after *Pocillopora* spp., followed by either *Leptastrea* spp. or *Lobactis scutaria.* It is likely that a combination of factors such as tissue depth, morphology, and nutritional value enable cushion seastars to extract higher energy per unit time from preferred coral species. These findings indicate which coral species may be subject to increased predation during cushion seastar outbreaks and how interactions between corallivorous stars and coral prey may shift as coral species are differentially affected by other stressors.

Keywords: *Culcita*, cushion seastar, corallivory, feeding preference, predation, seastar, coral reef

4.1 Introduction

Corallivores are animals that feed on coral by consuming their mucus, polyps and/or skeleton (Rotjan and Lewis 2008). Coral predators affect individual coral colonies directly through consumption. For example, the crown-of-thorns seastar (*Acanthaster planci*), a voracious coral predator, has been a leading cause of coral mortality on the Great Barrier Reef prior to major bleaching events (De'ath et al. 2012). Corallivores also affect coral colonies in indirect ways, which may be more subtle. Because corals are limited by metabolic resources, when they experience predation, they divert their energy to wound healing, causing reductions in growth and reproduction (Henry and Hart 2005). Corallivores also have the potential to transmit (Nicolet et al. 2018). At the reefscape scale, corallivores have been known to mediate interspecific interactions between corals by, for example, selectively feeding on faster growing coral species, thereby creating space for slower growing corals (Cox 1986).

The cushion seastar (*Culcita novaeguineae*) is a corallivore native to the Pacific region, including Hawaiʻi (Clark and Rowe 1971) which has two sister species, *Culcita schmideliana* found in the Indian Ocean and *Culcita coriacea* found in the Red Sea and Indian Ocean (Ahyong et al. 2024). All cushion seastars consume coral by extruding their stomach over the colony and secreting digestive enzymes which allow for the absorption of polyps (Birkeland 1989). Even though cushion seastars share similar life history traits with the more voracious and extensively studied crown-of-thorns seastar, there is comparatively less research on cushion seastars. Furthermore, the limited studies on cushion seastars are spread among three sister species found in different regions. Previous research has focused on the life history characteristics of *C. novaeguineae* (Birkeland and Lucas 1990), the distribution of *C. schmideliana* and *C.*

novaeguineae (Thomassin 1976, Grosenbaugh 1981, James 2004), drivers of *C. schmideliana* distribution (Montalbetti et al. 2022), and the thermal range of *C. novaeguineae* (Yokley 2016).

Cushion seastar feeding behavior has previously been researched, but these studies had some limitations. While Glynn and Krupp (1986) studied the feeding preferences of *C. novaeguineae* in Hawaiʻi, they tested only four coral species, *Montipora capitata*, *Porites compressa*, *Lobactis scutaria*, and *Pocillopora damicornis,* failing to test many of the other coral species commonly found around Hawaiʻi. More importantly, they tested only *Pocillipora damicornis* against all the other coral species, rather than testing all pairwise combinations, leaving gaps in knowledge about the prey hierarchy when potentially less desireable coral species are the only options. Furthermore, food was not withheld prior to experimental trials, which limits our understanding of prey choice when food is limited and there are few prey choices. Studies conducted in other regions with the same seastar species also tested few coral species and/or they tested genera, such as *Acropora*, which are not found around the Main Hawaiian Islands (Hawkins 2006, Bell 2008). Trial times in previous prey choice studies have also been short (e.g., approximately one day), leaving little time to observe whether cushion seastars would consume less desireable coral species (Glynn and Krupp 1986, Hawkins 2006, Bell 2008). Lastly, and most importantly, all previous feeding preference studies were either observational (Goreau et al. 1972, Thomassin 1976, Montalbetti et al. 2019a) or conducted in laboratory settings, where study species are removed from all their normal sensory cues and multiple artifacts are possible (Glynn and Krupp 1986, Hawkins 2006, Bell 2008).

All told, there are substantial gaps in our understanding of cushion seastar feeding preferences. For example, there is very limited information about predation on *Pavona* spp. and

Lepastrea spp. by the cushion seastar. Even though cushion seastars have been observed feeding on these genera in the field (Bruckner and Coward 2019, Montalbetti et al. 2019a), preference has never been tested under controlled conditions. Furthermore, disparities in feeding preferences have been observed among different species and regions. In the single-choice lab experiments conducted in Hawaiʻi, *C. novaeguineae* exhibited a higher consumption rate of *P. damicornis*, followed by *P. compressa* and *M. capitata* (Glynn and Krupp 1986). These findings diverged from observations of feeding behavior of *C. novaeguineae* and *C. schmideliana* in the Maldives, where cushion seastars more frequently consumed *Montipora* spp. over *Porites* spp. (Bruckner and Coward 2019, Montalbetti et al. 2019a). Indeed, biogeographical differences in behavior among sister species has been documented for other corallivorous seastars such as *Acanthaster* spp. (Burn et al. 2020).

In Hawaiʻi, Cushion seastars have recently been found in high densities at some sites around the island of Oʻahu. While Glynn and Krupp (1986) previously found less than 21 individuals per hectare off Waikīkī Beach in the mid 1980s, recent surveys found much higher densities ($\bar{x}$ ± SE = 30 ± 10 individuals per hectare) (D. Escontrela Dieguez unpubl. data). The corallivorous feeding behavior of the cushion seastar coupled with potentially increasing densities could have negative effects on Hawaiian coral reefs, which are already stressed (National Ocean Service 2018). Although the feeding rate of the cushion seastar is only about one-fifth the feeding rate of the crown-of-thorns seastar (Glynn and Krupp 1986), they can still undergo outbreaks with detrimental effects on coral reefs. For example, in the Maldives, *C. schmideliana* outbreaks may have delayed coral reef recovery after bleaching (Bruckner and Coward 2019). Persistent populations of cushion seastars have also coincided with patterns of coral loss (Quinn and Kojis 2003, Pratchett et al. 2011). Moreover, field observations and previous studies have shown cushion seastars seem to preferentially feed on juvenile colonies, which often results in full colony mortality, and could become a potential population bottleneck at larger spatial scales (Glynn and Krupp 1986, Montalbetti et al. 2019b). Although cushion seastars have not been studied directly in relation to coral restoration, corallivorous fishes are known to impede coral restoration efforts (Koval et al. 2020). Cushion seastar outbreaks therefore represent a potential local stressor to coral reefs which, if unchecked, could lead to high mortality rates among reef building corals, slow recovery after thermal stress events, and/or failed coral restoration efforts. Managing local, natural stressors such as excess corallivory could potentially help offset global changes or at least buy coral reefs time until carbon emissions are stabilized (Kennedy et al. 2013).

The goal of this study was to understand the hierarchy of coral prey choice by cushion seastars and whether or not prey choice was random. By testing more coral species than any previous study, many of which have not been experimentally tested, we can gain a comprehensive understanding of which coral species may be most vulnerable in the event of a cushion seastar outbreak. For example, *Pocillopora* spp. and *Acropora* spp. have experienced disproportionately severe impacts during crown-of-thorns seastar outbreaks, primarily due to their pronounced preference for these genera (Pratchett 2010). This knowledge can be a valuable guide for implementing effective management interventions.

We used experimental pairwise comparisons to study cushion seastar feeding behavior and choice. To overcome the limitations encountered in previous feeding studies, we conducted our experiments entirely *in situ*, thereby reducing the potential artifacts associated with lab experiments and ensuring that the seastars were exposed to their usual array of sensory cues. Additionally, we tested nine common Hawaiian coral species, a much more extensive range than any prior study. Finally, we withheld food prior to trials and subjected stars to longer trial times than previously conducted. Based on previous studies, field observations, and known coral characteristics, we hypothesized that cushion seastars consume coral species in a nonrandom manner. Specifically, we predicted that, based on coral characteristics such as tissue depth, colony morphology, nutritional value, and nematocyst size and density, as well as previous feeding observations among coral species, cushion seastars will exhibit the following hierarchy of prey choice, listed from most preferred to least preferred: *Pocillopora* spp., *Pavona varians, Pavona duerdeni*, *Montipora patula*, *M. capitata*, *Leptastrea* spp., *L. scutaria*, and *P. compressa* and mounding *Porites* tied at the bottom of the hierarchy (Table 4.1). Understanding the feeding preferences of the cushion seastar, which are potentially increasing in abundance in Hawaiʻi, at least at some sites such as Waikīkī Beach, will be important for future restoration and management interventions.

4.2 Materials and methods

Study site and experimental set-up

We conducted this study nearly 1 km offshore of Waikīkī Beach, on the south shore of Oʻahu, Hawaiʻi, between 12 - 15 m depth from October 2020 to November 2022 (Figure 4.1a). Experimental and holding cages were constructed of PVC pipe and garden fencing material (5 cm mesh) and were secured to the seafloor using rebar and zip ties. We deployed five 1.5 × 0.5 × 0.5 m experimental cages in a sand channel flat 10 m away from and parallel to the nearby pavement reef. We also deployed two holding cages, measuring 0.75 × 0.75 × 0.35 m, 3 m away from the experimental cages (Figure 4.1b). We cleaned all cages to remove algae on a biweekly basis or as needed. Throughout the duration of this study, one holding and seven experimental cages had to be replaced at various stages because they were lost during intense swell events.

Animal collection and experimental design

We collected corals of opportunity and cushion seastars from the reef adjacent to the experimental cages. Corals of opportunity are corals that have naturally dislodged from the reef or fragments that have broken off of the main colony (Department of Aquatic Resources Special Activities Permit No. 2021-06, 2023-06). Cushion seastar individuals were identified using the I^3S spot software (Reijns/I^3S) with a standardized protocol (Escontrela Dieguez et al., *in prep*). Size (maximum arm tip to arm tip distance), depth, and location were recorded at the point of collection. Cushion seastars were first placed in the holding cages for one week without food to standardize hunger levels. We then placed one cushion seastar in the center of each experimental cage with corals of different species zip tied to either end of the cage (Figure 4.1b). Paired corals for each trial had approximately the same surface area of live tissue. The following data were recorded for each coral at the beginning of each trial: species, maximum diameter, orthogonal diameter, height, and percent live tissue. After each one-week feeding trial, we recorded whether corals had been consumed and the percent live tissue. For preyed upon corals, any tissue left deep in the skeleton which was not successfully extracted was considered live tissue. We returned cushion seastars and unconsumed corals to the surrounding reef.

In total, we tested nine coral species and 21 pairwise combinations for a total of 170 trials. Each pairwise combination was tested at least five times (Table 4.2). Out of the 170 trials, nine were omitted from analysis because cushion seastars escaped, cages were lost, or corals were smothered by sand for most of the trial. Several coral genera had multiple species that were morphologically similar, especially when looking at pieces rather than whole colonies, and could not be distinguished from one another, so they were grouped into categories: mounding *Porites* was comprised of *Porites lobata* and *Porites evermanni, Pocillopora* spp. was comprised of *Pocillopora meandrina* and *Pocillopora grandis*, and *Leptastrea* spp. was comprised of *Leptastrea purpurea, Leptastrea transversa*, and *Leptastrea bewickensis.* Corals of opportunity of the species *Pavona varians, Pavona duerdeni*, and *Leptastrea* spp. were rare and difficult to find, so they were tested only against *Pocillopora* spp. and *Montipora patula*, which had been preferred in previous studies and field observations (Glynn and Krupp 1986, Montalbetti et al. 2019a).

Order of consumption and feeding information

Where cushion seastars consumed only one coral, the consumed coral was categorized as "consumed first," and the uneaten coral was categorized as "not consumed" in the field. When neither coral was eaten, both were categorized as "not consumed" in the field. In order to determine the order of consumption when both corals were consumed, the timing of feedings, and the order of visitation for each coral in our absence, we used programmable, automated cameras. CoralCams (Greene et al. 2020) were mounted on rebar 0.5 m away from the cage and were programmed to take one 15-second video clip every hour from dawn to dusk. KiloCams, which are less expensive, have longer battery life, and take photographs as opposed to video, were also deployed during the second half of the study when they became publicly available (Greene et al., *in prep*). KiloCams were attached to the cage and pointed down towards each coral. Each KiloCam was programmed to take one photograph every five to fifteen minutes from dawn to dusk. Photographs were stitched into a time lapse to efficiently process all images. Due to technical difficulties, footage was acquired for only 67 trials. To determine when a coral was consumed, we scanned the CoralCam videos and KiloCam timelapses for cushion seastars consuming coral during the day, which appeared as a cushion seastar covering a coral and resulted in a colony with full or partial mortality. When cushion seastars fed overnight, we looked for color changes in the coral (white indicative of consumed tissue). Eaten corals were then categorized as either “consumed first” or “consumed second.” Order of consumption could not be determined for some of the trials due to camera malfunctions and the order of consumption was therefore categorized as “unknown.” We placed the timing of feeding into three categories: 1) started feeding before dusk and finished before dawn, 2) fed exclusively at night, 3) started feeding before dawn and continued feeding into the day. Imagery was also analyzed to determine which coral they visited first. We considered a cushion seastar visited a coral when it traveled to the side of the cage with the coral before dusk on the first day of the trial.

Data analysis

All data were analyzed using R v4.3.1. We used an alpha of 0.05 for all statistical tests. We conducted a paired t-test to compare the surface area of live tissue of paired corals in each trial. We used the geometric approximations approach in (Naumann et al. 2009) to approximate the surface area of each coral: a geometric shape was assigned to each coral and the surface area was calculated using geometric formulas. The surface area of each coral was multiplied by the percent live tissue at the beginning of each trial.

A chi-square goodness-of-fit test determined whether cushion seastars fed randomly. For all chi-square tests (one test per coral species or genus), expected and observed values were calculated across three consumption categories: consumed first, consumed second, and not consumed. We determined the expected value by dividing by three the number of times each coral species or genus was tested. The expected value was the same for the three consumption categories and represents the number of times each species would be consumed either first, second, or not consumed if consumption was random. For the observed value, we determined how many times each coral species or genus was actually consumed first, second, or was not consumed. We aggregated the data from all the trials and removed those trials from which order of consumption could not be determined. Because we had uneven sample sizes for each pairwise combination and not all coral species were tested against each other (i.e., *P. varians, P. duerdeni*, and *Leptastrea* spp. were tested only against *Pocillopora* spp. and *M. patula* leading to small sample sizes), we conducted several chi-square tests to determine whether they gave different results: 1) with data from all trials, 2) without trials that tested *P. varians, P. duerdeni*, and *Leptastrea* spp., and 3) by genus. These were unbalanced tests in that the sample sizes differed for each coral species. A balanced test was also conducted without trials that tested *P. varians, P. duerdeni*, and *Leptastrea* spp. For all tests, we ran 1000 iterations randomly selecting five trials from each pairwise combination each time.

Corals were ranked using three methods to determine the general hierarchy of prey choice and whether there were deviations in the hierarchy depending on what ranking method was used. First, corals were ranked by the proportion of times each species was consumed first. Second, we ranked corals by the proportion of times each species was consumed, regardless of order. Lastly, we ranked coral species using a weighted score, where those corals that were consumed first received a score of 1, those that were consumed second received a score of 0.5, and those that were not consumed received a score of 0. Lastly, to determine how efficient cushion seastars were at consuming each coral species, we calculated the percent change in live tissue for those corals that were consumed.

4.3 Results

Summary statistics

Cushion seastars in the prey-choice experiments ranged in size from 12 to 24 cm in diameter ($\bar{x} \pm \mathrm{SE} = 18.11 \pm 0.17$ cm). In total, 89 (72.4%) cushion seastars were each used in one trial, 30 (24.4%) were each used in two separate trials, and 4 (3.2%) were each used in three separate trials. Corals ranged in size from 2.5 to 26 cm (10.02 ± 0.23 cm) in diameter. The starting surface area of live tissue of paired corals was not significantly different (208.07 ± 11.26 cm^2, $p >> 0.05$). Cushion seastars consumed both corals in 43 (26.7%) trials, one coral in 76 (47.2%) trials, and neither coral in 42 (26.1%) trials.

Non-random feeding

Cushion seastars fed in a non-random manner on all coral species (all aggregate data χ^2 test, $df = 2$, $p < 0.05$, Table 4.3) except for *Pavona varians* ($\chi^2 = 0.5$, $df = 2$, $p = 0.78$) and *Pavona duerdeni* ($\chi^2 = 0.15$, $df = 2$, $p = 0.93$, Table 4.3). A chi-square test excluding data from trials that tested *Pavona varians, Pavona duerdeni*, and *Leptastrea* spp. similarly confirmed that cushion seastars fed non-randomly on all other coral species ($df = 2$, $p < 0.05$). When aggregated by genus, feeding by cushion seastars on all the genera was significantly non-random ($df = 2$, $p < 0.05$) except for *Pavona* spp. ($\chi^2 = 0.32$, $df = 2$, $p = 0.85$).

In 100% of the iterations in the balanced chi-square test, feeding by cushion seastars was significantly non-random ($df = 2$, $p < 0.05$) for *Pocillopora* spp., *Porites compressa,* mounding *Porites,* and *Lobactis scutaria.* In 99% of the iterations, feeding was significantly non-random ($df = 2$, $p < 0.05$) for *Montipora capitata*, and in 91% of the iterations, feeding was significantly non-random ($df = 2$, $p < 0.05$) for *Montipora patula*.

Order of visitation

We acquired footage with KiloCams and/or CoralCams, cushion seastars consumed at least one coral, and the order of visitation could be determined for 57 trials. In 59.6% (34) of these trials, cushion seastars initially visited the coral they consumed first. In the remaining 40.4% (23) of the trials, cushion seastars initially visited either the coral they did not consume or the coral they consumed second.

Hierarchy of prey choice

To determine the order of consumption, coral species were ranked in three ways: by the proportion of times each species was consumed first, by the proportion of times they were consumed regardless of order, and by a weighted score (Table 4.4, Figure 4.2). Among the three methods, there was agreement in the hierarchy for *Pocillopora* spp., *P. duerdeni*, *M. capitata,* and mounding *Porites.* The order of the other species varied depending on the ranking method. The methods that ranked corals by a weighted score and by whether they were consumed had the most agreement. Using these two methods, *P. varians* and *P. duerdeni* both followed *Pocillopora* spp. in the hierarchy. *M. patula* and *M. capitata* both followed *Pavona* spp. and *P. compressa* ranked next to last. These two methods aggregated corals by genus, from most to least preferred as follows: *Pocillopora* spp., *Pavona* spp., *Montipora* spp., *Leptastrea* spp. or *Lobactis* spp., and *Porites* spp. In all three methods *L. scutaria*, *Leptastrea* spp. and *P. compressa* aggregated at the bottom of the hierarchy but always above mounding *Porites.*

Feeding efficiency

Cushion seastars showed different levels of efficiency when extracting tissue depending on the coral species. On average, over 75% of the coral tissue was extracted from all coral species except for mounding *Porites* and *P. compressa.* Cushion seastars, on average, removed less than 65% of live tissue for these two corals and they showed high variability in the amount of tissue they removed per feeding bout (Figure 4.3a). When feeding on *Pocillopora* spp., cushion seastars usually consumed close to 100% of the tissue. This is contrast to *Porites* spp. for which cushion seastars often left behind undigested, sloughing tissue (Figure 4.3b).

Timing of feeding

The timing of feeding could be determined using KiloCam or CoralCam footage for 98 consumed corals. Cushion seastars started feeding before dawn and continued feeding into the day on 52.0% (51) of the 98 corals. For 46.9% (46) of these corals, seastars fed exclusively at night, and for only one coral (1.1%), a star began feeding at dusk and continued feeding during the night. Cushion seastars did not feed exclusively during the day in any trial.

4.4 Discussion

Non-random feeding

Cushion seastars consumed most coral species in a non-random manner. *Pocillopora* spp. was almost always consumed first while mounding *Porites* and *Lobactis scutaria* was almost always avoided. The observed "not consumed" values for mounding *Porites* and *Lobactis scutaria* were 2.3 and 2.7 times greater than expected, respectively. Meanwhile, *Pavona varians* and *Pavona duerdeni* were consumed in a random manner.

Optimal diet theory attempts to explain forager diets by considering the trade-off between acquiring energy from feeding and the energy that is spent searching for, consuming, and processing food (Stephens and Krebs 1986). The decision to include a prey item in an animal's diet usually depends on prey profitability and availability, and as rule of thumb, as profitable prey decreases, predators become more generalized (Emlen 1966). This model has performed well for foragers that consume immobile prey (Sih and Christensen 2001). In the case of the cushion seastar, the decision to feed on certain coral species, or not, likely depends on what other prey are available and amount of time since their last meal. For example, cushion seastars will almost always consume *Pocillopora* spp. if it is available, and regardless of other options, because it appears to be the most profitable prey. On the other hand, stars will consume mounding *Porites*, *Porites compressa, Leptastrea* spp., and/or *L. scutaria* only in the absence of other options. However, the decision to feed on *Pavona* spp. may be more dependent on what other prey are available and the timing of their last meal. For example, *Pavona* spp. was more often consumed second when paired with the highly preferred *Pocillopora* spp. Alternately, *Pavona* spp. was consumed first in about the same proportion as when it was paired with *Montipora patula,* which falls close to *Pavona* spp. in the prey preference hierarchy (Figure 4.2).

Cushion seastars visited the non-preferred coral species first 40.4% of the time, further demonstrating that feeding was not random. Seastars use gustatory stimuli and olfaction to perceive and differentiate between prey items (Keesing 1990). Additionally, cushion seastars might employ ingestive conditioning, whereby food preference is related to previous successful feeding experiences. This phenomenon has been documented in the crown-of-thorns seastar with which cushion seastars share many life history strategies (Wood 1968). Ingestive conditioning could partially explain why more familiar prey items are consistently consumed first whenever they are encountered.

Prey preference

Cushion seastars overwhelmingly preferred *Pocillopora* spp., as previously shown in laboratory experiments (Glynn and Krupp 1986, Hawkins 2006), and they avoided *Porites* spp. altogether (Bell 2008). Coral species hierarchies from *in situ* observations of the closely related *Culcita schmideliana* in the Maldives also closely matched the results of our experiment

(Bruckner and Coward 2019, Montalbetti et al. 2019a). While there are some minor discrepancies in prey preference, this can likely be explained by regional differences in behavior or differences among sister taxa. Indeed, regional behavioral differences for corallivorous seastars have been previously described (Burn et al. 2020). Contrary to our study, which ranked *Porites* spp. as the least preferred corals, Glynn and Krupp (1986) found that *P. compressa* ranked right below *Pocillopora* spp., yet their study tested only four coral species (*Pocillopora damicornis, Montipora capitata, P. compressa*, and *L. scutaria*) and *P. compressa* was only tested against *P. damicornis*. Although cushion seastars mostly consumed *Pocillopora* spp., they switched to other coral species when their preferred choice was not available. Other corallivores have been known to include less preferred coral species in their diet when preferred prey is not available, although this ability decreases with increased specialization (Cole et al. 2008).

Prey choice mechanisms

Similar to the crown-of-thorns sea star, cushion seastars likely select their prey based on a variety of factors such as physiological state of the predator, abundance and distribution of corals, nutritional value of the coral prey, coral morphology, and coral tissue placement (Birkeland 1989). The biggest determinants of prey selection likely involve certain coral characteristics which make cushion seastars more successful at removing tissue in a consistent and predictable manner for some prey species over others. For example, while cushion seastars were very effective at removing most, if not all, of the tissue from *Pocillopora* spp., their attempts at consuming *Porites* spp. were less successful. When consuming *Porites* spp., not only did they remove less tissue than with other coral species, but there was also high variability in the amount of tissue successfully removed in each feeding bout. This lack of consistency when consuming *Porites* spp. was previously documented with the crown-of-thorns seastar (Keesing 1990).

Various coral characteristics have been explored to explain corallivore prey choice, but tissue depth seems to be one of the best predictors of cushion seastar prey choice. Less preferred coral species such as *M. capitata, P. compressa*, mounding *Porites*, and *L. scutaria* have perforate skeletons with vertical and lateral connections between corallites and deep tissue layers, making it difficult to extract polyps (Glynn and Krupp 1986, Domart-Coulon et al. 2006, Kuffner et al. 2012). In contrast, *Pocillopora* spp. has tissue that is not intricately connected or deeply penetrating, and instead forms a superficial layer over the corallum, making polyp extraction easier (Glynn and Krupp 1986, Yost et al. 2013).

The nutritional value of corals has also been explored as an explanation for prey choice in corallivores, yet results have been equivocal, as the energy content of coral species often does not match feeding hierarchies. Even though *Pocillopora* spp. was preferred, it has lower organic matter content than less preferred species such as *P. compressa, M. capitata,* and *L. scutaria* (Glynn and Krupp 1986). Additionally, nutritional value can be measured in a variety of ways, such as calories and/or amount and location of fat bodies (Glynn and Krupp 1986, Tricas 1989, Keesing 1990), making it difficult to match nutritional value to feeding hierarchies. Lastly, nutritional quality can greatly vary between colonies of the same species and depends on environmental factors such as light intensity and water movement (Cole et al. 2008). Cushion seastars may be balancing a trade-off between nutritional value and their ability to efficiently extract coral polyps.

A variety of other characteristics have been studied in relation to corallivore prey choice such as nematocyst size and quantity (Moore and Huxley 1976, Glynn and Krupp 1986, Tricas 1989), coral morphology (Birkeland 1989, De'ath and Moran 1998, Pratchett 2007, Bergsma 2012), colony size (Goreau et al. 1972, Glynn and Krupp 1986, Bruckner and Coward 2019, Montalbetti et al. 2019a), and number of defensive symbionts, such as guard crabs (DeVantier et al. 1986, Glynn and Krupp 1986, Morrison 2008, Mckeon et al. 2012, McKeon and Moore 2014, Rouzé et al. 2014, Montalbetti et al. 2019a). However, similar to nutritional value, the results are equivocal and often do not match the feeding hierarchy of cushion seastars or other corallivores.

Ultimately, it is likely that multiple characteristics lead cushion seastars to prefer certain coral species over others. Some tentative conclusions can be drawn for *Pocillopora* spp. and *Porites* spp*.,* which are the most and least preferred, respectively, and which have been intensively investigated in previous studies. *Pocillopora* spp. has shallow tissue layers (Glynn and Krupp 1986), exposed fat bodies (Tricas 1989), and small nematocysts (Glynn and Krupp 1986). Moreover, cushion seastars usually consume juvenile colonies which are easier to climb and grasp, and they harbor fewer and smaller defensive symbionts, such as guard crabs (Counsell et al. 2018). *Porites* spp., in contrast, has deep tissue layers and large nematocysts (Glynn and Krupp 1986). They also form large colonies with vertical walls, making it difficult to climb and adhere them. Combined, these characteristics likely lead to more efficient polyp extraction and therefore higher energy absorption per time spent feeding for *Pocillopora* spp. while the opposite is true for *Porites* spp. Indeed, when cushion seastars consumed *Pocillopora* spp. in this study, they left behind a bare, white skeleton without any remaining coral tissue. Conversely, when they fed on *Porites* spp., they often left behind large amounts of tissue that was sloughing off the skeleton.

Timing of feeding

Consistent with other studies, cushion seastars almost exclusively fed at night and were usually done within a few hours after dawn (Hawkins 2006, Bell 2008). Although the only adult predator of the cushion seastar, the Triton's Trumpet (*Charonia tritonis*), is also nocturnal (Hall et al. 2017), they are sparse around the island of O‘ahu (D. Escontrela Dieguez unpubl. data), likely due to overcollection by humans. Because of their patchy distribution, Triton's Trumpet may be an insignificant threat which allows cushion seastars to forage at night. However, the nocturnal feeding behavior exhibited by cushion seastars does coincide with tentacle expansion in some coral species, which also happens at night (Sweeney 1976), and which may allow for more efficient polyp extraction.

4.5 Conclusions

This is the most comprehensive study to date of feeding preferences of the cushion seastar. We examined nine coral species, evaluating 21 pairwise combinations, shedding light on potential winners and losers in the event of a substantial cushion seastar outbreak. Because we conducted our study entirely *in situ*, the seastars were exposed to their typical sensory cues, thereby mitigating any potential artifacts that can arise from lab experiments. Lastly, we conducted the first controlled experiments ever to assess the feeding preferences of cushion seastars for *Pavona* spp. and *Leptastrea* spp.

Future studies should focus on expanding sample sizes, especially for less common genera such as *Pavona* spp. and *Leptastrea* spp. Furthermore, it would be beneficial to distinguish among all tested coral species, rather than grouping them as was done with some species in this study. It will also be important to further investigate the underlying basis of these preferences and to determine the details of feeding behavior, such as handling times, for each coral species.

When available to them, cushion seastars almost exclusively preferred *Pocillopora* spp., a coral genus which harbors a wide array of fishes and invertebrates that use its branches for shelter (Counsell et al. 2018). Reductions in *Pocillopora* spp., which could occur as a result of excess predation, will lead to less habitat for these highly reef associated species. Cushion seastars also prefer to consume juvenile colonies (Glynn & Krupp 1986, Montalbetti et al. 2019, pers. obs.) which likely would not survive to reproductive size before they are consumed, creating a potential population bottleneck for *Pocillopora* spp. in areas with high seastar densities. Moreover, *Pocillopora* spp. is one of the first genera to bleach during thermal stress events (Burgess et al. 2021). Following a coral bleaching event, *Pocillopora* spp. mortality could be exacerbated if there is excess coral predation. Cushion seastar predation can also hinder recovery after bleaching events because they preferentially consume newly settled corals, as has been documented in the Maldives (Bruckner and Coward 2019). Because cushion seastar abundances have increased on the south shore of O’ahu since the 1980s, where coral cover is already sparse, continual monitoring will be imperative for signs of excess predation and/or seastar outbreaks. In the event of an outbreak, this study equips coral reef managers with the knowledge needed to implement timely and effective management interventions. By understanding in advance which coral species are likely to experience disproportionate mortality from cushion seastar predation, they can make informed decisions to protect these vulnerable reefs.

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Author Contributions

All authors contributed to the study conception and design. Material preparation and data collection were performed by DED and EGB. Data analysis and the first draft of the manuscript was written by DED. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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4.7 Tables

Table 4.1 Predicted hierarchy of prey choice by the cushion seastar from most preferred (rank 1) to least preferred (rank 9) based on coral tissue depth, type of skeleton, colony morphology, nutritional value, and nematocyst size and density, as well previous feeding observations. Cells are color coded with the most desired characteristics in green followed by orange, yellow, and red being the least preferred. Species specific information was unavailable for some species therefore we used information from other species in the genus or family information.

Rank: Species	Tissue depth and skeleton	Colony morphology	Nutritional value	Nematocyst size and density	Observations of predation	References
1: ***Pocillopora* spp.**	Very shallow, imperforate	Branching, difficult to access	Exposed fat bodies, low calorie content	Small, high density	Preferred in prior field observations and controlled experiments	(Glynn and Krupp 1986, Tricas 1989, Loya et al. 2001)
2: ***Pavona varians***	Shallow, imperforate	Encrusting, very easy to access	No information	No information	Preferred after *Pocillopora* in prior field observations	Powers & Rohlf 1972, Montalbetti et al. 2019, pers. obs
3: ***Pavona duerdeni***	Shallow, imperforate	Lobate, easy to access	No information	No information	Preferred after *Pocillopora* in prior field observations	Powers & Rohlf 1972, Montalbetti et al. 2019, pers. obs
4: ***Montipora patula***	Medium, perforate	Encrusting, very easy to access	Low calorie content	Large, low density	Preferred after *Pavona* in prior field observations	Glynn & Krupp 1986, Loya et al. 2001, Montalbetti et al. 2019, pers. obs.
5: ***Montipora capitata***	Medium, perforate	Encrusting with knobby projections, easy to access	Low calorie content	Large, low density	Preferred after *Pavona* in prior field observations	Glynn & Krupp 1986, Loya et al. 2001, Montalbetti et al. 2019, pers. obs.
6: ***Leptastrea* spp.**	Imperforate	Encrusting, very easy to access	No information	No information	No prior observations reported	(Powers and Rohlf 1972).

Table 4.1 (Continued) Predicted hierarchy of prey choice by the cushion seastar from most preferred (rank 1) to least preferred (rank 9) based on coral tissue depth, type of skeleton, colony morphology, nutritional value, and nematocyst size and density, as well previous feeding observations. Cells are color coded with the most desired characteristics in green followed by orange, yellow, and red being the least preferred. Species specific information was unavailable for some species therefore we used information from other species in the genus or family information.

Rank: Species	Tissue depth and skeleton	Colony morphology	Nutritional value	Nematocyst size and density	Observations of predation	References
8: ***Lobactis scutaria***	Deep, perforate	Free living, often in crevices, difficult to access	Low calorie content	Large, low density	Few incidences of predation in prior field observations and controlled experiments	Powers & Rohlf 1972, Glynn & Krupp 1986, Montalbetti et al. 2019, pers. obs.
9 (tie): ***Porites compressa***	Deep, perforate	Branching, difficult to access	Low calorie content	Large, high density	Few incidences of predation in prior field observations and controlled experiments	Powers & Rohlf 1972, Glynn & Krupp 1986, Loya et al. 2001, Montalbetti et al. 2019, pers. obs.
9 (tie): **Mounding *Porites***	Deep, perforate	Mounding with steep walls, difficult to access	Low calorie content	Large, high density	Few incidences of predation in prior field observations and controlled experiments	Powers & Rohlf 1972, Glynn & Krupp 1986, Loya et al. 2001, Montalbetti et al. 2019, pers. obs.

Table 4.2 Sample sizes for all pairwise combinations tested (161 trials total). The nine trials that were discarded because of disturbance are not included. Several species were too similar to distinguish from each other and were grouped into the following categories: mounding *Porites* includes *Porites lobata* and *Porites evermanni*, *Pocillopora* spp. includes *Pocillopora meandrina* and *Pocillopora grandis*, and *Leptastrea* spp. includes *Leptastrea purpurea*, *Leptastrea transversa*, and *Leptastrea bewickensis*.

	***Pocillopora* spp.**	***Montipora patula***	***Montipora capitata***	***Porites compressa***	**Mounding *Porites***	***Lobactis scutaria***	***Pavona varians***	***Pavona duerdeni***	***Leptastrea* spp.**
***Pocillopora* spp.**	—	10	10	16	12	5	8	7	7
Montipora patula		—	10	7	13	5	6	6	7
Montipora capitata			—	5	6	5	—	—	—
Porites compressa				—	5	6	—	—	—
Mounding *Porites*					—	5	—	—	—
Lobactis scutaria						—	—	—	—
Pavona varians							—	—	—
Pavona duerdeni								—	—
***Leptastrea* spp.**									—

Table 4.3 Chi-square tests using aggregate data from all trials. “Expected” was calculated by dividing number of trials by three and represents the number of times each species would be consumed first, second, or not consumed if consumption was random.

Coral species	Number of Trials	Expected	Observed: Consumed First	Observed: Consumed Second	Observed: Not consumed	χ^2	p-value
***Pocillopora* spp.**	71	23.67	58	7	6	74.73	<0.0001
Montipora patula	59	19.67	27	7	25	12.34	0.002
Pavona duerdeni	13	4.33	5	4	4	0.15	0.926
Pavona varians	12	4.00	4	5	3	0.50	0.779
Montipora capitata	35	11.67	8	4	23	17.2	<0.001
Lobactis scutaria	26	8.67	4	2	20	22.46	<0.0001
Porites compressa	38	12.67	4	1	33	49.32	<0.0001
***Leptastrea* spp.**	12	4.00	1	2	9	9.5	0.009
Mounding *Porites*	40	13.33	1	3	36	57.95	<0.0001

Table 4.4 Coral species ranked from most to least preferred using three methods (from left to right): by the proportion of times each species was consumed first, by the proportion of times each species was consumed, regardless of order, and by a weighted score. Cells highlighted in green show agreement among all three methods and cells highlighted in yellow show agreement between two of the methods.

	Ranked by: Consumed first	**Ranked by: Consumed**	**Ranked by: Weighed score**
Most preferred	*Pocillopora* spp.	*Pocillopora* spp.	*Pocillopora* spp.
	Montipora patula	*Pavona varians*	*Pavona varians*
	Pavona duerdeni	*Pavona duerdeni*	*Pavona duerdeni*
	Pavona varians	*Montipora patula*	*Montipora patula*
	Montipora capitata	*Montipora capitata*	*Montipora capitata*
	Lobactis scutaria	*Leptastrea* spp.	*Lobactis scutaria*
	Porites compressa	*Lobactis scutaria*	*Leptastrea* spp.
	Leptastrea spp.	*Porites compressa*	*Porites compressa*
Least preferred	Mounding *Porites*	Mounding *Porites*	Mounding *Porites*

4.8 Figures

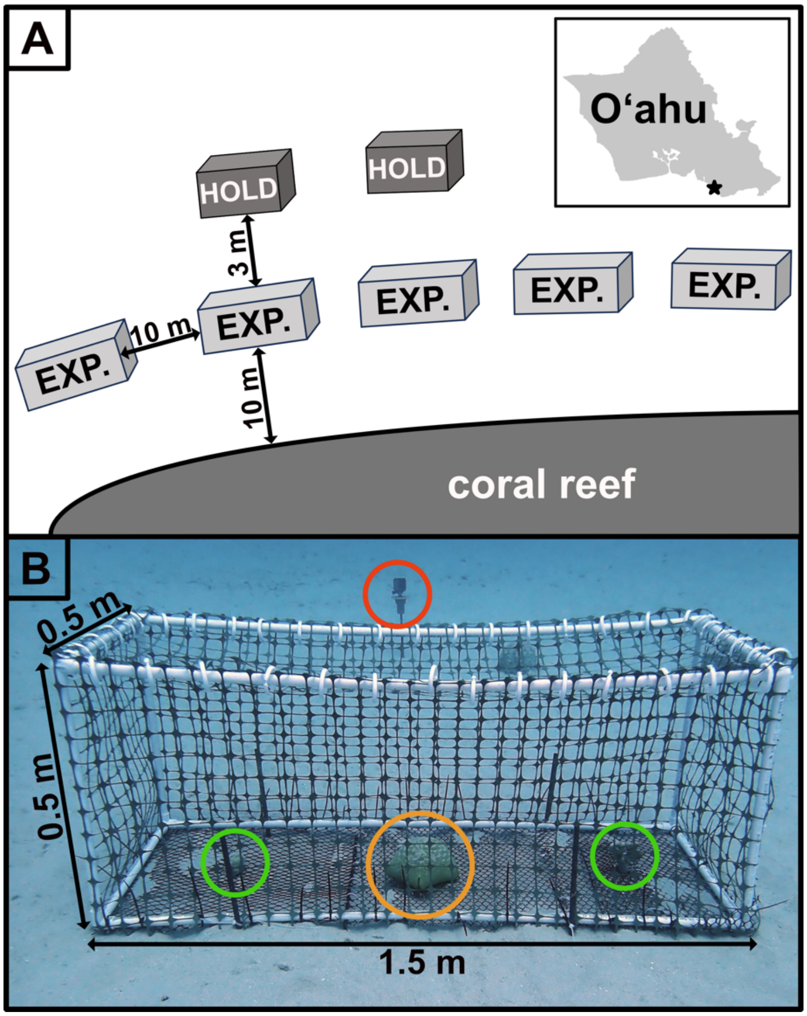

Figure 4.1 (A) Map of the experimental design at the study site offshore of Waikīkī Beach, on the south shore of O‘ahu. Experimental cages were deployed on sand 10 m off and parallel to the reef and holding cages were deployed 3 m away from the experimental cages. EXP denotes experimental cages. (B) An experimental cage containing a cushion seastar (yellow circle), corals of different species (green circles), and a CoralCam (red circle).

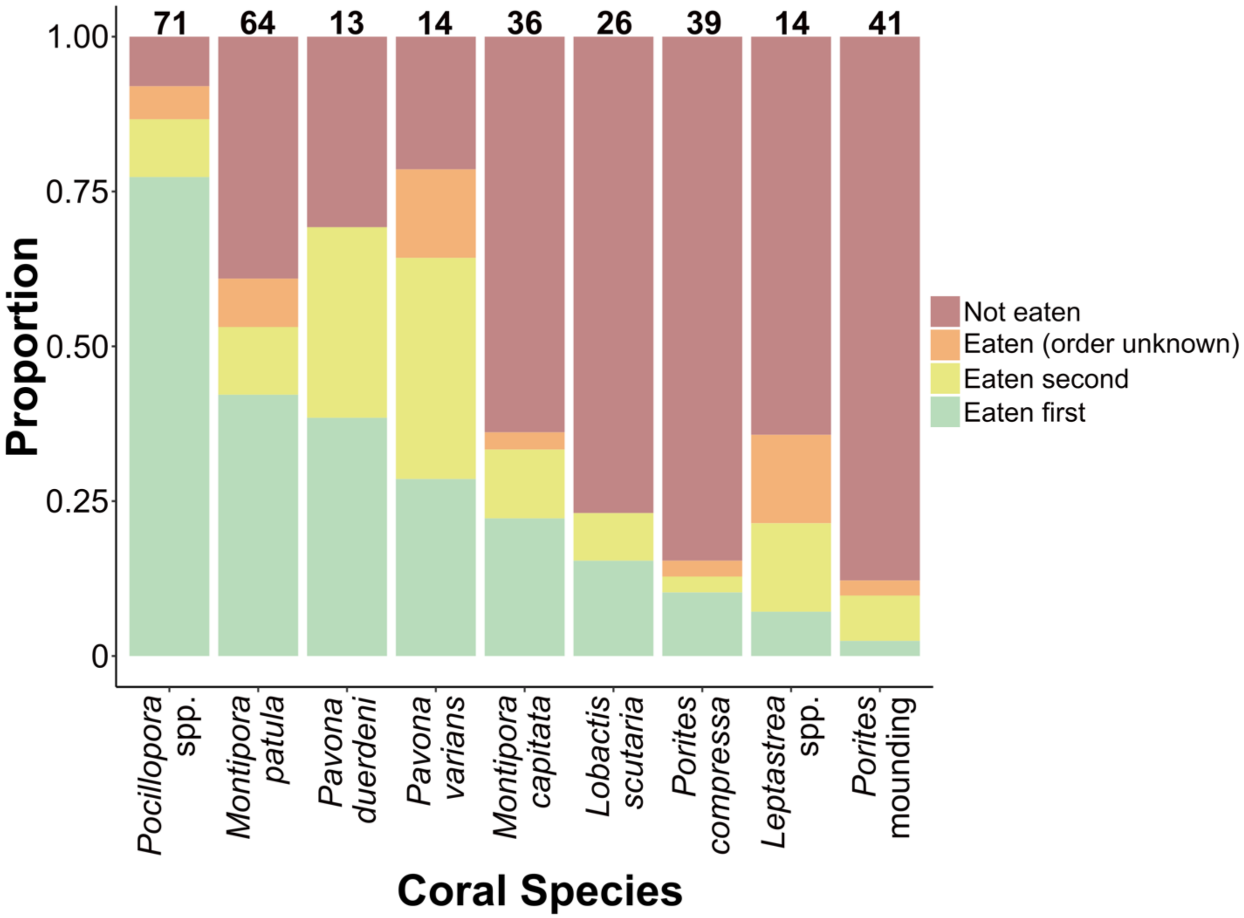

Figure 4.2 Hierarchy of cushion seastar prey choice for coral species (aggregate data from all trials). Numbers across the tops of the bars give the total number of times each coral was tested across all trials. Green bars represent corals that were consumed first, yellow bars represent corals that were consumed second, orange bars represent corals where the order of consumption could not be determined, and red bars represent corals that were not consumed.

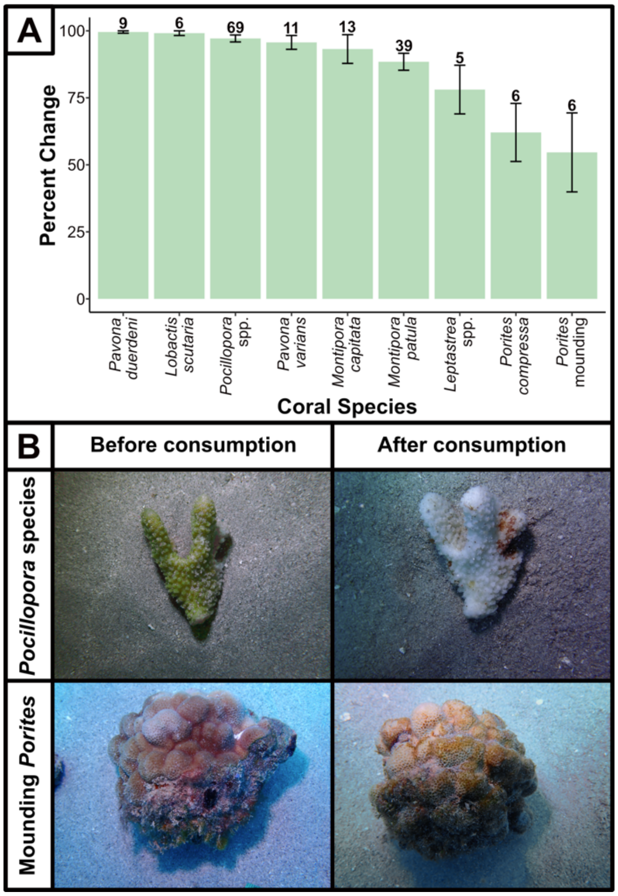

Figure 4.3 (A) Cushion seastar feeding efficiency by coral species represented by the percent change in surface area of live tissue for consumed corals ($\bar{x}$ ± SE). (B) *Pocillopora* spp. (above) before and after consumption shows how effective cushion seastars are at removing tissue from these corals for which they leave behind a bare, white skeleton. This is in contrast to mounding *Porites* (below) for which large amounts of tissue still remain after cushion seastars have fed.

Chapter 5 – General Conclusions

Daniela Escontrela Dieguez

Corallivores are animals that consume living coral tissue, which in some circumstances may confer benefits to both coral colonies (Glynn 1976, Stewart et al. 2013) and entire coral reefs (Cox 1986, Miller and Hay 1998). However, corallivores are also widely known to have negative effects. For example, they can cause reductions in colony growth and reproduction as limited metabolic resources are diverted to wound healing (Henry and Hart 2005) and at high densities, they can cause mass mortality of corals (De'ath et al. 2012). Despite its ecological importance, corallivory has often been overlooked in reef management interventions (Ladd and Shantz 2020), potentially undermining their efficacy. Hawaiʻi is one region where corallivory research has received limited attention (Rotjan and Lewis 2008), impairing our ability to incorporate corallivory into reef management decisions. This dissertation, conducted around the island of Oʻahu, Hawaiʻi, explored the accuracy of structure from motion (SfM) photogrammetry as a corallivory monitoring tool, documented patterns and drivers of corallivory, and investigated the feeding ecology of a prominent corallivore, the cushion seastar (*Culcita novaeguineae*).

The second chapter of this dissertation explored whether SfM served as an accurate tool to quantify corallivory. I found a significant difference in bite mark counts between SfM and *in situ* visual surveys, with more bite marks recorded through SfM. This discrepancy between methods in counting small features is consistent with (Charendoff et al. 2023), who found that SfM annotations resulted in higher counts of small, cryptic juvenile coral colonies compared to *in situ* surveys. Despite differences between methods, relative patterns of corallivory across sites were consistent, that is, sites with high bite mark densities *in situ* also had high bite mark densities with SfM, and vice versa. Consistency in site rankings between methods indicates that SfM can accurately identify high corallivory sites for prioritization in management interventions.

This difference in methods led me to explore how time constraints experienced by divers affected recorded bite mark counts. For all corallivore types, I found that as depth and hard coral cover increased, bite marks recorded through SfM annotations increased at a faster rate than bite marks recorded through *in situ* surveys. This bias likely resulted from limitations divers faced during *in situ* surveys in that deeper sites limited underwater time due to air and physiological constraints and high coral cover sites required more time to survey. In contrast, SfM surveyors had unlimited time to inspect all imagery, allowing them to find more bite marks. These differences were especially apparent for blenny and parrotfish bite marks, which are small, densely concentrated, and often overlap, demanding more survey time (Bruckner et al. 2000, Carlson 2012).

Between-method differences also varied depending on the coral species for blenny, scraper, and excavator bite marks. This variation likely resulted from methodological nuances in documenting specific types of predation on different coral species. For instance, the pale branch tips on *Pocillopora meandrina* could be mistaken for healing excavator or scraper bite marks. Because photos pixelated upon zooming in, identifying missing skeletal parts was challenging with SfM, so these pale branch tips were excluded from bite mark counts when missing skeletal parts were not discernible. Conversely, during *in situ* surveys, divers could closely inspect coral branches to identify whether parts of the skeleton were absent, potentially leading to higher and more accurate counts. Both methods involve trade-offs specific to each coral species and corallivore type which researchers will have to carefully consider depending on the questions being asked.

Overall, I captured high-resolution imagery that allowed me to count and identify different types of bite marks. SfM surveys overcame the time limitations that divers face, making this methodology potentially more precise than *in situ* surveys. Despite drawbacks like long processing and annotating times and high up-front costs, using SfM allows extraction of numerous reef metrics from a single model beyond corallivory estimates (Burns et al. 2015, Bryson et al. 2017, Ferrari et al. 2017, House et al. 2018, Lange and Perry 2020, Couch et al. 2021, Kornder et al. 2021), reducing long-term fieldwork costs. Ultimately, the choice of methodology will depend on factors such as the specific questions being asked, availability of resources, and the urgency with which data are needed.

Given the precision with which I quantified corallivory using SfM models, for chapter three I leveraged the SfM data from chapter two to study patterns and drivers of corallivory. Of 16 coral species documented during surveys, I found that only six species were widely consumed: *Montipora capitata*, *M. patula*, *Porites compressa*, *P. evermanni*, *P. lobata*, and *Pocillopora meandrina*. This finding aligns with studies from other regions, which have identified these three genera as among the most commonly consumed (Rotjan and Lewis 2008). Furthermore, prey choice varied by predator and matched results from previous studies in Hawaiʻi (DiSalvo et al. 2007, Jayewardene et al. 2009, Carlson 2012, Palacios et al. 2014). Prey choice is likely linked to coral characteristics such as caloric content (Tricas 1989), nematocyst size and quantity (Gochfeld 2004), macroborer and symbiont presence (Rotjan and Lewis 2005), and tissue depth (Glynn and Krupp 1986). Corallivores probably choose coral species based on specific characteristics that enable them to effectively extract coral polyps according to their feeding behavior or mode.

I further explored how coral cover either diluted or concentrated corallivory and found that as hard coral cover increased, predation intensity also increased for all corallivore types. Coral availability may limit corallivore population growth as coral serves as both a food source (Rotjan and Lewis 2008) and a place of refuge (Cole et al. 2008). The positive relationship identified here for all predator types suggests that coral availability affects corallivore populations as a dual resource. When I disaggregated these relationships by predator type and coral species, I found more positive relationships between species-specific coral cover and predation intensity for the preferred coral species of each predator. This pattern supports the idea that coral as a food source may be a more important limiting factor for corallivore population growth than coral as a place of refuge. Understanding how hard coral either dilutes or concentrates predation can help inform restoration design, especially given that coral cover increases over time at restoration sites (Hein et al. 2020).

I also investigated the healing status of bite marks and found that predator type, rather than coral species, was a more important determinant of bite mark healing. Excavators and scrapers, which leave behind deeper and more extensive wounds, had a lower proportion of heal bite marks compared to those made by parrotfish and blennies. Excavator and scraper marks take longer to heal or heal incompletely (Carlson 1992, Jayewardene and Birkeland 2006, Cameron and Edmunds 2014) and have larger surface areas (Rice et al. 2019), making them more vulnerable to colonization by macroalgae. While algae colonization does not impede full recovery, unless regeneration occurs rapidly, the probability of re-growth diminishes (Bak and Steward-Van Es 1980). Despite these differences, I found an overall high proportion of healing bite marks, which is a positive indicator for O‘ahu reefs and also offers an insight into coral recovery after small-scale disturbances.

For the fourth chapter of this dissertation, I focused on the cushion seastar (*Culcita novaeguineae*), a prominent corallivore around O‘ahu. Although less voracious than the crown-of-thorns seastar, *Acanthaster planci* (Glynn and Krupp 1986, Birkeland 1989), cushion seastar outbreaks may have delayed reef recovery in other regions (Bruckner and Coward 2019) and they commonly consume juvenile coral colonies (Glynn and Krupp 1986, Birkeland 1989). Although cushion seastars have not been studied directly in relation to coral restoration, the crown-of-thorns seastar has been known to negatively affect coral reef restoration efforts (Mbije et al. 2013, Knoester et al. 2023). The negative effects of cushion seastars on coral reefs, combined with potentially increasing abundances around O‘ahu (Glynn and Krupp 1986) and their potential to hinder restoration efforts, necessitate a deeper understanding of their feeding ecology to guide future management interventions.

Using *in situ* prey-choice experiments, I found cushion seastars consumed all coral species, except *Pavona varians* and *Pavona duerdeni*, in a non-random manner. For instance, *Pocillopora meandrina* was consumed first more frequently than would be expected by chance, while mounding *Porites* was generally avoided. Optimal diet theory explains forager diets by considering the tradeoff between the energy gained from feeding and the energy expended searching for, consuming, and processing food (Stephens and Krebs 1986). As a rule of thumb, when profitable prey decreases in abundance, predators become more generalized (Emlen 1966) and this general model has performed well for foragers that consume immobile prey (Sih and Christensen 2001). For cushion seastars, the decision to feed on certain coral species likely depends on the availability of other prey and the time since their last meal.

This non-random feeding behavior resulted in a clear hierarchy of prey choice, ranked from most preferred to least preferred: *Pocillopora* spp., *Pavona* spp., *Montipora* spp., *Leptastrea* spp. or *Lobactis scutaria*, *Porites compressa*, and mounding *Porites*. Feeding hierarchies developed in previous lab and observational studies generally followed the same order (Glynn and Krupp 1986, Hawkins 2006, Bell 2008, Bruckner and Coward 2019, Montalbetti et al. 2019). Like other corallivores, cushion seastars likely select their prey based on various factors such as the physiological state of the predator, coral abundance and distribution, and a variety of coral characteristics (Birkeland 1989). Coral characteristics like tissue depth (Glynn and Krupp 1986), corallite morphology (Domart-Coulon et al. 2006, Kuffner et al. 2012, Yost et al. 2013), and nutritional value (Tricas 1989, Keesing 1990) have been extensively studied and linked to corallivore hierarchies of prey choice (Glynn and Krupp 1986, Tricas 1989, De’ath and Moran 1998). However, past results have been inconsistent for the cushion seastar (Glynn and Krupp 1986).

Ultimately, a combination of characteristics, rather than a single factor, likely contributes to the hierarchy of prey choice observed. The limited availability of data on all the coral species studied here prevented me from directly linking coral characteristics to the constructed hierarchy of prey choice. However, insights can be drawn from the extensively studied *Pocillopora* spp. and *Porites* spp., which were the most and least preferred, respectively. *Pocillopora* spp. typically possess shallow tissue layers (Glynn and Krupp 1986), exposed fat bodies (Tricas

1989), and small nematocysts (Glynn and Krupp 1986). Furthermore, cushion seastars tend to consume juvenile colonies of *Pocillopora* spp., which are easier to climb and grasp, and they harbor fewer and smaller defensive symbionts (Counsell et al. 2018). In contrast, *Porites* spp. have deep tissue layers and large nematocysts (Glynn and Krupp 1986) and they form large colonies with vertical walls, making it challenging for cushion seastars to climb and adhere to them. These combined characteristics likely result in more efficient polyp extraction and, consequently, higher energy absorption per unit of time spent feeding for *Pocillopora* spp. compared to *Porites* spp.

Corallivory was found to be an important trophic interaction across Oʻahu reefs, and the findings of this research offer valuable insights that can inform future management and restoration interventions. For instance, the SfM corallivory monitoring tool can be used to create time-series data and extract other coral reef metrics, helping us better understand drivers of corallivory. Furthermore, recognizing that only a subset of coral species were vulnerable to predation, restoration practitioners should prioritize growing these vulnerable species to larger size classes prior to outplanting to avoid the early life stage bottleneck observed in previous studies (Penin et al. 2010, Rivas et al. 2021). Lastly, understanding the cushion seastar hierarchy of coral prey choice equips managers with the knowledge needed to prioritize coral species for restoration in the event of a seastar outbreak. By integrating knowledge about corallivores into coral reef management, we can design interventions that yield more successful outcomes.

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Appendix A – Chapter 2 Supplemental Tables

Table S2.1 Table detailing site names, surveyed habitat types (with transect counts in parentheses), and the average and range of percent hard coral cover and depths recorded.

Site	**Habitat types (n)**	**% hard coral cover Avg ± SE (range)**	**Depth (m) Avg ± SE (range)**
Haleʻiwa	Pavement (2)	4.29 ± 1.84 (2.45 – 6.12)	13.37 ± 0.56 (12.80 – 13.93)
Mokulēia	Pavement (2)	7.35 ± 2.45 (4.90 – 9.80)	12.45 ± 3.92 (8.53 – 16.37)
Pūpūkea	Pavement (4)	13.78 ± 1.78 (10.61 – 17.96)	6.76 ± 0.56 (5.27 – 7.92)
Kāneʻohe	Aggregate reef (6)	46.53 ± 8.23 (11.43 – 71.02)	2.34 ± 0.44 (0.79 – 3.26)
Lanikai	Aggregate reef (4)	19.19 ± 2.46 (16.33 – 26.53)	1.42 ± 0.09 (1.22 – 1.62)
Hanauma	Aggregate reef (4)	42.25 ± 10.95 (9.8 – 57.55)	10.46 ± 2.58 (5.18 – 17.47)
Waikīkī	Pavement (4)	2.86 ± 0.44 (1.63 – 3.67)	8.18 ± 0.83 (5.88- 9.75)
Kewalo	Aggregate reef (2) Pavement (3)	27.92 ± 6.20 (4.49 – 40)	9.13 ± 0.47 (7.53 – 10.36)
Kahe	Pavement (4)	11.12 ± 4.26 (4.08 – 22.96)	5.54 ± 0.77 (3.66 – 7.32)
Mākaha	Pavement (4)	15.21 ± 4.84 (5.71 – 27.35)	6.17 ± 0.45 (5.39 – 7.10)

Table S2.2 Likelihood Ratio Test Results for GLMMs and LMMs. Significant fixed effects are bolded ($p < 0.05$). Tests where excavator and scraper bite marks were combined are underlined.

Response variable	Test	Fixed effect	Likelihood ratio	*p*
Number of bite marks (total)	GLMM	**Depth × method**	**82.38**	**<0.0001**
		Hard coral cover × method × bite mark category	**476.97**	**<0.0001**
		Hard coral cover × method × bite mark category (excavator & scraper grouped)	**457.25**	**<0.0001**
Number of bite marks (blenny)	GLMM	**Hard coral cover × method**	**31.91**	**<0.0001**
Number of bite marks (parrotfish)	GLMM	**Hard coral cover × method**	**270.96**	**<0.0001**
Number of bite marks (excavator)	GLMM	**Hard coral cover × method**	**10.14**	**0.0015**
Number of bite marks (scraper)	GLMM	**Hard coral cover × method**	**7.23**	**0.0072**
Number of bite marks (scraper & excavator)	GLMM	**Hard coral cover × method**	**14.35**	**<0.0001**
Between method difference (blenny)	LMM	**Hard coral cover × coral species**	**10.82**	**0.013**
Between method difference (blenny excluding *M. capitata*)	LMM	**Hard coral cover × coral species**	**8.16**	**0.017**
Between method difference (parrotfish)	LMM	Hard coral cover × coral species	4.04	0.26
		Hard coral	**9.22**	**0.0024**
		Coral species	3.15	0.37
Between method difference (excavator)	LMM	Hard coral cover × coral species	4.99	0.29
		Hard coral	1.50	0.22
		Coral species	**12.28**	**0.015**
Between method difference (scraper)	LMM	Hard coral cover × coral species	3.89	0.42
		Hard coral	1.39	0.24
		Coral species	**16.74**	**0.0022**
Between method difference (scraper & excavator)	LMM	Hard coral cover × coral species	4.36	0.36
		Hard coral	2.03	0.15
		Coral species	**19.61**	**<0.001**

Table S2.3 Table of results for post-hoc Tukey's test for pairwise comparison. Bold indicates significant fixed effects ($p < 0.05$).

Response	Predictor	Slope Pairwise comparison	Z ratio	*p*
Number of bite marks	Depth × method	**SfM vs *in situ***	**-8.81**	**<0.0001**
	Hard coral cover × method	**SfM vs *in situ* for blenny bite marks**	**5.66**	**<0.0001**
		SfM vs *in situ* for parrotfish bite marks	**12.57**	**<0.0001**
		SfM vs *in situ* for excavator bite marks	**3.17**	**0.0015**
		SfM vs *in situ* for scraper bite marks	**2.68**	**0.0075**
		SfM vs *in situ* for scraper & excavator bite marks	**3.77**	**0.0002**

Appendix B – Chapter 3 Supplemental Tables

Table S3.1 Table of permutational multivariate analysis of variance (PERMANOVA) results testing pairwise differences between coral predators. Bold indicates significant differences between pairs ($p < 0.05$).

Pairwise comparison	**f statistic**	***p***
Excavator versus Scraper	**9.10**	**0.001**
Excavator versus Parrotfish	**3.96**	**0.002**
Excavator versus Blenny	**5.05**	**0.001**
Scraper versus Parrotfish	**9.35**	**0.001**
Scraper versus Blenny	**8.31**	**0.001**
Parrotfish versus Blenny	1.07	0.36

Table S3.2 Similarity percentage analysis (SIMPER) identifying the contribution of coral species to differences between predator types. Bold indicates significant contributions from species ($p < 0.05$).

Coral species	**Contribution (%) to differences between species**					
	Excavator versus Scraper	**Excavator versus Parrotfish**	**Excavator versus Blenny**	**Scraper versus Parrotfish**	**Scraper versus Blenny**	**Parrotfish versus Blenny**
Pocillopora meandrina	**32.8**	8.06	6.47	**27.3**	**23.0**	0.39
Porites compressa	20.5	**22.2**	12.9	17.9	11.7	10.6
Massive *Porites*	18.6	**39.5**	**48.3**	24.5	32.6	**46.9**
Montipora capitata	6.31	4.92	3.44	6.09	5.67	4.40
Montipora patula	5.25	5.06	**14.1**	7.08	**13.6**	**15.0**

Table S3.3 Pairwise slope comparisons between coral predators with and without outliers. Bold indicates significant differences between pairs ($p < 0.05$).

Response	Predictor	Pairwise comparison	With outliers		Without outliers	
			z ratio	*p*	z ratio	*p*
Bite mark density	Hard coral cover × type of predator	Blenny versus Excavator	**3.19**	**0.008**	**4.71**	**<0.0001**
		Blenny versus Scraper	**10.65**	**<0.0001**	**13.71**	**<0.0001**
		Blenny versus Parrotfish	-2.23	0.12	**3.06**	**0.01**
		Excavator versus Scraper	**3.44**	**0.003**	**-4.88**	**<0.0001**
		Excavator versus Parrotfish	**-4.38**	**0.0001**	2.45	0.07
		Scraper versus Parrotfish	**-11.46**	**<0.0001**	**9.94**	**<0.0001**

Table S3.4 Pairwise slope comparisons between coral species with and without outliers. Bold indicates significant differences between pairs (p < 0.05). Excavators did not have outliers.

Response	Predictor	Type of predator	Coral species 1	Coral species 2	With outliers		Without outliers	
					z ratio	*p*	z ratio	*p*
Bite mark density	Species-specific coral cover × coral species	Blenny	*Montipora capitata*	*Montipora patula*	**-2.81**	**0.03**	-2.33	0.09
			Montipora capitata	*Porites compressa*	**4.07**	**0.0003**	**4.66**	**<0.0001**
			Montipora capitata	Massive *Porites*	**4.58**	**<0.0001**	**4.93**	**<0.0001**
			Montipora patula	*Porites compressa*	**7.77**	**<0.0001**	**8.55**	**<0.0001**
			Montipora patula	Massive *Porites*	**12.26**	**<0.0001**	**12.31**	**<0.0001**
			Porites compressa	Massive *Porites*	-0.56	0.94	-1.06	0.71
		Parrotfish	*Montipora capitata*	*Montipora patula*	-1.17	0.77	-1.40	0.63
			Montipora capitata	*Porites compressa*	**4.01**	**0.0006**	**3.79**	**0.001**
			Montipora capitata	Massive *Porites*	**3.30**	**0.009**	**2.78**	**0.04**
			Montipora capitata	*Pocillopora meandrina*	0.03	1.00	0.28	1.00
			Montipora patula	*Porites compressa*	**6.80**	**<0.0001**	**6.74**	**<0.0001**
			Montipora patula	Massive *Porites*	**6.36**	**<0.0001**	**6.06**	**<0.0001**
			Montipora patula	*Pocillopora meandrina*	0.13	1.00	0.40	0.99
			Porites compressa	Massive *Porites*	-1.01	0.85	-1.55	0.53
			Porites compressa	*Pocillopora meandrina*	-0.25	1.00	0.02	1.00
			Massive *Porites*	*Pocillopora meandrina*	-0.22	1.00	0.07	1.00
		Scraper	*Montipora capitata*	*Montipora patula*	-0.06	1.00	1.16	0.78
			Montipora capitata	*Porites compressa*	**6.11**	**<0.0001**	**3.81**	**0.001**
			Montipora capitata	Massive *Porites*	**5.94**	**<0.0001**	**4.05**	**0.0005**
			Montipora capitata	*Pocillopora meandrina*	-1.62	0.49	-0.10	1.00
			Montipora patula	*Porites compressa*	**4.22**	**0.0002**	**4.36**	**0.0001**

Table S3.4 (Continued) Pairwise slope comparisons between coral species with and without outliers. Bold indicates significant differences between pairs (p < 0.05). Excavators did not have outliers.

Response	Predictor	Type of predator	Coral species 1	Coral species 2	With outliers		Without outliers	
					z ratio	*p*	z ratio	*p*
			Montipora patula	Massive *Porites*	**4.85**	**<0.0001**	**5.00**	**<0.0001**
			Montipora patula	*Pocillopora meandrina*	-1.46	0.59	-1.46	0.59
			Porites compressa	Massive *Porites*	1.41	0.62	1.44	0.60
			Porites compressa	*Pocillopora meandrina*	**-4.59**	**<0.0001**	**-4.68**	**<0.0001**
			Massive *Porites*	*Pocillopora meandrina*	**-4.87**	**<0.0001**	**-4.96**	**<0.0001**
		Excavator	*Montipora capitata*	*Montipora patula*	0.14	1.00	NA	NA
			Montipora capitata	*Porites compressa*	**3.76**	**0.002**	NA	NA
			Montipora capitata	Massive *Porites*	**3.54**	**0.004**	NA	NA
			Montipora capitata	*Pocillopora meandrina*	0.17	1.00	NA	NA
			Montipora patula	*Porites compressa*	1.10	0.81	NA	NA
			Montipora patula	Massive *Porites*	1.08	0.82	NA	NA
			Montipora patula	*Pocillopora meandrina*	-0.01	1.00	NA	NA
			Porites compressa	Massive *Porites*	-0.18	1.00	NA	NA
			Porites compressa	*Pocillopora meandrina*	-1.68	0.44	NA	NA
			Massive *Porites*	*Pocillopora meandrina*	-1.65	0.47	NA	NA

Table S3.5 Results of post-hoc Tukey's test for pairwise comparisons. Bold indicates significant differences between pairs ($p < 0.05$).

Response	Predictor	Coral species 1	Coral species 2	t ratio	*p*
Proportion of healed bite marks	Type of predator + coral species	*Montipora capitata*	*Montipora patula*	0.58	0.98
		Montipora capitata	*Porites compressa*	0.05	1.00
		Montipora capitata	Massive *Porites*	1.97	0.28
		Montipora capitata	*Pocillopora meandrina*	-1.35	0.66
		Montipora patula	*Porites compressa*	-0.52	0.99
		Montipora patula	Massive *Porites*	1.33	0.67
		Montipora patula	*Pocillopora meandrina*	-1.96	0.29
		Porites compressa	Massive *Porites*	1.96	0.29
		Porites compressa	*Pocillopora meandrina*	-1.41	0.62
		Massive *Porites*	*Pocillopora meandrina*	**-3.92**	**0.001**

Table S3.6 Results of post-hoc Tukey's test for pairwise comparisons. Bold indicates significant differences between pairs ($p < 0.05$).

Response	**Predictor**	**Pairwise comparisons**	**t ratio**	***p***
Proportion of healed bite marks	Type of predator + coral species	Blenny versus Excavator	**7.56**	**<0.0001**
		Blenny versus Scraper	**4.89**	**<0.0001**
		Blenny versus Parrotfish	1.20	0.63
		Excavator versus Scraper	**-3.77**	**0.001**
		Excavator versus Parrotfish	**-7.50**	**<0.0001**
		Scraper versus Parrotfish	**-4.45**	**0.0001**

Table S3.7 Table of results for post-hoc Tukey’s test for pairwise comparison with and without outliers. Bold indicates significant differences between pairs ($p < 0.05$). Excavators did not have outliers.

Response	Predictor	Type of predator	Coral species 1	Coral species 2	With outliers		Without outliers	
					z ratio	p	z ratio	p
Proportion of healed bite marks	Coral species	Scraper	*Montipora capitata*	*Montipora patula*	0.80	0.93	0.55	0.98
			Montipora capitata	*Porites compressa*	1.20	0.75	1.90	0.32
			Montipora capitata	Massive *Porites*	1.06	0.83	1.54	0.54
			Montipora capitata	*Pocillopora meandrina*	-0.76	0.94	-0.32	1.00
			Montipora patula	*Porites compressa*	0.31	1.00	1.09	0.81
			Montipora patula	Massive *Porites*	0.10	1.00	0.85	0.91
			Montipora patula	*Pocillopora meandrina*	-1.66	0.47	-0.97	0.87
			Porites compressa	Massive *Porites*	-0.29	1.00	-0.53	0.98
			Porites compressa	*Pocillopora meandrina*	-1.98	0.28	-2.28	0.16
			Massive *Porites*	*Pocillopora meandrina*	-2.56	0.09	-2.73	0.06
		Excavator	*Montipora capitata*	*Montipora patula*	-0.44	0.99	0.11	1.00
			Montipora capitata	*Porites compressa*	-1.52	0.55	-0.52	0.99
			Montipora capitata	Massive *Porites*	-0.001	1.00	0.46	0.99
			Montipora capitata	*Pocillopora meandrina*	-0.95	0.88	-0.21	1.00
			Montipora patula	*Porites compressa*	-0.82	0.92	-0.94	0.88
			Montipora patula	Massive *Porites*	0.61	0.97	0.58	0.98
			Montipora patula	*Pocillopora meandrina*	-0.47	0.99	-0.52	0.99
			Porites compressa	Massive *Porites*	2.43	0.12	2.59	0.09
			Porites compressa	*Pocillopora meandrina*	0.43	0.99	0.52	0.99
			Massive *Porites*	*Pocillopora meandrina*	-1.65	0.47	-1.70	0.45

Appendix C – Chapter 3 Supplemental Figures

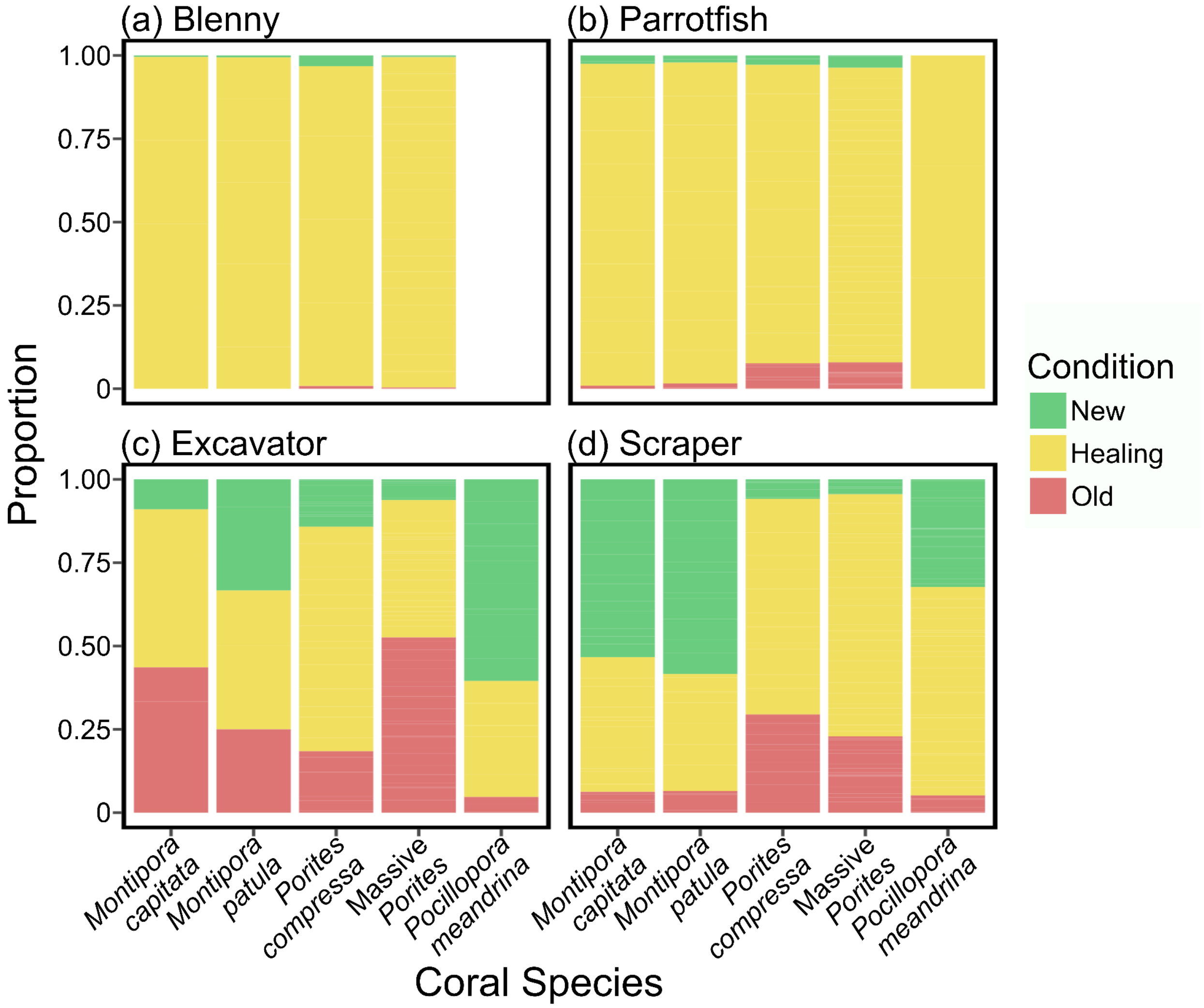

Figure S3.1 Bar graphs illustrating proportion of new, healing, and old bite marks by coral species for (a) blenny, (b) parrotfish, (c) excavator, and (d) scraper bite mark categories ($\bar{x}$ ± SE).

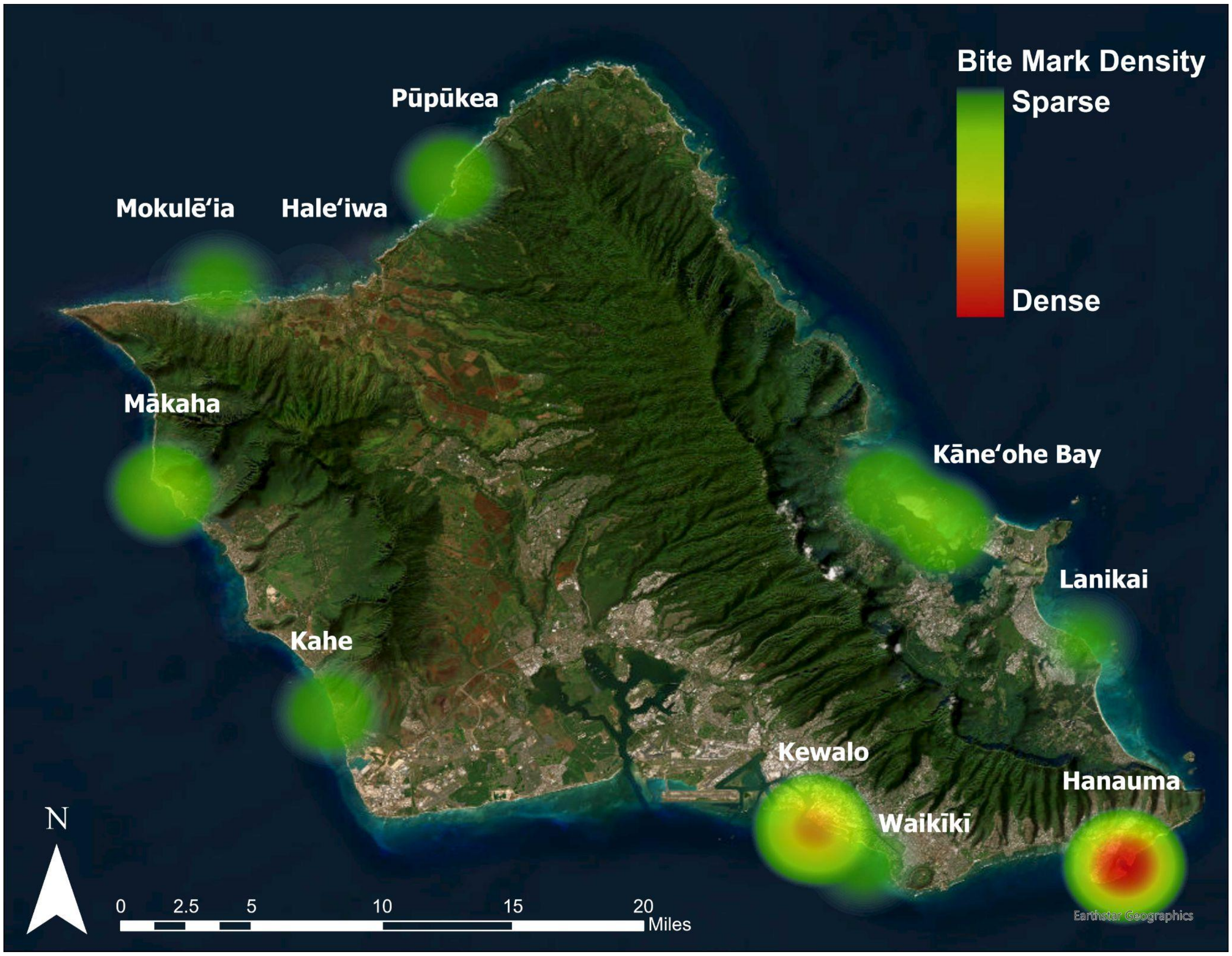

Figure S3.2 Heat map of bite mark density at ten sites surveyed around Oʻahu.

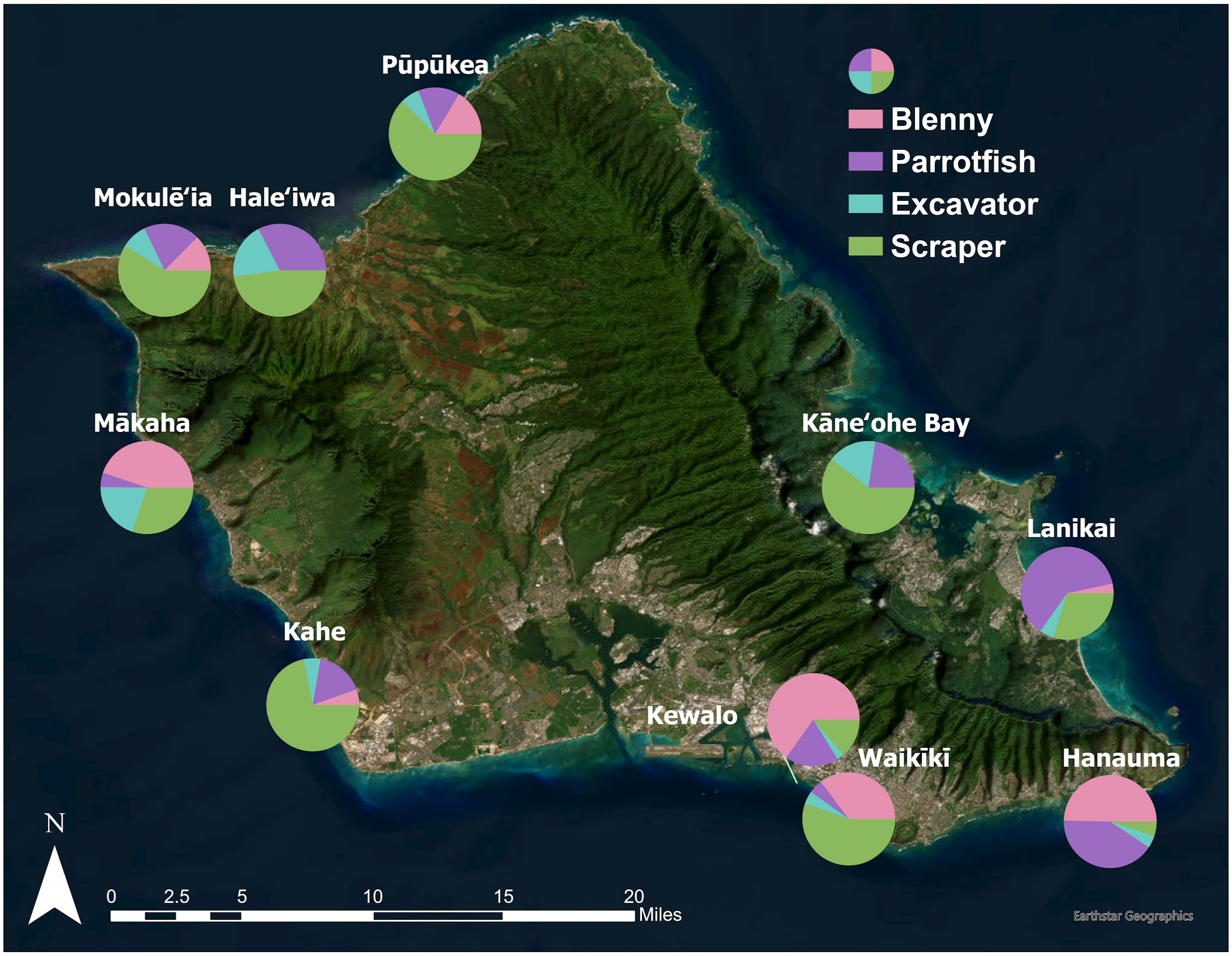

Figure S3.3 Map with proportion of bite marks inflicted by predator type observed at surveyed sites around Oʻahu.

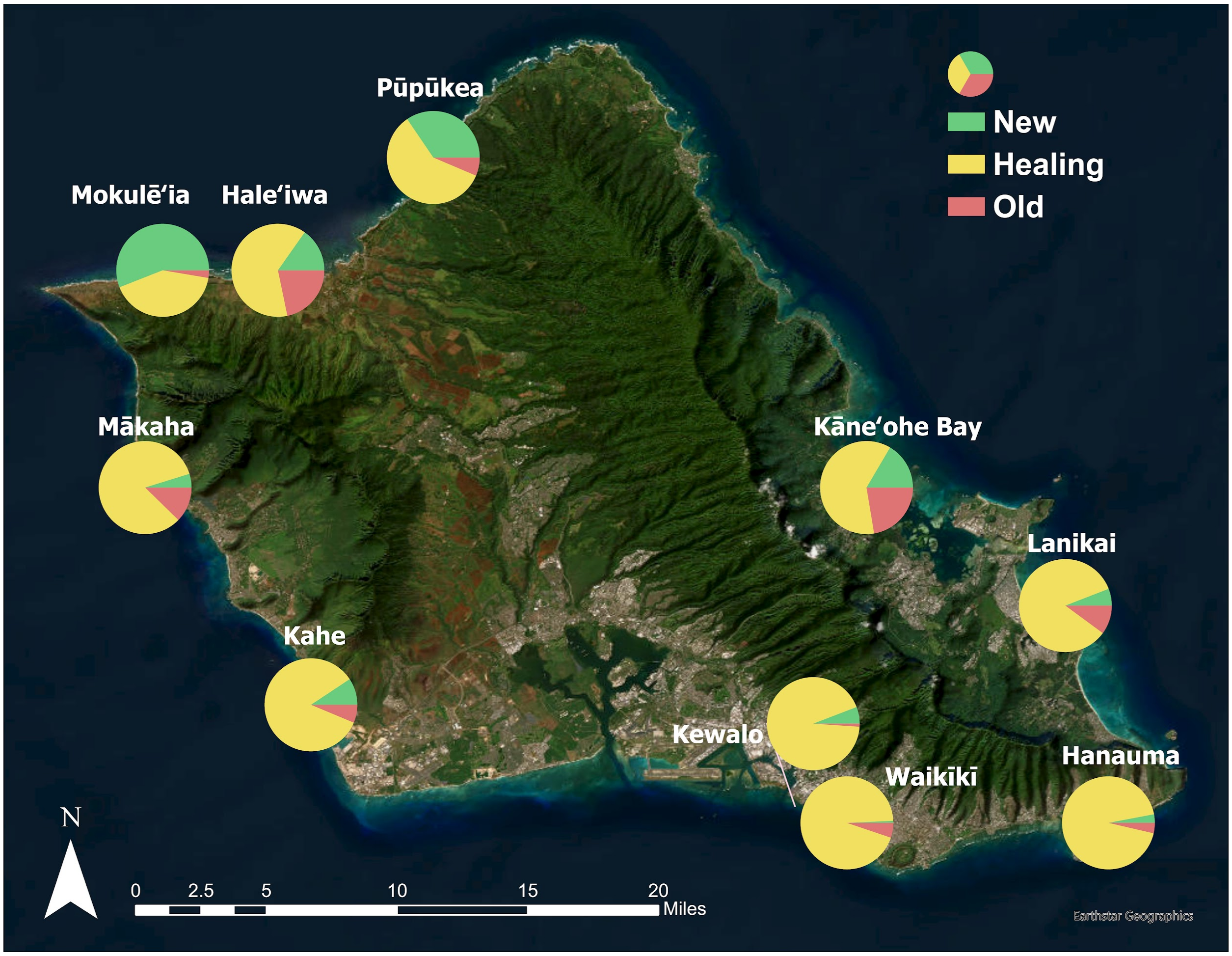

Figure S3.4 Map with proportion of bite mark conditions observed at surveyed sites around Oʻahu.

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