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Corso di Laurea Magistrale

Gestione delle epidemie di *Drupella* spp. (Mollusca, Gastropoda): conseguenze ecologiche nella barriera corallina di Koh Tao (Thailandia)

Managing *Drupella* spp. (Mollusca, Gastropoda) Outbreaks: ecological consequences in the Koh Tao coral reef (Thailand)

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SUMMARY

RIASSUNTO

Le barriere coralline sono tra gli ecosistemi più ricchi di biodiversità e produttivi della Terra, offrendo benefici ecologici, economici e culturali essenziali. Tuttavia, sono sempre più minacciate dai cambiamenti climatici, dall'acidificazione degli oceani e dalle pressioni antropiche, tra cui la pesca eccessiva, l'inquinamento e la distruzione dell'habitat. Una delle minacce meno studiate ma significative per le barriere coralline è la predazione da parte dei gasteropodi corallivori di *Drupella spp.*, capace di cause danni estesi alle colonie di corallo, in particolare quelle di *Acropora cervicornis (*Lamarck, 1816). Questa tesi indaga l'impatto ecologico delle epidemie di *Drupella* sulle barriere coralline, con un focus sull'isola di Koh Tao, in Thailandia, una regione fortemente colpita da fattori di stress sia naturali che antropici. Lo studio è stato condotto da aprile a settembre 2024 in tre siti sull'isola di Koh Tao: Chalok Bay, Taa Cha Bay e Laem Thian Bay. La ricerca mirava a (1) studiare il comportamento di *Drupella* durante le epidemie, (2) monitorare i coralli colpiti e (3) confrontare gli effetti a breve e lungo termine della rimozione analizzando i dati delle precedenti campagne di rimozione. Il lavoro sul campo ha comportato l'uso di transetti, quadrati e fotografia subacquea per monitorare la salute dei coralli, la densità di *Drupella* e gli effetti della predazione.

Inoltre, sono stati condotti esperimenti per confrontare il recupero delle colonie di *Acro*pora con e senza rimozione di *Drupella,* nonché il ruolo del pesce damigella (*Plectroglyphidodon lacrymatus*) nella colonizzazione delle cicatrici dei coralli da parte delle macroalghe. I risultati hanno rivelato una significativa variabilità spaziale nella salute dei coralli e nella densità di *Drupella* nei siti di studio. Chalok Bay ha mostrato la percentuale più alta di colonie di Acropora sane (36,1%), ma anche la più alta densità di predazione di *Drupella*. Al contrario, Laem Thian Bay ha mostrato la salute dei coralli più bassa, con il 56,9% di colonie morte o ricoperte da macroalghe. Il tasso di alimentazione di *Drupella* è stato più alto a Laem Thian (4,65 cm^2/giorno in colonie senza rimozione), seguito da Chalok (2,53 cm^2/giorno) e Taa Cha (1,17 cm^2/giorno). La rimozione manuale di *Drupella* ha ridotto i tassi di consumo dei coralli, ma si è scoperto che la pratica accelera la colonizzazione delle alghe da parte dei pesci damigella, portando alla degradazione dei coralli a lungo termine. Le colonie in cui *Drupella* è stata rimossa hanno mostrato un recupero iniziale, ma le cicatrici sono state rapidamente colonizzate da macroalghe, ostacolando la ricrescita dei coralli. Lo studio evidenzia le complesse interazioni tra la predazione di *Drupella*, il comportamento dei pesci damigella e la salute dei coralli. Mentre la rimozione manuale di *Drupella* può fornire un sollievo a breve termine per le colonie di coralli, può inavvertitamente esacerbare

la degradazione della barriera corallina a lungo termine facilitando la crescita eccessiva delle alghe. I risultati suggeriscono che una gestione efficace delle epidemie di *Drupella* richiede un approccio olistico, che includa il monitoraggio e il controllo delle popolazioni di damigelle, nonché sforzi più ampi per migliorare la resilienza della barriera corallina attraverso pressioni antropogeniche ridotte e una migliore gestione dell'ecosistema. In conclusione, questa ricerca sottolinea la necessità di strategie di conservazione integrate che affrontino sia gli impatti diretti che indiretti della predazione di *Drupella* sulle barriere coralline. Grazie alla comprensione delle dinamiche ecologiche delle epidemie di *Drupella* e delle loro interazioni con altri organismi della barriera corallina, questo studio fornisce preziose informazioni per la gestione sostenibile degli ecosistemi delle barriere coralline di fronte alle crescenti sfide ambientali e antropogeniche.

ABSTRACT

Coral reefs are among the most biodiverse and productive ecosystems on Earth, providing critical ecological, economic, and cultural benefits. However, they are increasingly threatened by climate change, ocean acidification, and anthropogenic pressures, including overfishing, pollution, and habitat destruction. One of the lesser-studied but significant threats to coral reefs is the predation by corallivorous gastropods of *Drupella rugosa* (Born, 1778), which can cause extensive damage to coral colonies, particularly those of *Acropora cervicornis* (Lamarck, 1816*)*. This thesis investigates the ecological impact of *Drupella* outbreaks on coral reefs, with a focus on Koh Tao Island, Thailand, a region heavily impacted by both natural and anthropogenic stressors. The study was conducted from April to September 2024 across three sites on Koh Tao Island: Chalok Bay, Taa Cha Bay, and Laem Thian Bay. The research aimed to (1) study the behavior of Drupella during outbreaks, (2) to monitor the grazed corals and (3) to compare short- and long-term effects of culling by analyzing data from previous removal campaigns. Fieldwork involved the use of transects, quadrats, and underwater photography to monitor coral health, Drupella density, and the effects of predation. Additionally,

experiments were conducted to compare the recovery of *Acropora* colonies with and without *Drupella* removal, as well as the role of damselfish (*Plectroglyphidodon lacrymatus*) in the colonization of coral scars by macroalgae. The results revealed significant spatial variability in coral health and *Drupella* density across the study sites. Chalok Bay exhibited the highest percentage of healthy *Acropora* colonies (36.1%), but also the highest density of *Drupella* predation. In contrast, Laem Thian Bay showed the lowest coral health, with 56.9% of colonies dead or covered by macroalgae. The feeding rate of *Drupella* was highest in Laem Thian (4.65 cm^2/day in colonies without removal), followed by Chalok (2.53 cm^2/day) and Taa Cha (1.17 cm^2/day). Manual removal of Drupella reduced coral consumption rates, but the practice was found to accelerate algal colonization by damselfish, leading to long-term coral degradation. Colonies where *Drupella* were removed showed initial recovery, but scars were quickly colonized by macroalgae, hindering coral regrowth. The study highlights the complex interactions between *Drupella* predation, damselfish behavior, and coral health. While manual removal of *Drupella* can provide short-term relief for coral colonies, it may inadvertently exacerbate long-term reef degradation by facilitating algal overgrowth. The findings suggest that effective management of *Drupella* outbreaks requires a holistic approach, including the monitoring and

control of damselfish populations, as well as broader efforts to improve reef resilience through reduced anthropogenic pressures and enhanced ecosystem management. In conclusion, this research underscores the need for integrated conservation strategies that address both direct and indirect impacts of *Drupella* predation on coral reefs. By understanding the ecological dynamics of *Drupella* outbreaks and their interactions with other reef organisms, this study provides valuable insights for the sustainable management of coral reef ecosystems in the face of increasing environmental and anthropogenic challenges.

INTRODUCTION

1. Coral reefs

1.1.1 The importance of coral reefs

Coral reefs are one of the world's most productive ecosystems, with enormous ecological, economic and cultural value for hundreds of millions of people, contributing $2.7 trillion annually (Spalding et al. 2017). Their functionality is closely linked to the complex interactions between the marine organisms that inhabit them. Scleractinian corals (belonging to the order Scleractinia within the Class Anthozoa and the Phylum Cnidaria) and coralline algae, constitute a complex three-dimensional structure (Graham & Nash 2013), due to their ability to lay down enormous amounts of calcium carbonate (Hoegh-Guldberg 2011a). Thus structures provide multiple ecosystem benefits (Iwasaki et al. 2016); 1. natural resources, both for food and aquarium needs, 2. coastal protection from waves and tsunamis (Kunkel et al. 2006), 3. cultural resources with increased tourism, cultural and religious heritage, and medical resources 4. multiple types of microhabitats utilized as shelter from predators, food resources, spawning and nesting areas (Seraphim et al. 2020) , thus supporting a greater diversity and

abundance of associated marine organisms (Graham & Nash 2013) Indeed, although coral reefs occupy less than 0.2% of the world's ocean surface, they support 25% of the biodiversity, hosting approximately 170,000 known marine species, including 4,000 species of fish, 165,000 species of invertebrates and 845 species of corals (Carpenter et al. 2008, Stella et al. 2011). This ecological success is made possible thanks to the symbiosis between the coral and an intracellular microalgae commonly called zooxanthellae, belonging to the genus *Symbiodinium spp*. This mutualistic symbiosis allows the coral to obtain nourishment, oxygen and carbon dioxide removal in exchange for shelter and the availability of nutrients from waste elements (Iwasaki et al. 2016).

1.1.2 Distribution of coral reefs

Coral reefs, encompassing an area of approximately 151,390 km², are largely concentrated in the Indo-Pacific region, thriving within a latitudinal band of 30°S to 30°N. This distribution is dictated by the specific environmental requirements necessary for coral growth and survival. As highlighted by Sing Wong et al. and Hoegh-Guldberg, these requirements include:

- Sea Temperature: The ideal temperature range for corals is typically between 18–29°C, optimal for the metabolic processes of both the coral animal and its symbiotic algae (zooxanthellae).
- Oligotrophic Conditions: Excess nutrients can fuel the growth of macroalgae, which can outcompete corals for space and light.
- Salinity: The ideal range is 23.3–40 ppt is crucial for coral health and proper skeletal formation.
- Water Clarity and Alkalinity: These are essential for coral survival. Clear water allows sufficient sunlight to reach the zooxanthellae within the coral tissue, enabling photosynthesis. Alkaline conditions are necessary for the deposition and maintenance of the coral's calcium carbonate skeleton.

1.2 **Threats to coral reefs**

1.2.1 Climate change and acidification

Coral reefs are extremely vulnerable ecosystems, currently threatened by expanding and intensifying impacts of human activities (He & Silliman, 2019). Over the last 30 years, the main drivers of pressure on coral reefs have been rising temperatures, ocean acidification and sea level rise (He & Silliman, 2019), caused

by high greenhouse gas emissions and climate change (Mumby & Van Woesik 2014), anthropogenic phenomena initiated during industrial development (He & Silliman, 2019). In particular, excessive irradiation (Hoegh-Guldberg 2011) and high temperatures disrupt the symbiotic relationships between corals and the dinoflagellates living within them, thus leading to coral bleaching. This is considered extreme photoinhibition, which can lead to the weakening of corals and thus their inability to fight disease (El-Naggar 2020) and the production of harmful photosynthetic by-products. Bleaching may be a temporary and/or reversible event for some species, but fatal for those species that rely heavily on symbionts. Furthermore, the persistence of high temperatures may reduce growth rates (hence calcification) or lead to weaker skeletal formation. Reduced calcification and bleaching events may reduce the resilience of coral-dominated ecosystems (El-Naggar 2020) . The increased acidity of ocean waters due to the absorption of carbon dioxide (CO_2) produced by the combustion of fossil fuels, deforestation and increased agricultural runoff (Hoegh-Guldberg 2011b), is directly affecting the reproductive capacity, growth rate and survival of some calcifying reef organisms, including corals, molluscs and coralline algae (Hoegh-Guldberg 2011a). Although coral reef populations have adapted to increasingly higher temperatures, events such as global warming and ocean acidification are

changing the composition and distribution of species, with uneven effects among different ocean areas (Hoegh-Guldberg 2011a).

1.2.2 Anthropogenic pressures

Although climate change is the most prevalent threat (He & Silliman, 2019). While global stressors independently affect 11% of reefs worldwide, twice as many (22%) coral reefs are impacted by local impacts. Local disturbances (i.e., water quality, sedimentation, human use, fishing pressure) may potentially influence coral reef responses to and recovery from climatic threats. (Guan et al. 2020). Several studies have shown that water pollution and fishing are affecting 32.3% and 30.8% of global coral reefs, respectively, followed by coastal population (19.7%), tourism (14.6%) and industrial development (4.6%) (Andrello et al. 2022). Over the past two centuries, these factors have been recognised as the responsible of ecosystem shift from a dominance of scleractinian corals, fish and coralline algae to algal turf, non-calcifying macrophytes and non-calcifying symbiotic cnidarians (Ellis et al. 2019; Mumby & Van Woesik 2014) (Fig.1).

Figure 1: Changes in coral reef health due to multiple stressor interactions associated with climate stress, overfishing and nutrient enrichment. Artist Credit: Ivan Gromicho

Recent studies by the Global Coral Reef Monitoring Network claim that up to 2018, 19% of coral reefs have been destroyed, 15% severely damaged and 20% could disappear within less than 40 years (GCRMN).

1.2.3 Eutrophication and coral disease

Coral reefs face numerous biotic stressors, including algal overgrowth, outbreaks of infectious diseases, and predation. These factors, acting individually or synergistically, have significantly reduced coral cover. Among the primary human-induced impacts, land-use changes and terrestrial runoff stand out, as they

have increased sedimentation and eutrophication in nearshore reefs (Jørgensen 1996). Sedimentation poses a range of threats to coral reefs, causing both lethal and sub-lethal effects. As described by Rogers & Ramos- Scharrón (2022) sediment can smother and bury corals, abrade their tissues, reduce light penetration critical for photosynthesis, and inhibit coral recruitment by interfering with larval settlement and survival. Eutrophication, the excessive enrichment of nutrients like nitrogen and phosphorus, also endangers coral reefs. While eutrophication can occur naturally (Akinnawo 2023), it has been exacerbated by human activities, such as the intensive use of fertilizers in agriculture, concentrated animal feeds, and effluents from livestock and aquaculture (Fabricius 2011; Akinnawo 2023). In coral ecosystems, eutrophication fosters competition for resources like light and nutrients between macroalgae and corals. The resulting increase in water turbidity—caused by suspended particles and phytoplankton growth—further reduces light availability for zooxanthellae photosynthesis. Additionally, studies have shown that eutrophication can promote coral disease outbreaks (Bruno et al. 2003; Fabricius 2011).

Infectious coral diseases, caused by pathogens such as bacteria, viruses, and protozoa, lead to tissue loss, reduced reproductive capacity, and destabilized reef communities (Sokolow 2019; Harvell et al. 2007; Renzi et al. 2022). While these

diseases occur naturally, their prevalence has increased due to anthropogenic stressors and global changes (Sokolow 2019; Moriarty et al. 2020). Eutrophication weakens coral immunity, and coral predators may serve as vectors for disease transmission (Renzi et al. 2022; Bruckner 2002).

1.2.4 Corallivory

Corallivory is the consumption of live coral tissue, and sometimes skeleton, by several taxonomic groups, including fishes, echinoids, crustaceans, molluscs, and annelids (Rice et al. 2019) . Corallivory is a natural process that plays a complex role in reef ecosystems, influencing coral growth, distribution, and community structure (Renzi et al. 2022). Predation on corals by corallivore organisms is a natural process in coral ecosystems that contributes to their diversity and adaptive capacity (Rotjan & Lewis 2008). However, ecological imbalances resulting from factors such as human activities or climate change can make this activity destructive to coral reefs (Rotjan & Lewis 2008; Lenihan et al. 2011). Corallivores are a heterogeneous group of species (vertebrates and invertebrates) that can consume both soft and hard corals, making them more vulnerable and thus increasing their exposure to infection and disease (Renzi et al. 2022). They can be

subdivided into; 1. ‘Mucus-feeders’ that are only able to consume the coral's mucus; 2. ‘Browsers’ for those corallivory that remove coral tissue without damaging the skeleton; 3. ‘Excavators’ that feed on the skeleton by removing coral tissue; 4. ‘Scrapers’ that are able to remove living coral tissue and take a small portion of the underlying skeleton (Rotjan & Lewis 2008). These four strategies cause different types of damage to live corals, with injury size and shape significantly affecting their recovery. Their activity has direct negative effects on coral growth, survival, and reproductive traits (fertility, fecundity, gonad numbers, and egg production). Indirectly, corallivores facilitate algal competition and interact synergistically with other stressors, both natural and anthropogenic, further reducing coral fitness (Rice et al. 2019; Renzi et al., 2022).

1.2.5 Gastropods corallivory

Corals are subject to predation by various macro-consumers, such as fish (Cole et al. 2008), echinoderms, (Kroon et al. 2021) and gastropods (Dalton & Godwin 2006). Among the corallivorous gastropods that feed on hard corals are the families *Architectonicidae*, *Epitoniidae*, *Pediculariidae* and *Muricidae*; the latter is one of the richest in species and morphologically most diverse (Barco et al. 2010).

Large aggregations and outbreaks of corallivore gastropods often have a negative effect on the fitness of corals, leading to a decrease in live coral cover on affected reefs (Ayling & Ayling 1987; Rotjan & Lewis 2008; Onton et al. 2011). The gastropods of the genus *Drupella* (Muricidae) is particularly voracious, having caused a 35% decline in coral cover over two years in Toga Bay, Japan and an 86% decline in less than a decade in parts of Ningaloo Reef, Australia (Ayling & Ayling 1987; Rotjan & Lewis, 2008). *Drupella* is specialized in feeding on hard corals using a specialized radula and a cuticle-covered proboscis (Claremont et al. 2011), more details on these features are provided later. The feeding behavior of these gastropods creates wounds that can lead to extensive necrosis and colony death. Additionally, *Drupella* facilitates the spread of coral diseases like Brown Band Disease by enabling pathogen entry through feeding injuries, accelerating reef decline (Scott et al. 2017b; Nicolet et al. 2013). This disproportionate impact on stressed coral reefs highlighted the need for management strategies, including manual removal and population monitoring, in heavily affected areas (Nicolet et al. 2018).

1.3 Gastropods of genus *Drupella* Thiele, 1925

1.3.1 Phylogenesis and global distribution

Originated in the late Miocene (Claremont et al. 2011), the genus *Drupella* belongs to the family Muricidae, class Gastropoda, and phylum Mollusca. The currently best-known species include *D. rugosa* **(Born, 1778),** *D. cornus* **(Röding, 1798***)*, *D. fragum* **(Blainville, 1832***)*, *D. eburnea (***Küster, 1862***)* (Saponari et al. 2021) and *D. margariticola* **(Broderip, 1833***)* (Zhang et al. 2024) (Fig.2). These marine molluscs are mainly distributed in the Indo-Pacific Ocean, in tropical ecosystems between eastern Africa, south-east Asia and the western Pacific (Fig.3). *Drupella* genus commonly occurs on corals (like *Acropora*) or hard substrate (such as coral rubble or dead coral) in lower intertidal and shallow sublittoral zones (Zhang et al. 2024) with densities of 0-2 ind/m2 (Cumming 2009) that decline with depth (Schoepf et al. 2010). However, the deterioration of coral reefs caused by climate change, pollution and other anthropogenic pressures has led to several proliferation or aggregation events. During these events, densities of up to 20 individuals per square meter or 250 individuals per colony have been observed, with significant consequences on the health of coral reefs and local ecology (Saponari et al. 2021). Aggregation events have been reported and well described

in several geographical areas, including the Great Barrier Reef (Morton et al. 2002; Cumming 2009), Kenya (McClanahan 1997), Hong Kong (Morton et al. 2002), the Red Sea (Schoepf et al. 2010), Thailand (Scott et al. 2017; Moerland et al. 2016), Taiwan (Tan et al. 2024) India (Marimuthu & Tripathy 2018) and the Maldives (Saponari et al. 2021).

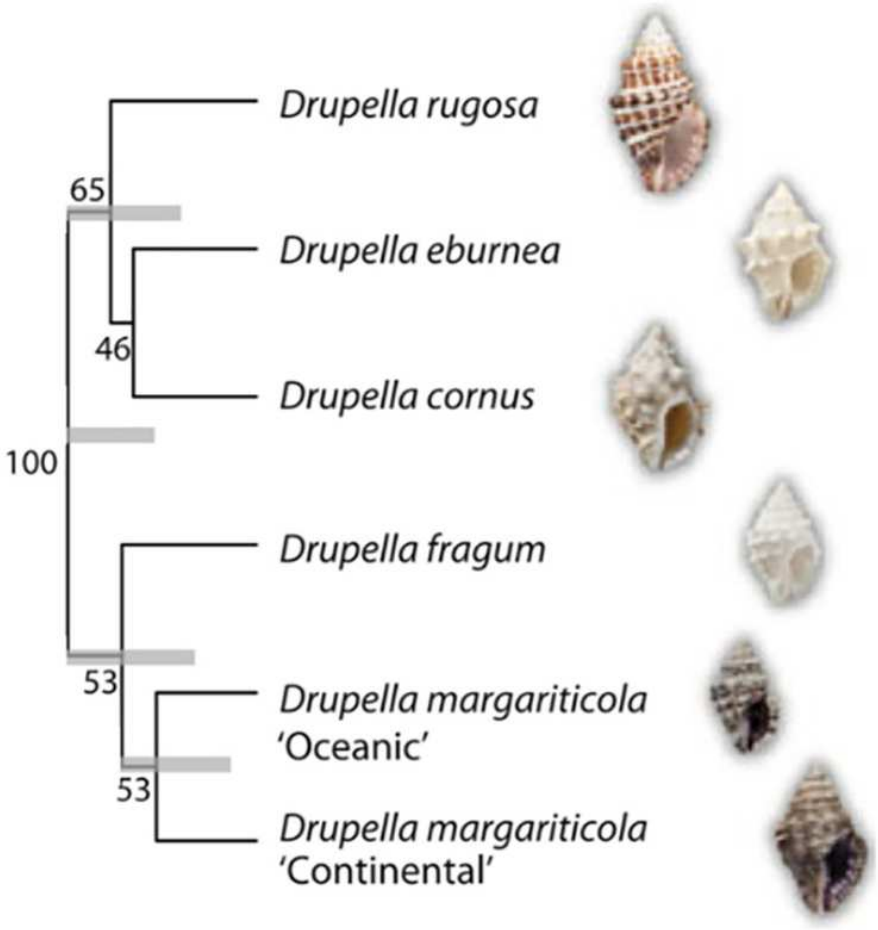


Figure 2: BEAST phylogeny of *Drupella* snails, from Zhang et al. 2024

Figure 3: *Drupella* genus distribution, 2000-2024 from: GBIF Secretariat (2023). GBIF Backbone Taxonomy. Checklist dataset https://doi.org/10.15468/39omei accessed via GBIF.org on 2024-11-28.

1.3.2 Morphology of Drupella

The fusiform/cylindrical shell (Tan et al. 2024) of *Drupella* can be divided into two parts: the spire, or the tip of the shell, and the body whorl, which is the main part that houses the mollusc (Fig.4). At the level of the body whorl is the opening of the shell (operculum), the size of which varies with the age of the individual (Ismail et al. 2000). This operculum (cream-white in colour) allows the mollusc to exit and withdraw and is characterised, on the inner edge of the outer lip, by a row of 5-6 small teeth (Zhang et al. 2024). The body whorl has 4/5 rows of spirals

(complete 360° rotations of the shell), each adorned with a different number of pointed ribs that vary according to the size of the shell and that decrease towards the siphonal canal. The spire, on the other hand, is composed of 4 rows of spirals, with ribs less accentuated than the lower part. Each protuberance is equipped with riblets or sculptures that form an axial or longitudinal pattern. The identification of *Drupella* shells is complex due to the presence of coralline algae and assorted epifauna that often cover the external surface, giving them a pink or burgundy color (Scott et al. 2017c; Saponari et al. 2021; Zhang et al. 2024). The colour of the shell is white but may vary depending on the species considered; *D. rugosa* and *D. margariticola* in fact have darker tones corresponding to the ribs. These characteristics make the *Drupella* shell not only functional but also an indicator of its growth stage (Ismail et al. 2000) and its ecological habitat.

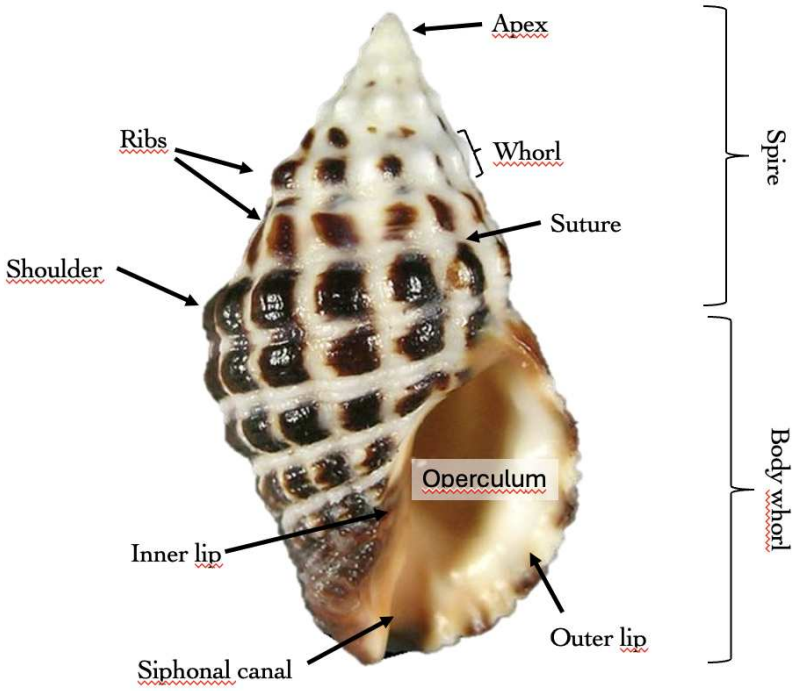


Figure 4: Shell morphology of *Drupella rugosa,* modified from: WoRMS

Drupella rugosa (Born,1778)	Drupella margariticola (Broderip, 1833)	Drupella cornus (Röding, 1798)
		

Figure 5: Morphological differences between the most common *Drupella* species in the Indo-Pacific Ocean. Images tmodified from WoRMS and modified.

Inside the shell, the mollusc possesses a foot for movement and a head equipped with two eye stalks, a siphon, and a proboscis (Fig.6). The siphon, part of the mantle, functions as a snorkel to channel water to the gills and detect proteins and other substances released by prey, aiding in food location. The proboscis, with a keratinized tip that protects against nematocyst punctures (Claremont et al. 2011), ends in a mouth containing a specialized radula (Fujioka 1984; Zhang et al. 2024). This radula is adapted for scraping and consuming live coral tissue, allowing efficient removal of coral polyps (Zhang et al. 2024). Additionally, some species exhibit sexual dimorphism, with males having more complex radulae and larger rachidian teeth than females (Claremont et al. 2011).

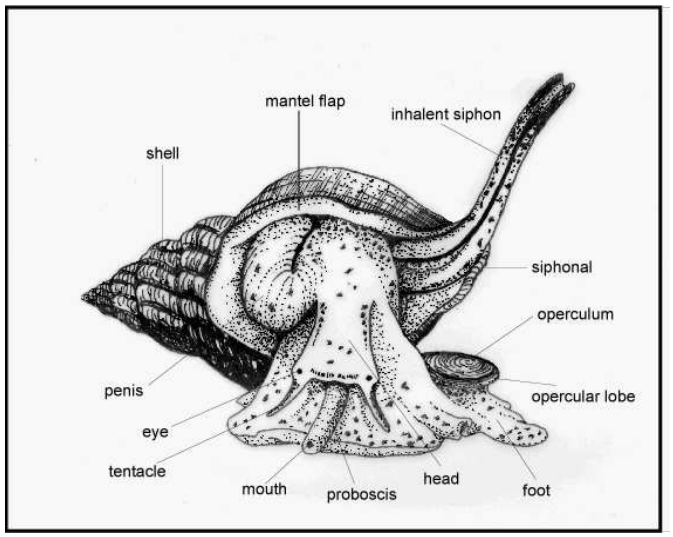


Figure 6: Gastropods morphology, modified from: Sohl 1979

Based on size, *Drupella* can be divided into three categories: “recruits”, with shells smaller than 1 cm; “juveniles”, between 1 and 2 cm; and “adults”, which reach 4.8 cm (Saponari et al., 2021). Several studies have reported an average length between 0.6 and 3.63 cm with an average shell weight of 1335 mg and a dry body weight of 33 mg (Ismail et al. 2000; Zhang et al. 2024).

1.3.3 Life cycle and reproduction

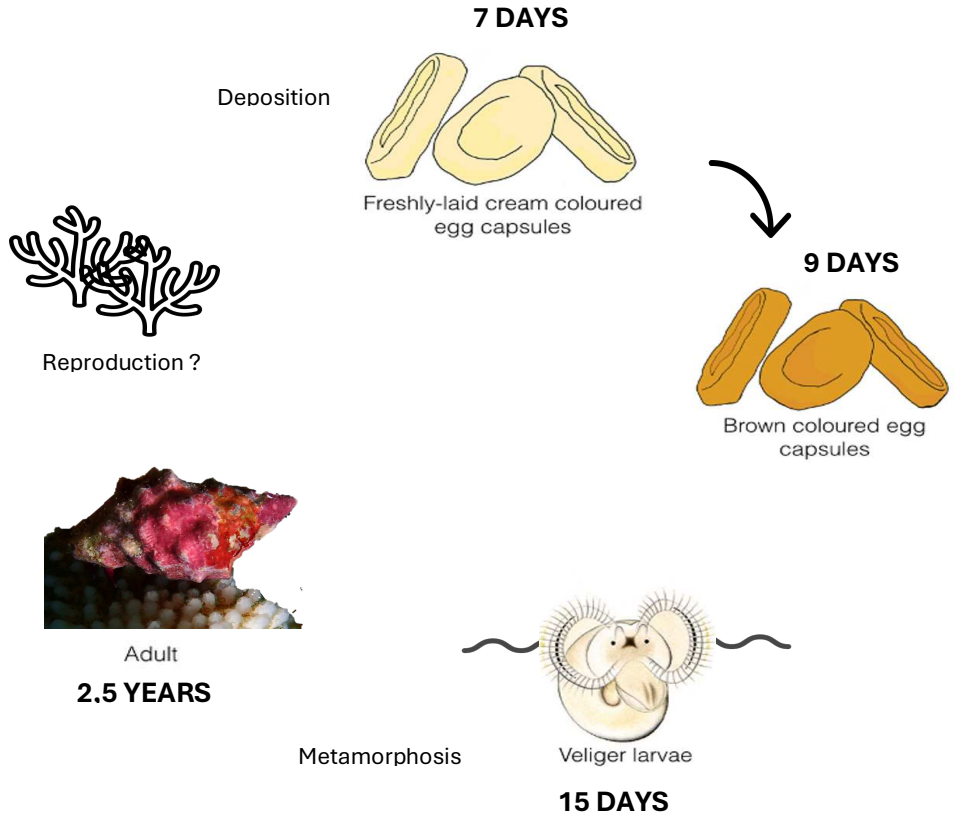


Figure 7: Life cycle of *Drupella* genus, modified from Sam et al. 2017

As illustrated by the image (Fig.7), the life cycle of *Drupella* begins when the female lays small egg capsules measuring 2.43 ± 0.14 mm by 2.39 ± 0.09 mm by 0.97 ± 0.12 mm (L × W × H) (Sam et al. 2017). Spawning occurs in December in the southern hemisphere and June in the northern hemisphere (Zhang et al. 2024) with a water temperature range of 23.3° (Haslam et al. 2024) to 30° degrees (Baomer & Al.Sofyani 2016). Water temperature appears to play a key role in the development of *Drupella* snails; studies indicate that their embryos can develop normally inside the capsules even during winter when the temperature drops to 18°C (Koido et al. 2017). However, a drop in temperature could significantly hinder egg laying (Zhang et al. 2024). These translucent ampullary or vasiform capsules (Sam et al. 2017) have concave tops (Sam et al. 2017) and are deposited in clusters on the skeleton of worn coral or hidden under dead corals (such as mushroom corals) (Scott et al. 2017 c) that can serve as substrates for egg-capsule attachment. Each capsule has an average of 64-67 creamy-white/light yellow spherical embryos (Sam et al. 2016; Sam et al. 2017). Seven days after spawning, pre-spawning veligers have developed transparent shells with visceral mass and yolk. They move slowly within the confines of the still cream-coloured egg capsules. After a further 2 days, the inner egg capsules turned brown and opaque (Sam et al. 2017).

15 days after oviposition, the pelagic veliger larvae (shell size averaged 328 ± 19 μm by 245 ± 19 μm, length × depth) are able to swim freely in the water column, concentrating mainly near the surface, probably due to phototaxis (Sam et al. 2017) and the presence of phytoplankton (as they are considered filter-feeders). At hatching, the yolk is absent, while structures such as the foot, operculum and internal organs, including the stomach, are already formed (Sam et al. 2017). Due to the predation, illness and lack of food, embryonic and larval stages constitute the most critical moments in the life cycle of *Drupella* (Zhang et al. 2024), during which only 5% of individuals manage to survive beyond the first year of life (Sam et al. 2017). Approximately 15 days after hatching, veliger larvae migrate to the bottom to settle on suitable substrate, a behaviour influenced by the sail reduction and by competition with other invertebrates (Sam et al. 2017). Individuals that pass these critical stages transform into juveniles through metamorphosis and, within 2.5 years, reach sexual maturity, with an overall life expectancy of 7-8 years (Zhang et al. 2024).

The different species of the genus *Drupella* show significant variations in size, laying times, morphology of the ovarian capsules, and the number of eggs and embryos contained in each capsule. In the case of *D. rugosa*, capsules with a

bulliform (bladder-shaped) morphology were observed, in contrast to the more common ampulliform or vasiform forms typical of other species in the genus. As highlighted by Sam et al. (2017), *D. rugosa* produces the smallest capsules in terms of length and width, the fewest number of capsules per deposition event (between 47 and 67 capsules), and the fewest embryos per deposition, with an average of 3484 embryos per event. This represents the lowest value among all the species studied. However, this apparent limitation is compensated for by the relatively large size of the newly hatched veligers (Zhang et al., 2024), a factor that significantly increases their survival rate and, consequently, the probability of more individuals to reach the metamorphosis stage (Sam et al. 2017).

1.3.4 Feeding behaviour

Most species of the genus *Drupella* (e.g., *D. cornus*, *D. eburnea*, *D. fragum*, and *D. rugosa*) exhibit distinctive morphological adaptations, such as a specialized radula and a cuticular proboscis, enabling efficient coral tissue consumption and obligate corallivory (Moerland et al. 2016; Zhang et al. 2024). Their feeding behavior leaves behind white scars—exposed skeletons—which are quickly colonized by filamentous algae (Nardi 1991). In contrast, *D. margariticola* is

considered an opportunistic corallivore or scavenger, feeding primarily on damaged corals and lacking these specialized features (Claremont et al. 2011). *Drupella* snails are opportunistic generalist corallivores with high dietary plasticity, selecting corals based on availability, nutritional value, and environmental conditions (Hoeksema et al. 2013; Lei et al. 2022). Preferences are influenced by factors such as high protein and lipid content, tissue biomass, branching morphology, and intermediate tissue nutritional value (Lei et al. 2022; Tan et al. 2024). They show a marked preference for *Acropora* species, which are rapid growers but vulnerable to diseases, structural damage, and predation (Hobbs & Frisch 2010). On average, *Acropora* tissue consumption is 1.81 cm^2 per individual per day (Zhang et al. 2024), with some species reaching a maximum consumption of 6.5 cm^2 (Bessey et al. 2018). Studies have also shown that this rate can increase with increasing temperatures (Al-Horani et al. 2011). *Drupella* snails often aggregate on large coral colonies (≥30 cm) during mass reproductive events or in response to chemical signals from stressed corals. They prey nocturnally, moving within a radius up to two meters, and retreat during the day to sheltered areas like undersides or between branches (Bessey et al. 2018; Cumming 2009). Aggregation behavior is driven by attraction to conspecifics,

compounds from damaged corals, and shared settlement histories within cohorts (Schoepf et al. 2010).

1.3.5 Drupella snails' population dynamics and distribution

The population dynamics of *Drupella* exhibit distinct behaviors between juvenile (1–2 cm) and adult (>2 cm) individuals, leading to differing impacts on coral communities. Colony shape plays a critical role in prey selection, offering varying levels of protection (Schoepf et al. 2010). Juveniles typically occupy cryptic positions at the base of tightly branching corals like *Acropora* and *Pocillopora* (Bettarel et al. 2018; Saponari et al. 2021), seeking shelter from predators and wave motion. As they mature, adults gain greater mobility and begin occupying more exposed positions on corals, expanding their feeding range. Their thick, epifauna-covered shells make them less conspicuous and reduce their vulnerability to predation, enabling more frequent movement between colonies (Cumming 2009; Schoepf et al. 2010). Juveniles, in contrast, tend to cluster in small groups to enhance survival and minimize competition with adults (Schoepf et al. 2010), while adults often form larger aggregations, particularly during breeding periods, exerting greater ecological pressure on coral reefs (Saponari et al. 2021).

Population studies of *Drupella* reveal a predominance of adults, which, under resource-limited conditions (e.g., food and shelter), can lead to intraspecific competition and increased juvenile mortality (Saponari et al. 2021; Zhang et al. 2024).

1.3.6 Causes of Drupella outbreaks

Although the causes of *Drupella* outbreaks are not yet widely comprehended, Zhang et al. (2024) suggest some factors that could contribute to this phenomenon. Among these he analyzes the excessive nutrient input given by terrestrial runoff, overfishing by *Drupella* predators, and increased stressors to the reef.

1. Terrestrial runoff results in reduced salinity and increased nutrients, leading on the one hand to stress corals subjected to low salinity conditions and on the other hand to increased phytoplankton given by increased temperatures and increased nutrients, which improves the chance of survival of *Drupella* larvae and juveniles, ensuring that the veliger larvae have sufficient energy to complete to metamorphosis. In addition, the increase in macroalgae results in an excessive release of organic carbon that promotes microbial proliferation,

weakening by decreasing the rate of photosynthesis of corals' Symbiodiniaceae (Kaullysing et al. 2016).

2. Another factor that would seem to have contributed to the increase in *Drupella* is overfishing, which, by reducing balistids, wrasses, and predatory invertebrates (such as the fish *Coris aygula*, the Napoleon fish *Cheilinus undulatus* and smaller predators such as *Alpheus lottini* and *Cymo andreossyi*) would have resulted in the reduction of natural control over *Drupella* populations, facilitating their over-expansion . The decrease in herbivorous fish due to intensive fishing, caused an overgrowth of macroalgae (Leckraz 2015), which are natural competitors of corals in terms of recruitment, light and nutrients.
3. Stressors given by climate change such as rising temperatures and coral bleaching events decrease the resilience of coral reefs , making them more vulnerable to predator attacks (Rice et al. 2019). In addition, extreme natural events such as cyclones can physically damage corals, creating possible microhabitats or increasing rubbles that could favour the establishment and the proliferation of *Drupella* (Ayling & Ayling 1992).

4. Finally, increased recreational activities such as scuba diving and snorkeling physically harm corals, causing injuries that could facilitate the settlement of the snail or the secretion of substances attracting *Drupella* (Cumming, 2002).

It would seem that *Drupella* outbreaks are the result of complex interactions between environmental and anthropogenic factors that compromise the health and balance of coral reefs. According to studies carried out by Canteri (2024), *Drupella rugosa* outbreaks in Koh Tao are closely linked to a combination of environmental factors and anthropogenic stresses affecting coral reefs. Increased CO2 concentration has been identified as one of the main stressors, with significant effects on coral survival. CO2 contributes to ocean acidification, which reduces coral calcification and lowers the heat tolerance threshold, making them more vulnerable to bleaching and degradation. These changes compromise the integrity of coral ecosystems, creating favorable conditions for the proliferation of *D. rugosa*. Another relevant factor is increased phosphate (PO4) levels, often associated with agricultural and urban runoff. Although high PO4 concentrations can promote algal growth, resulting in coral stress, the study found a negative correlation between PO4 and *D. rugosa* abundance. This suggests that the reduction in water quality negatively affects the species, while worsening the

overall condition of the reef. Furthermore, the increase in salinity in the area showed a positive correlation with the presence of *D. rugosa*, indicating that higher levels of salinity could favor their proliferation.

1.3.6 Prevention and management strategies for Drupella outbreaks

Drupella snail outbreaks require targeted management to mitigate damage to coral reefs. One of the most immediate practices is manual removal (Fig.8a), which involves identifying and collecting both adults and egg capsules. This method has been successfully implemented in several regions, such as in Japan, where seasonal interventions have controlled *Drupella* populations and preserved *Acropora spp*. colonies, even during winter stress conditions. Similarly, in Thailand, manual removal by volunteer divers significantly reduced snail density, demonstrating the effectiveness of this practice in the short term (Scott et al. 2017b) However, the method is limited by the resources required, high costs, and the difficulty of operating in deep water, making it a temporary rather than a permanent solution. Currently, the only long-term monitoring study on Koh Tao Island about *Drupella* shell removal was conducted by Canteri (2024). This study

analyzed data collected between 2010 and 2023 by the New Heaven Reef Conservation, integrated with Scott's data from 2009-2014 (Scott et al. 2017b). The results show that *Drupella* shell removal activity has had a positive impact on coral cover, with a recovery of 812,569.72 m² in 10 years on a total area of 11,364.71 m². Furthermore, the study proposed the production of natural dyes from *Drupella* shells, promoting a sustainable economy and possible economic benefits for local communities. A complementary method for the control of *Drupella* is represented by biological control, which uses their natural predators, such as the giant snail *Charonia tritonis* and the guardian crabs of the genus *Trapezia*. These organisms, through direct predation or aggressive behavior towards corallivores, can help to contain the spread of epidemics. In Australia, for example, the coral guardian crab (*Trapezia cymodoce*) has been shown to reduce the feeding rate of *D. rugosa* by 22.9% (Samsuri et al. 2018).

Another long-term strategy is to improve the resilience of coral reef ecosystems. Interventions such as reducing agricultural runoff, which decreases the proliferation of macroalgae, and protecting marine areas through restrictions on human activities promote the overall health of the reefs. In addition, increasing the abundance of herbivorous and predator fish by regulating the overfishing may restore a natural control of *Drupella*. Integrating these approaches, along with new

technologies for monitoring and restoring marine habitats, is a promising way to sustainably address the problem of *Drupella* outbreaks, ensuring the preservation of coral reefs for future generations.

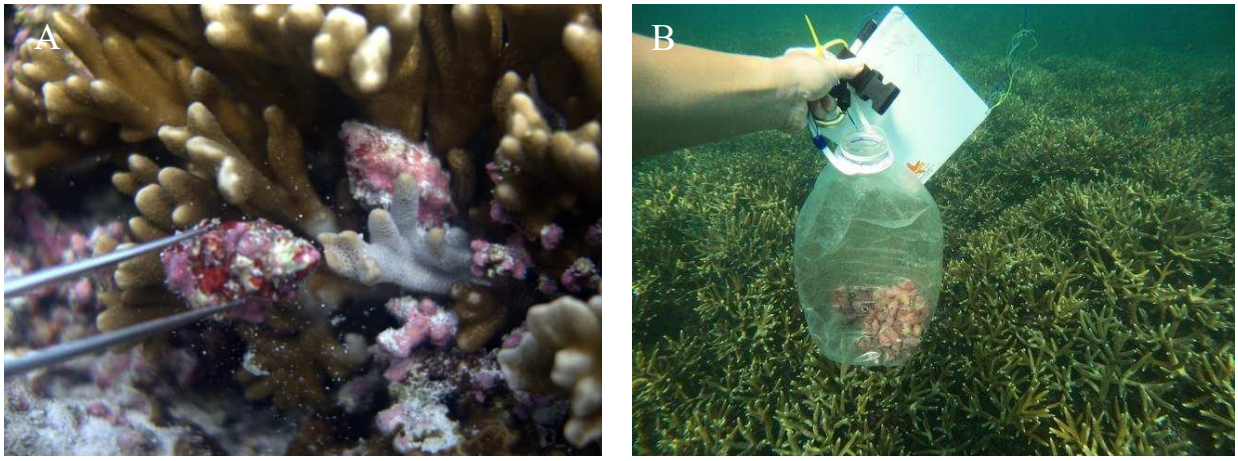


Figure 8: *Drupella* removal; A: *Drupella* removal from Montipora spp. Image from https://gili-lankanfushi.com/gili-veshi-environmental-initiatives/marine-biology-blog/drupella-removal-expedition-gili-hosts-help-save-our-coral/. B: *Drupella* removal from *Acropora spp*. Image taken in Chalok 19/05/24.

1.4 Koh Tao island, Thailand

1.4.1 Geographical and Ecological information

Thailand, located in Southeast Asia between latitudes 6° and 13° N, has a 2,614 km long coastline that provides ideal environmental conditions for the

development of coral reefs. The country is home to approximately 153 square kilometers of coral reefs and over 300 small islands (Yeemin et al. 2006). Koh Tao, the study area, is a small island located along the western coast of Thailand, in the province of Surat Thani (Weterings 2011). With a total area of 21 square kilometers, the island is located in the Gulf of Thailand, a shallow bay with an average depth of 58 meters and a maximum of 85 meters. These physical characteristics limit water exchange and favor a significant influx of freshwater that reduces salinity and increases the rate of sedimentation of the gulf (Khongchai et al. 2003). In the 1980s, the island began to emerge as a tourist destination due to its numerous bays surrounded by coral reefs, which today constitute the main economic support of the island (Weterings 2011; Szuster & Dietrich 2014). Currently, Koh Tao is known as one of the most popular destinations for scuba diving in Southeast Asia, with over 60 dive centers (Scott et al. 2017a). The thriving diving industry has led to a rapid development of supporting infrastructure such as restaurants, bars and resorts, resulting in an annual tourist flow that varies between 300,000 and 500,000 visitors. (Scott et al. 2017a).

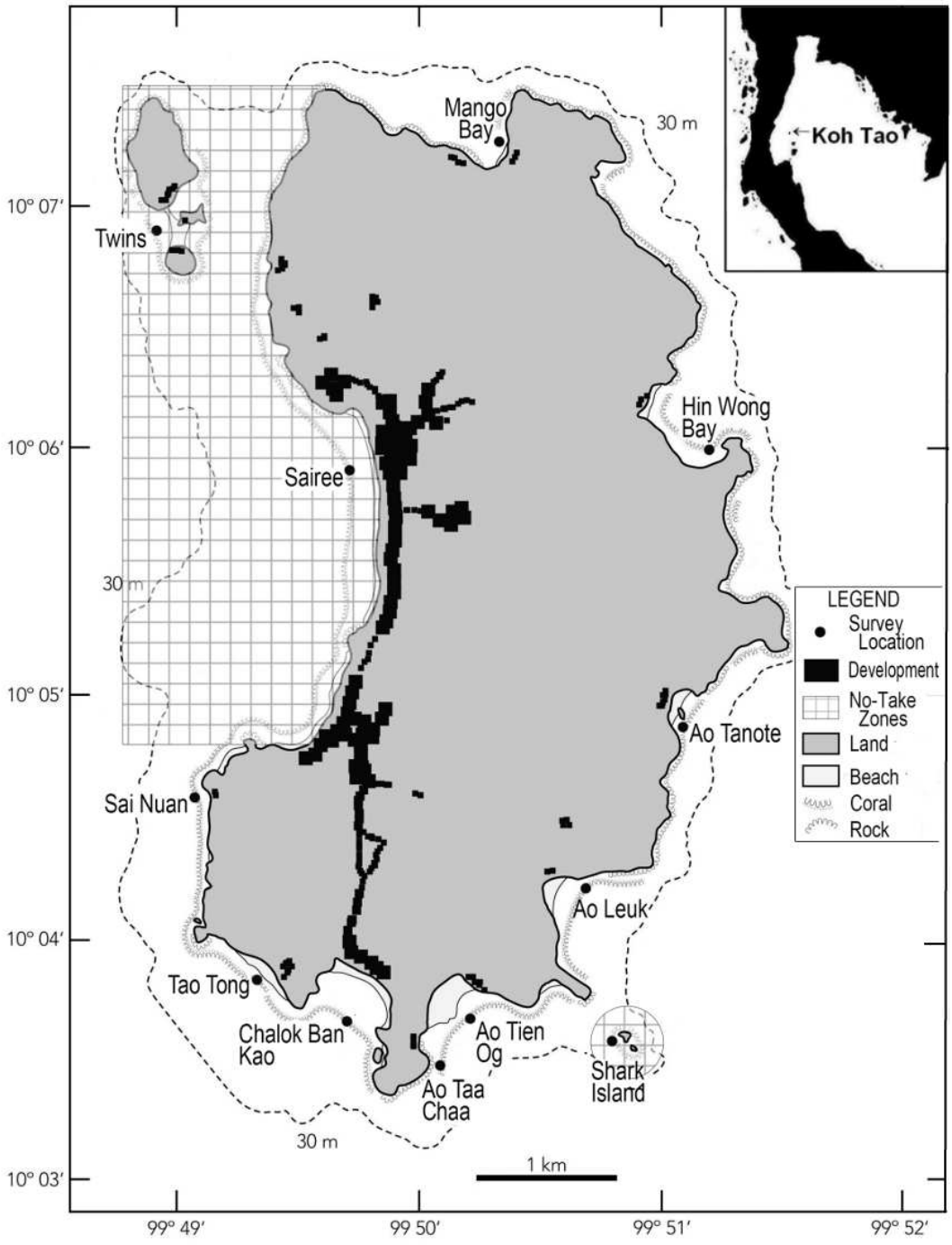


Figure 9: Modified map of Koh Tao showing survey locations used in Scott C. et al. 2017a

1.3.2 Coral reefs in Koh Tao

The coral reefs of Koh Tao extend to a depth ranging from 1 to 40 meters, mainly along the western and southern coasts of the island. In terms of biodiversity, Koh Tao has a significantly higher rate than its neighbors Koh Phangan and Koh Samui. Among the corals surrounding the island, there are several types (Hoek et al. 1980), such as massive, encrusting, tabular, branching and mushroom corals. Regarding the associated fauna, 56% of the 365 species observed in the Gulf of Guinea have been found in Koh Tao (Wongthong 2013). Currently, the island offers over 30 dive sites distributed along the entire coast of the island, each with unique geological characteristics.

1.4.3 Impacts on Koh Tao coral reefs

The coral reefs of Koh Tao have been under significant stress in recent years, due to a combination of local and global factors (Tapsuwan & Rongrongmuang 2015). One of the most significant factors has been the mass coral bleaching events that occurred in 1998, 2010, 2014 (Wetering 2011; Scott et al. 2017a), 2016 and 2019

(NOAA). The most significant case was in 2010, when 72.17% of corals were affected by bleaching due to high sea temperatures (Chavanich et al. 2012), which reached 32.4°C for over five months (NOAA). Deforestation, mainly related to tourism development and the expansion of roads, settlements and coconut plantations (Weterings 2011), has accelerated soil erosion, causing increased sedimentation (Scott et al. 2017a). Added to this is boat traffic, which not only increases pollution but also causes direct physical damage to corals (Wongthon 2013) . The high amount of human activity both on land and at sea has led to an increase in coral disease rates, and as reef-based tourism continues to increase, coral disease is expected to become an increasingly important problem (Lamb et al. 2014). Finally, recreational activities, such as snorkeling and diving, contribute to the degradation of reefs (Scott et al. 2017a). Snorkeling, in particular, is often more destructive than diving, as it is practiced mainly on shore and therefore responsible for the breaking and scarring of corals, leading to mortality in 2-20% of cases (Cumming 2002).

1.4.4 Drupella outbreaks in Koh Tao

Drupella outbreaks, now known for their devastating impact on coral reefs, have occurred worldwide, with documented episodes in the Pacific and Indo-Pacific Oceans. In these areas, *Drupella* populations have reached densities in the millions (Zhang et al. 2024). Since the 1990s (Hoeksema et al. 2013; Scott et al. 2017b), Koh Tao Island has also experienced several outbreaks of *Drupella*, with effects comparable to those of the crown-of-thorns star *Acanthaster planci* (Moerland et al. 2016). These episodes, combined with other stressors, have accelerated coral degradation, recognizing coral predation as a threat to coral reefs and dive tourism (Scott et al. 2017b). According to a study by Scott et al. 2017b, the *Drupella* population and its fluctuations were found to be homogeneous throughout Koh Tao Island, with the largest outbreak recorded in 2010 and between 2013 and 2014, following large bleaching events (Hoeksema et al. 2013; Moerland et al. 2016; Scott et al. 2017b). An outbreak is defined as such when more than 1.4-2 individuals/m² are observed (Cumming 2009; Zhang et al., 2024), related to feeding rate and coral growth (Zhang et al. 2024). At Koh Tao, the density of *Drupella* reached 7.9 individuals per m² in 2010, decreasing to 5.6 individuals/m²

in 2011 due to removal efforts by volunteer divers (Scott et al. 2017b). Branching *Acropora suffered* 60-75% reduction (Cumming 2009; Scott et al. 2017b) at depths of 3-6 meters, due to predation and severe bleaching events. The direct effect of this lost is a modification of target prey of *Drupella*, in fact *Drupella*'s high dietary plasticity allowed it to adapt, leading it to colonize free-living mushroom corals (fig.x) at greater depths (5-9 meters) (Hoeksema et al. 2013). The most affected species were *Fungia fungites*, followed by Lithophyllon *repanda*, *Ctenactis echinata*, and *Pleuractis granulosa* (Hoeksema et al. 2013; Scott et al. 2017c). Despite manual removal efforts by volunteers, which resulted in the collection of approximately 26,000 *Drupella* specimens between 2010 and 2014 (Canteri 2024), a doubling of their population was observed in all areas analyzed (Scott et al. 2017a). This increase was particularly evident in Chalok Bay, Koh Tao dominated by *Acropora* corals and free-living mushroom corals (Scott et al. 2017a). As highlighted in the figure from Hoeksema et al. 2013's study, most *Drupella* snails were observed hiding under free-living mushroom corals. This appears to offer protection from predators and suggests an attraction for feeding during the night hours.

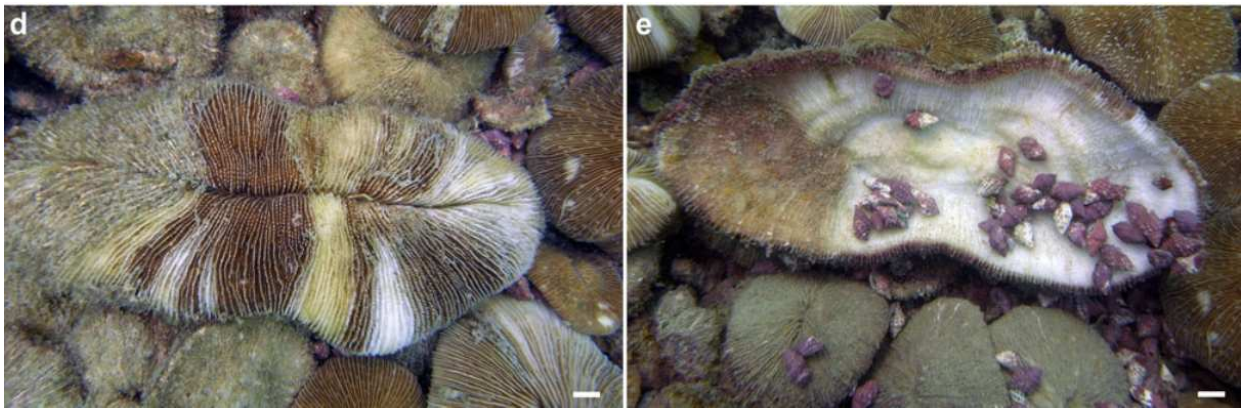


Figure 10: Specimen of Fungia fungites in daylight with one snail and tissue loss. D: Ctenactis echinata coral showing tissue loss in typical radial pattern. E: Same specimen turned over to show *Drupella* infestation (90 individuals). Scale bars: 2 cm, from: Scott et al. 2017c.

1.5. The species interacting with *Drupella* spp.

1.5.1. *Acropora spp*.

The order Scleractinia *(Cnidaria, Anthozoa*) , consists of hard-bodied corals, which are essential for the formation and maintenance of coral reefs. The family *Acroporidae* includes *Acropora*, a genus with more than 400 nominal species (Renema et al. 2016; Ball et al. 2021). These species are distributed in shallow, well-lit, high-energy waters (Bonin 2012), typical of tropical and subtropical regions (between 30°N and 30°S), with a concentration in the central Indo-Pacific

(Wallace & Rosen 2006). Represented by corals known as staghorn or elkhorn corals (Ball et al., 2021), adult colonies of *Acropora* are characterised by numerous branch bifurcations (Fig.11a). The branching morphology of *Acropora* plays a crucial role in the ecology of coral reefs as it not only forms their three-dimensional structure (Bonin 2012), but also contributes to providing food (in the form of coral tissue, mucus and associated detritus) (Gibson et al. 2011) and shelter for numerous fish and invertebrates (Patton 1994; Bruckner 2003; Ball et al. 2021). Each branch is equipped with a terminal axial polyp, lacking zooxanthellae, which contributes to the construction of a solid structure subsequently calcified by the radial polyps below (Fig. 11b) (Ball et al. 2021). Colony growth occurs through the formation of new branches and axial polyps branching off from pre-existing ones, or through the conversion of radial polyps into axial polyps (Wallace 1999).

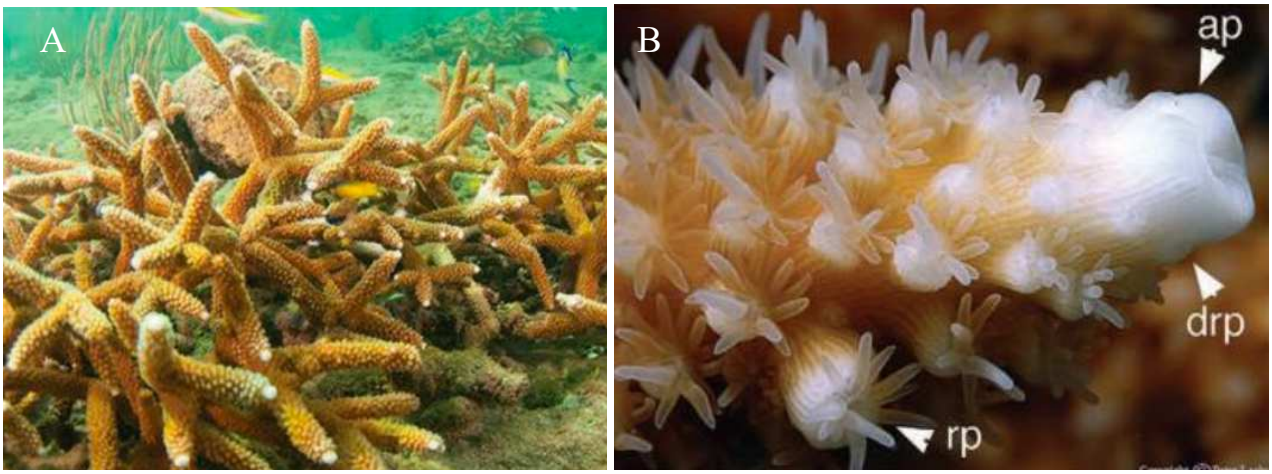


Figure 11: A: *A. cervicornis* (Florida); B: Tip of the branch of A. cervicornis, showing the arrangement of the two types of polyps. At the tip of the branch is the large axial polyp (ap) which has no zooxanthellae; behind it are small developing radial polyps (drp) and more proximally are normal-sized radial polyps(rp). Image from Ball E. et al. 2021

Acropora species are characterised by a high growth rate (Hobbs & Frisch 2010) and a high nutritional content within the skeleton that includes proteins, polysaccharides and lipids. (Ball et al. 2021). According to Willis et al. (2004), fast-growing corals tend to show reduced resistance to disease, a phenomenon due to the fact that growth requires a considerable energy investment, which is mainly achieved through mutualistic symbiosis with endosymbionts of the family *Symbiodiniaceae* (Ball et al. 2021). Excessive use of resources towards growth, however, can limit those available for immune defence, making corals more vulnerable to attack by pathogens and diseases (Jackson 1979). Although *Acropora* have a high growth rate that allows them to recover within 5-10 years of disturbance (Baker et al. 2008; Bonin 2012), chronic stresses can hinder the recovery of *Acropora* communities. These can include: bleaching events induced by rising temperatures (Bonin 2012), ocean acidification, water quality deterioration, outbreaks of corallivorous predators (such as *Acanthaster planci,*

and/or *Drupella*)((Bonin 2012), sedimentation (Wolanski et al. 2004; Fabricius et al. 2005; Wooldridge 2009), destructive fishing (Caras & Pasternak 2009) and recreational activities. These phenomena can lead to a decline in associated biodiversity and significant changes in the composition of marine habitats (Ball et al. 2021), causing a dominance of massive, encrusted corals over branching corals (Loya et al. 2001; Gibson et al. 2011; Bonin 2012). To date, 50% of *Acropora* species are classified as high risk of extinction according to IUCN Red List criteria (Bonin 2012).

1.5.2. Damselfish*, Pomacentridae*

Damselfishes (family *Pomacentridae*) are a diverse and widespread group of fish inhabiting coral reefs across tropical and temperate seas (50° N and S) (McCord et al. 2021). Their greatest diversity is found in the central Indo-Pacific, followed by the eastern Pacific, Atlantic, and Mediterranean regions (Frédéric & Parmentier 2016). These fishes typically live close to coral reefs, with their distribution influenced by factors such as depth, the presence or absence of conspecifics, predators, and substrate type (Frédéric & Parmentier 2016). With over 300

species, *Pomacentridae* display remarkable diversity in morphology and behavior (Fishelson 1998; McCord et al. 2021). They range from small, 4.5 cm fish in shallow coastal waters to larger species up to 45 cm, found at depths of 200 meters (McCord et al. 2021). Damselfishes can be broadly classified as solitary or gregarious. Gregarious species, which form groups of 10–50 individuals, exhibit diverse social structures, including monogamous and polygamous behaviors (Fishelson 1998; Frédéric & Parmentier 2016). In contrast, solitary species are highly territorial, defending small, well-defined areas (Frédéric & Parmentier 2016). Small damselfishes in shallow benthic habitats exhibit "farmer" behavior (Fig.12), actively cultivating and promoting the growth of algal patches (Gibson et al. 2001). This behavior plays a key role in shaping benthic community structures on coral reefs (Tebbett et al. 2020; McCord et al. 2021). These damselfishes scrape away living coral tissue to establish algal growth on coral skeletons, often cultivating algae distinct from those found on surrounding substrates (Randazzo et al. 2019). Their aggressive territoriality deters conspecifics, rivals, and potential egg predators, influencing the distribution of grazing fish and invertebrates (Gibson et al. 2001). Gibson et al. (2001) describe four key strategies damselfishes use to maintain their "gardens":

1. **Selective weeding**: Removing less-preferred algae to promote the growth of favored species.
2. **Substrate preparation**: Scraping away coral tissue to create surfaces suitable for algal colonization (Hata et al. 2020).
3. **Fertilization**: Enriching nutrients for algal growth through defecation.
4. **Herbivory reduction**: Defending territories to discourage grazing by other organisms (Vermeij et al. 2015).

This farming behavior highlights the significant ecological role of damselfishes in coral reef ecosystems.

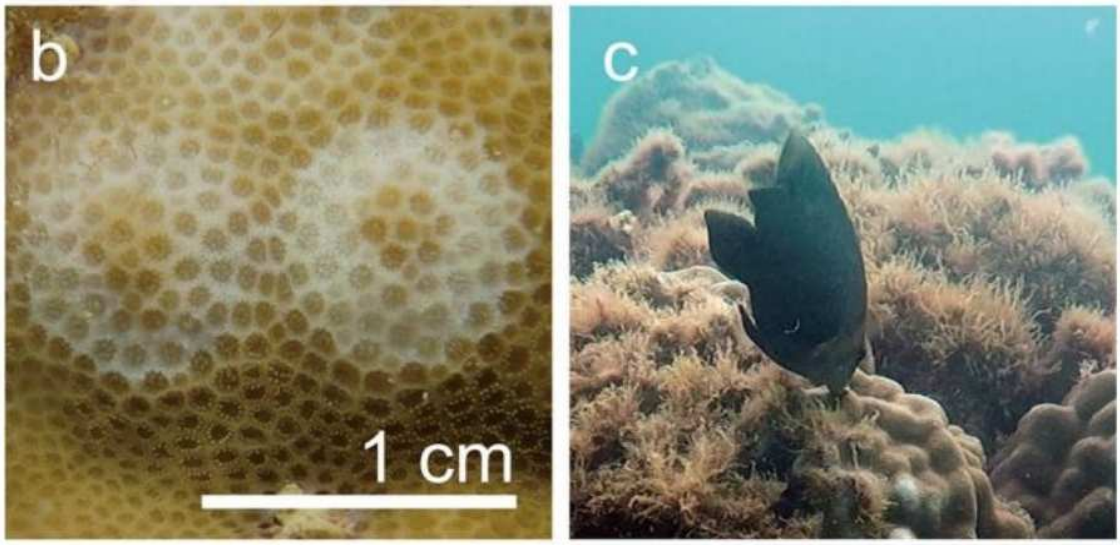


Figure 12: (b,c) Close-ups of white scars: bite lesions of *S. nigricans* on the coral Porites (c) S. nigricans biting live Porites adjacent to its territory, from Hata H. 2020

This behavior significantly influences benthic algal assemblages, system productivity, nitrogen fixation, and species composition. It promotes the dominance of filamentous rhodophytes and cyanophytes over branching and encrusting calcified corals (Gibson et al. 2001). The accumulation of sediment trapped in algal mats damages the basal tissues of corals, while bacteria hosted within the turf can lead to disease outbreaks, further deteriorating coral health (Vermeij et al. 2015). Territorial damselfishes primarily rely on *Acropora* coral colonies, which provide protection from predators and ideal microhabitats for growth and reproduction (Bonin 2012). However, *Acropora* is highly vulnerable to disturbances, including predation by corallivores (e.g., *Acanthaster planci* and *Drupella* spp.), tropical cyclones, and mass bleaching events (Hata et al. 2020). In such cases, damselfish may move to less favorable substrates, such as massive corals or structures of dead and/or damaged coral from other corallivorous organisms, which, although they cannot guarantee the same level of protection (Bonin 2012), can be used as a substrate for algal meadows (Gibson et al. 2001). The activity of damselfishes often prevents coral recovery within their territories, as their algal farming inhibits tissue regrowth and the reestablishment of coral cover. Coral recovery typically occurs only after damselfishes abandon their territories due to intraspecific competition or seasonal changes (Letourneur 2000;

Hata et al. 2020). Bleaching events, often triggered by thermal stress or environmental changes, further exacerbate these dynamics by drastically reducing the availability of *Acropora* colonies, intensifying competition among damselfishes for the few remaining suitable habitats (Bonin 2012).

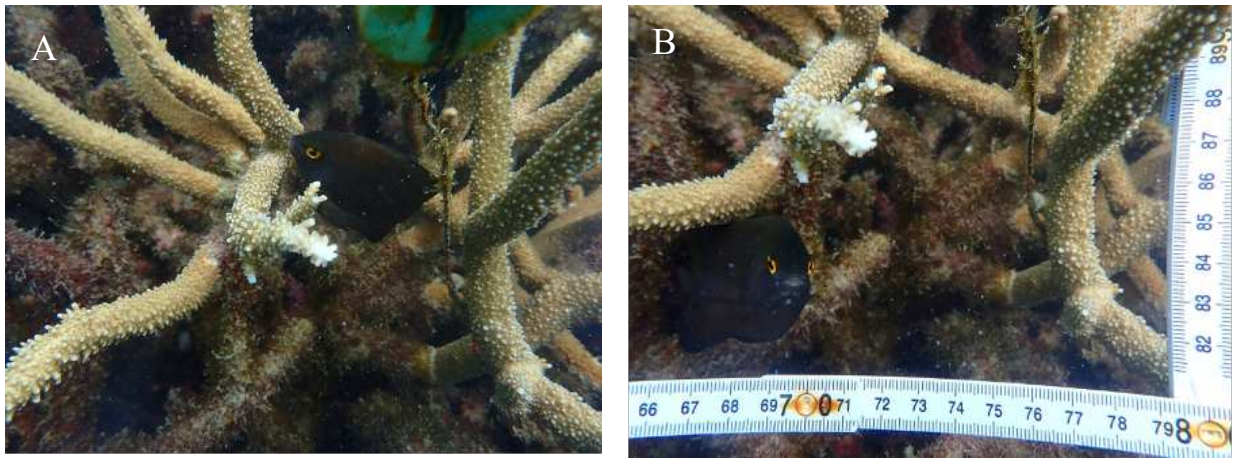


Figure 13: A,B: *Plectroglyphidodon lacrymatus* protecting territory on a colony of *Acropora cervicornis* previously preyed upon by *Drupella* spp. Photo taken 8/07 at Taa Cha

OBJECTIVES

Over the last century, coral reefs have undergone significant deterioration due to climate change and numerous anthropogenic factors, including unregulated diving tourism, destructive fishing, increased marine nutrients and resulting eutrophication, uncontrolled construction of infrastructure, and excess sedimentation (Scott et al. 2017b). These factors have caused an imbalance in food webs in the reef habitat and the excessive proliferation of some corallivorous species. Corallivory refers to predation by fish and invertebrates on coral mucus, tissue, and skeletons, causing chronic stress for many coral species. Such predation tends to be persistent over time, generating significant wounds (Renzi et al. 2022). Gastropod molluscs belonging to the genus *Drupella*, although they constitute only a small fraction of all corallivorous species, are often associated with overgrazing phenomena due to their ability to rapidly and large-scale degrade coral reefs (Scott et al. 2017b; Moerland, et al. 2016; The coral reef of Koh Tao, Thailand, is particularly affected by excessive grazing by *Drupella spp.* The coastal environment and the reef of Koh Tao have undergone profound alteration in recent years to increase the tourist offer, with drastic consequences on the integrity and health of the reef (Scott et al. 2017a) that could have contributed to

the hyper-proliferation of *Drupella spp.* Although some reports have been made on the gastropod observed in Koh Tao, most of these studies focuses on the manual removal of the gastropod from the host coral; there is still a lack of in-depth studies on the trophic strategy of *Drupella spp.* and the response to overgrazing of organisms in the Thai reef. The goal of this research is to contribute to understanding the long-term effects of snail culling on the tropical reefs and to supply useful information for the management of the gastropod. Specific objectives are 1. to study the behavior of *Drupella* during outbreaks; 2. to monitor the grazed corals, 3. to compare short- and long-term effects of culling by analyzing data from previous removal campaigns.

The present study firstly examines several aspects related to *Drupella* such as behavior, ability to move from one coral colony to another, trophic strategy, zonation and density of *Drupella* per coral colony. Another aspect considered is whether and how the predatory activity of *Drupella* influences the behavior of another reef-associated organism: the damselfish *Plectroglyphidodon lacrymatus.* Finally, we tried to understand the factors triggering the outbreaks of the gastropod. Observations of preyed corals showed that *Acropora cervicornis* is the coral species preferred by *Drupella* from Koh Tao, and only colonies that had areas devoid of living tissue (wounds) were attacked by gastropods. It was therefore

hypothesized that mechanical impact from recreational divers and excessive sedimentation at the survey sites could increase the damaged areas of the coral and therefore favor attack by *Drupella*. Phenomena such as bleaching and disease could contribute to the decline of the coral reef of Koh Tao, in terms of size and live coral cover.

MATERIALS AND METHODS

Fieldwork was conducted from April to September 2024 at three sites distributed in the eastern and southern parts of Koh Tao Island. These included respectively (1) Taa Cha (10°03'59 “N, 99°50'00 ‘E) and (2) Ao Laem Thian (10°05'20.0 ’N, 99°51'20.7 ‘E) bays in the east (3) and Chalok Bay (10°04'04 ’N 99°49'29 ”E) in the south. Chalok Bay is a beach more than 400 meters long, generally protected from stronger winds that often hit the east and north coasts of the island. During the dry season (February to September), temperatures range from 28° to 34° and winds coming from the northeast are generally weak/moderate. However, the bay is subject to a high tidal range where, from June, the sea recedes more than 10 meters. Although the physical conditions make Chalok Bay quiet, the waters are shallow, warm (29°-31°) and suitable for snorkeling activities thus attracting many tourists, despite the fact that it is not the most attractive dive sites in Koh Tao Island. Laem Thian, located on the east coast of Koh Tao, is a small beach and accessible by sea. Depths range from 5 to 35 meters, with a water temperature of 28°C to 30°C, offering ideal conditions for year-round diving. Currents in the Laem Thian area are generally weak but can intensify under certain weather conditions, that can occur when winds come from the southwest. Taa Cha is a

small beach of about 300 meters, renowned as a foraging area for sea turtles and blacktip reef sharks. Located in the southeastern part of the island, it enjoys natural protection from winds from the northeast, making it less exposed to weather disturbances. However, the area has been severely affected by coral bleaching events, caused in part by rising sea temperatures, which have significantly compromised the biodiversity of its ecosystem

2.1.1 Determination of Acropora and rubbles' densities and substrate characterization

Photographs were taken using 1 m x 1 m plastic squares, randomly positioned along 10 m x 3 m transects. Six transects were positioned at each site: three in areas characterized mainly by the presence of *Acropora spp*. (dense *Acropora* area) and three in patchy *Acropora* area dominated mainly by rubble. These areas were analyzed separately, both for differences in *Acropora spp*. density and to determine which area was best for conducting the *Drupella* study. Photos of the squares were taken from above and subsequently analyzed using ImageJ software. This tool allow to calculate the density of *Acropora spp*. or rubbles, dividing the area occupied by *Acropora* or rubble by the total area of the quadrants (1 m^2). In

addition, the same software was used to characterize the substrate of each site. The substrate characterization allowed us to distinguish different categories of coral, assigned based on the predominant condition: healthy (H) when they had healthy coral tissue, predated on *Drupella rugosa* (DRUP) when scars were visible, covered by damselfish farmedalgae (MA), bleached (B) when polyps were present but lacking zooxanthellae and therefore with a faded and dead appearance (DC) when they were dead and covered by peat algae associated with necrotic tissue). These algae were distinct from those laid by the damsel *Plectroglyphidodon lacrymatus* (Quoy & Gaimard, 1825), particularly widespread in *Acropora cervicornis* (Lamarck, 1816) beds where the colony was mainly covered by *Polysiphonia* sp. recognizable by its tufted arrangement (Hata & Kato, 2006) and other unidentified macroalgae. Following this process, underwater surveys for fish and invertebrates were conducted along the same transect line (10 m x 3 m) for each bay.

2.1.2 Behaviour of Drupella spp. and effects on the predated corals

Field research was conducted from April to September 2024, with support and equipment provided by the New Heaven Dive School center. To monitor the

behavior of *Drupella rugosa* (Born, 1778) feeding on branching *Acropora* corals, twelve randomly selected *Acropora* colonies were examined and tagged at each selected site. These colonies were located at depths of 3 to 5 meters in areas with similar environmental conditions, such as slope and sedimentation. A small red buoy was attached to a dead section of the coral colony using a metal wire, ensuring no contact with healthy areas of the scleractinian. Each colony was then documented through photographs taken with a GoPro Hero9 and an Olympus TG6 digital camera, with a meter included for scale. Colonies were identified using a combination of numbers (1, 2, 3) and letters (A, B, C). Data were collected once or twice a month. Collection sessions were scheduled based on weather conditions, equipment availability from the New Heaven center, and the center's planned activities. In Taa Cha Bay, data were collected on 6/05, 14/05, 3/06, 11/07, 8/07, and 1/08; in Laem Thian Bay on 23/04, 15/05, 31/05, 16/07, and 7/08. In Chalok Bay, however, sampling was conducted only three times (21/05, 7/06, and 28/06) due to significant tidal fluctuations recorded during the study period, which had less impact on the other two sites. To assess the effect of *Drupella* removal on *Acropora* recovery, the gastropods were manually removed from three coral colonies, identified as 1A, 2A, and 3A.

Removal was conducted using 30-cm steel tongs, with collected snails stored in a zippered plastic bag. Some *Drupella* were transferred to a 30x30 cm aquarium with an oxygenation system to study their feeding and social behavior, with water manually replaced weekly. Others, captured from colonies 1B, 2B, and 3B, were marked and released. A total of 48 snails were collected and marked using green plastic cable ties (3x100 mm) attached to the widest, central part of the shell. The excess tie was trimmed to avoid interference with movement before the snails were returned to their original locations. This marking method was first tested in the aquarium, where *Drupella* showed no adverse effects and continued moving normally. Observations revealed that when placed on healthy coral branches, the snails were stung by the coral's nematocysts, causing them to retreat into their shells and fall, making recovery difficult.

To observe the healing process of scars left by *Drupella* on *Acropora* branches, a predator-exclusion experiment was conducted using three hexagonal plastic cages (0.5m high × 5m long) with a 19mm mesh. Due to challenges in securing the cages over the *Acropora* garden, only two cage types were used: one fully enclosed cylindrical cage with closed bases to prevent entry of both *Drupella* and damselfish, and another with open bases, allowing damselfish access. The experimental setup (Fig.14) aimed to assess coral recovery in the absence of algal-

gardening fish. Both cage types were installed on the same colonies (1C, 2C, and 3C) but on different branches, following the removal of any *Drupella* shells.

Next, photographs were taken for each colony, taken on different dates and with uniform framing to ensure maximum comparability. For each photograph, the condition of the colony (hard coral, bleached, dead, and/or algae-covered by damselfishes) and the length and the status of the scars left by *Drupella* were recorded and classified according to the following parameters: damaged (scars), dead area, and algae-covered area scar. A “scar” is an area of bare white skeleton, devoid of pigmentation and not yet colonized by the meadow algae that usually cover the exposed parts of the skeleton (Cumming 2009). Each of these was measured in cm and cm2 by analyzing the photos taken and using the ImageJ software.

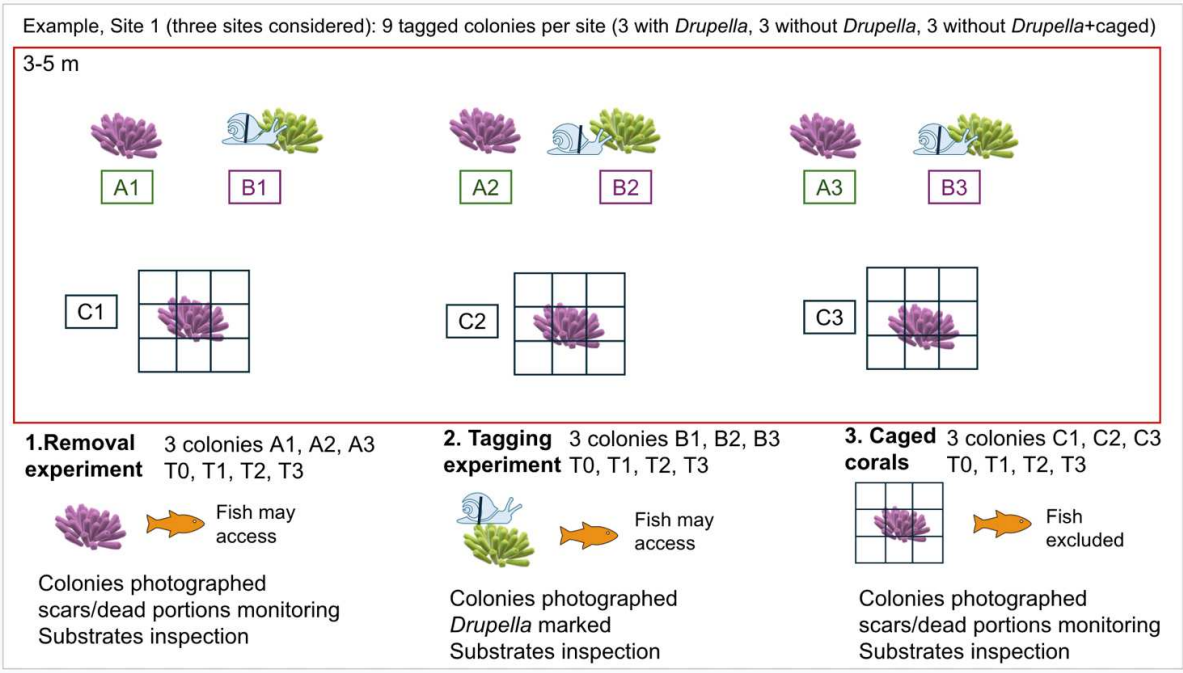


Figure 14: The sampling design is visually represented, with colonies categorized as follows: *A* indicates those where *Drupella* were removed, *B* represents colonies where the snails were marked, and *C* denotes colonies where *Drupella* were removed, followed by cage installation to exclude damselfish. Each category was replicated three times per site at depths of 3–5 m. While colonies were interspersed in the field, the diagram is simplified for clarity.

In order to understand the reproductive dynamics leading to outbreaks of *Drupella spp*., during each dive, rubbles and free-living mushroom corals were carefully observed to detect eggs, laid on dead coral fragments (Scott et al. 2017c).

2.1.3 Feeding rate

At each site, nine additional colonies, randomly selected at depths of 3–5 meters, were analyzed to assess the feeding rate of *Drupella*. Each colony was marked with a small red buoy, secured with a metal wire to a dead section of the coral, and documented through multiple photographs taken with a GoPro Hero9 and an Olympus TG6 digital camera, using a meter for scale. Colonies were identified using a combination of numbers (1, 2, 3) and letters (D, E, F).

The colonies were categorized into three groups to examine coral consumption rates (branches per day^{-1}) by damselfish and *Drupella*:

- Colonies D: represented colonies damaged by damselfish. A yellow cable tie (4x150 mm) was placed at the level of the coral branch scar caused by the fishes to indicate the margins.
- Colonies E: represented the colonies on which *Drupella* were not removed. Again, a cable tie was placed on the worn branch to mark the margins of the scar.
- Colonies F: represented colonies from which *Drupella* were removed. For these colonies, the consumed branches were tied with a yellow cable tie at the level of the scar to identify the margins.

This classification was used to understand the impact of damselfish and the difference between colonies in which *Drupella* were not removed versus those from which they were removed. Cable ties placed on the consumed branches were used as reference points during image analysis. Every time some photographs were taken to be analyzed. The photographs of the colonies were analyzed using ImageJ software, which allowed calculation of the length of the scars (measured from the outer side of the cable tie to the base of the damaged branch) and their area in cm^2.

2.1.4 Damselfish behaviur

Fifteen *Acropora* colonies were selected to observe damselfish (*Plectroglyphidodon lacrymatus)* behavior. The observations were conducted by volunteer scuba divers. Once a colony was chosen, the divers determined the size of its territory by using a tank banger around the *Acropora* colonies and observing the fish's chasing behavior. The boundary of the territory was identified when the damselfish stopped displaying aggressive behavior. After establishing the territory, the divers began a 15 minute observation period (Hata & Kato, 2006; Schopmeyer & Lirman 2015). During this time, they recorded the number of bites on farmed

algae, chasing behavior directed at other damselfish or other species (including fish and invertebrates), and rubbing behavior on the corals.

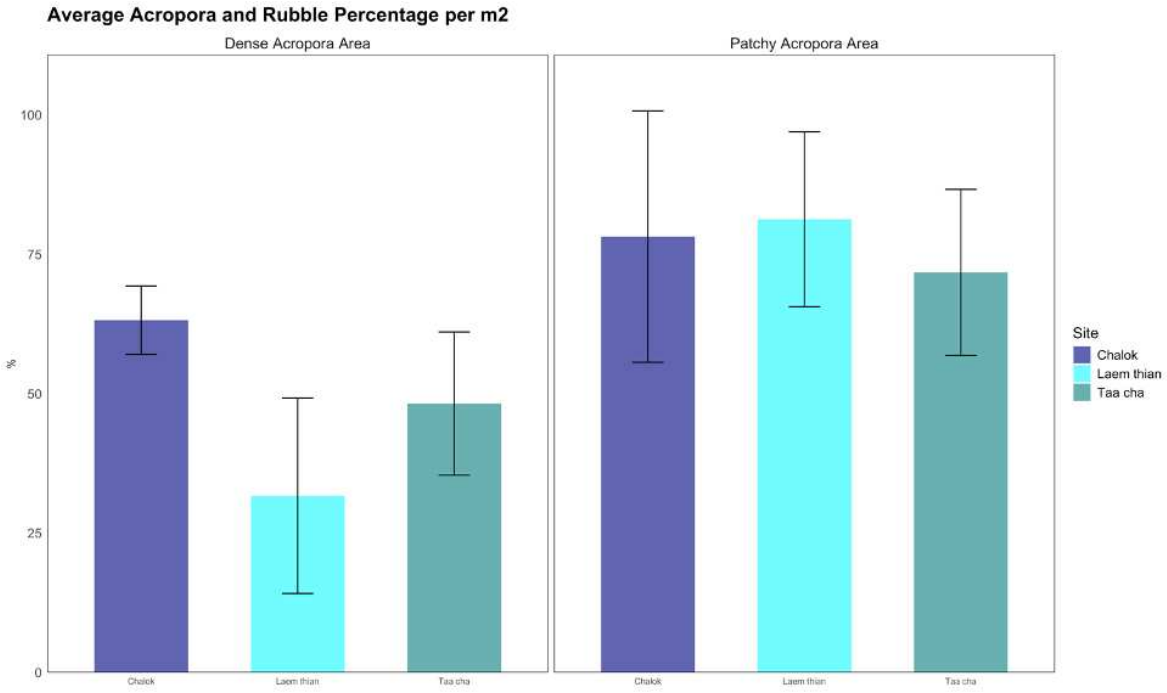
2.1.5 Determination of the density of Drupella spp. on branching corals spp. and the effect of Drupella removal

Drupella removal, while in the other two areas constant manual shell removal was performed. Data were collected from 2010 to 2024 and were kindly provided by the New Heaven center. Each volunteer was equipped with 30-cm-long steel tongs and a 3-liter plastic bottle with small holes on top to collect *Drupella*. Next, the collected specimens were counted, measured and classified into three size categories (≤1 cm, 1<x≤2 cm, >2 cm), as suggested by the literature (Saponari et al. 2021) and the density of each size class was expressed as n. of gastropod m-2. Data on the number of shells removed per action and per year and the number of collectors involved were processed and compared to estimate sampling effort and to verify the effectiveness of removal campaigns.

2.1.6 Determination of the density of Drupella spp. on branching corals and comparison of Acropora gardens with and without Drupella spp.

In Taa Cha and Chalok bays, three 5 m x 5 m areas were delimited using threads to assess the density of *Drupella spp*. feeding on *Acropora spp*. The areas, identified by the colors yellow, blue, and green, were located at a depth of 3-5 meters, with the green area serving as the control zone. One of these areas was used as a control, without performing *Drupella* removal, while in the other two areas constant manual shell removal was performed. This activity was carried out every two weeks for the months of March and April at the Chalok site and the months of August and September at Taa Cha by volunteers from the New Heaven Conservation Centre. Each volunteer was equipped with 30-cm-long steel tongs and a 3-liter plastic bottle with small holes on top to collect *Drupella*. Next, the collected specimens were counted, measured and classified into three size categories ($\leq$1 cm, 1<x$\leq$2 cm, >2 cm), as suggested by the literature (Saponari et al. 2021) and the density of each size class was expressed as n. of gastropod m^2.

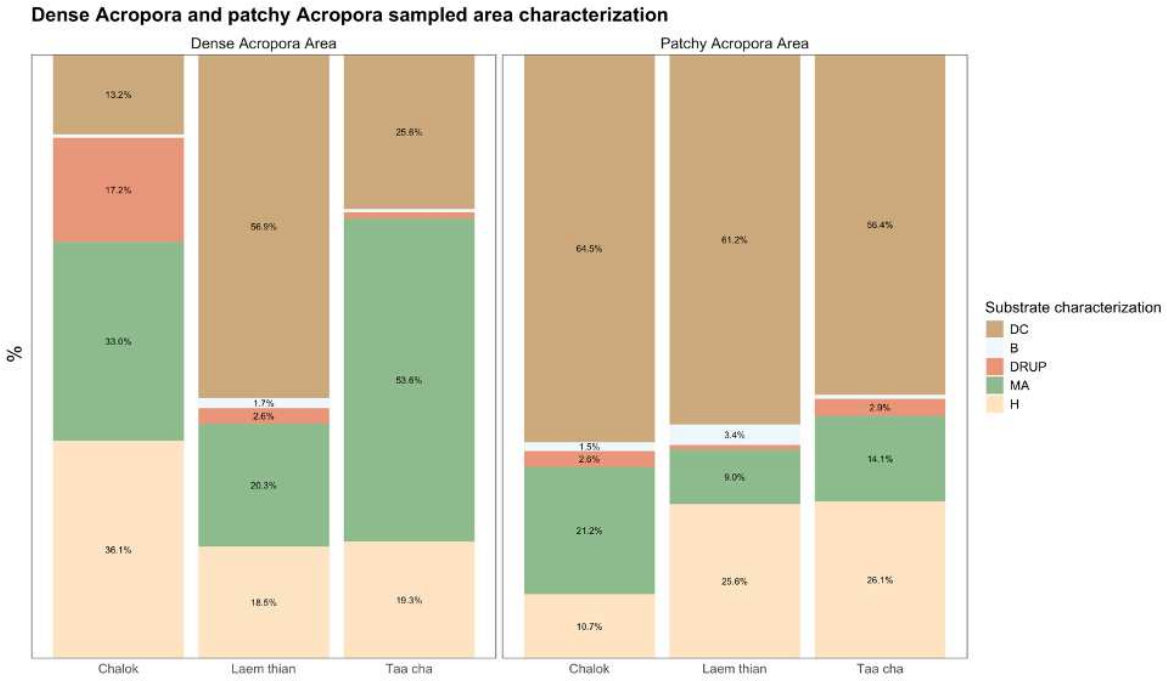
RESULTS



Graph 1: Average percentage of *Acropora spp*. Per m2 in region with high *Acropora* density and percentage of rubble per m2 in patchy *Acropora* areas

The survey conducted in Koh Tao shows the characterization of the study areas (Graph 1) across three bays: Chalok, Taa Cha, and Laem Thian. In all three locations, areas with high *Acropora* density are surrounded by regions where *Acropora* distribution is patchy and dominated by rubble. Chalok stands out with the highest *Acropora* coverage in the dense area (63.1 ± 6.1%), while the patchy area contains 78.1 ± 22.1% rubble. Conversely, Taa Cha exhibits the lowest

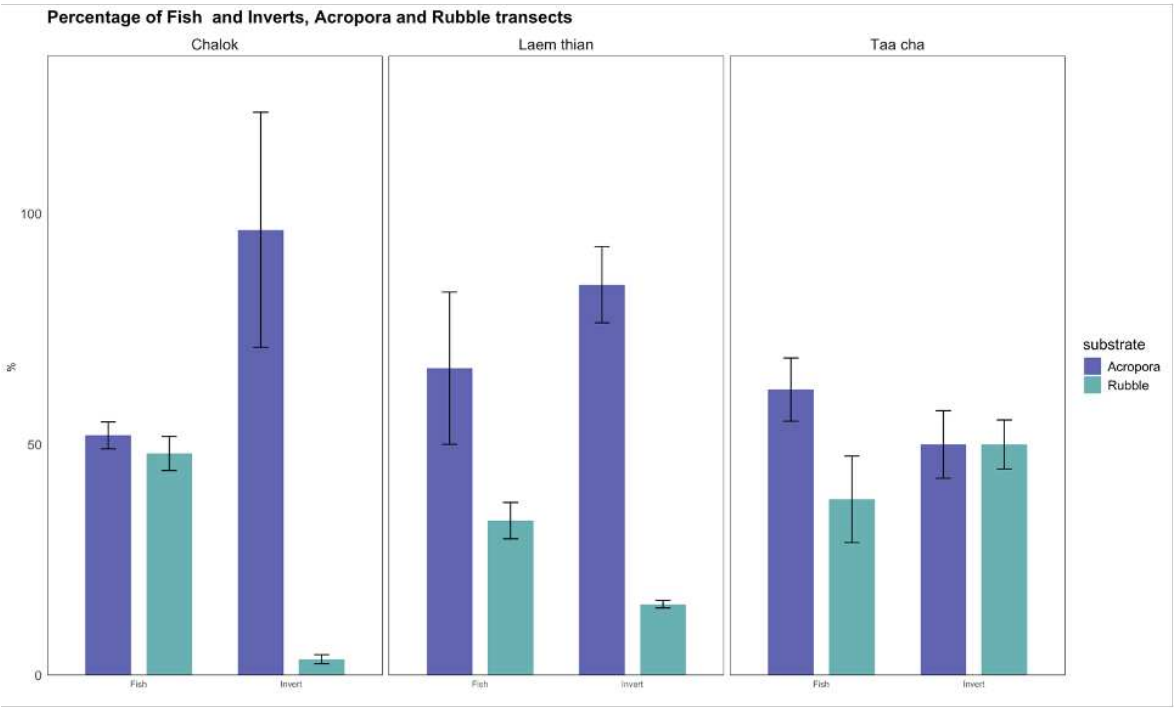
Acropora coverage in the dense area (48.2 ± 12.8%) and a high rubble density (71.7 ± 14.8%) in the patchy area. Finally, Laem Thian recorded the lowest *Acropora* coverage (31.6 ± 17.5%) and the highest rubble percentage in the patchy area (81.2 ± 15.6%).



Graph 2: Characterization of dense and patchy *Acropora spp*. Areas in three different bays (Chalok, Laem Thian and Taa Cha). The two areas classification includes: H=healthy, MA= algal coverage, especially farmed by damselfish, DRUP= preyed on by *Drupella* spp., B=bleached and DC =dead coral.

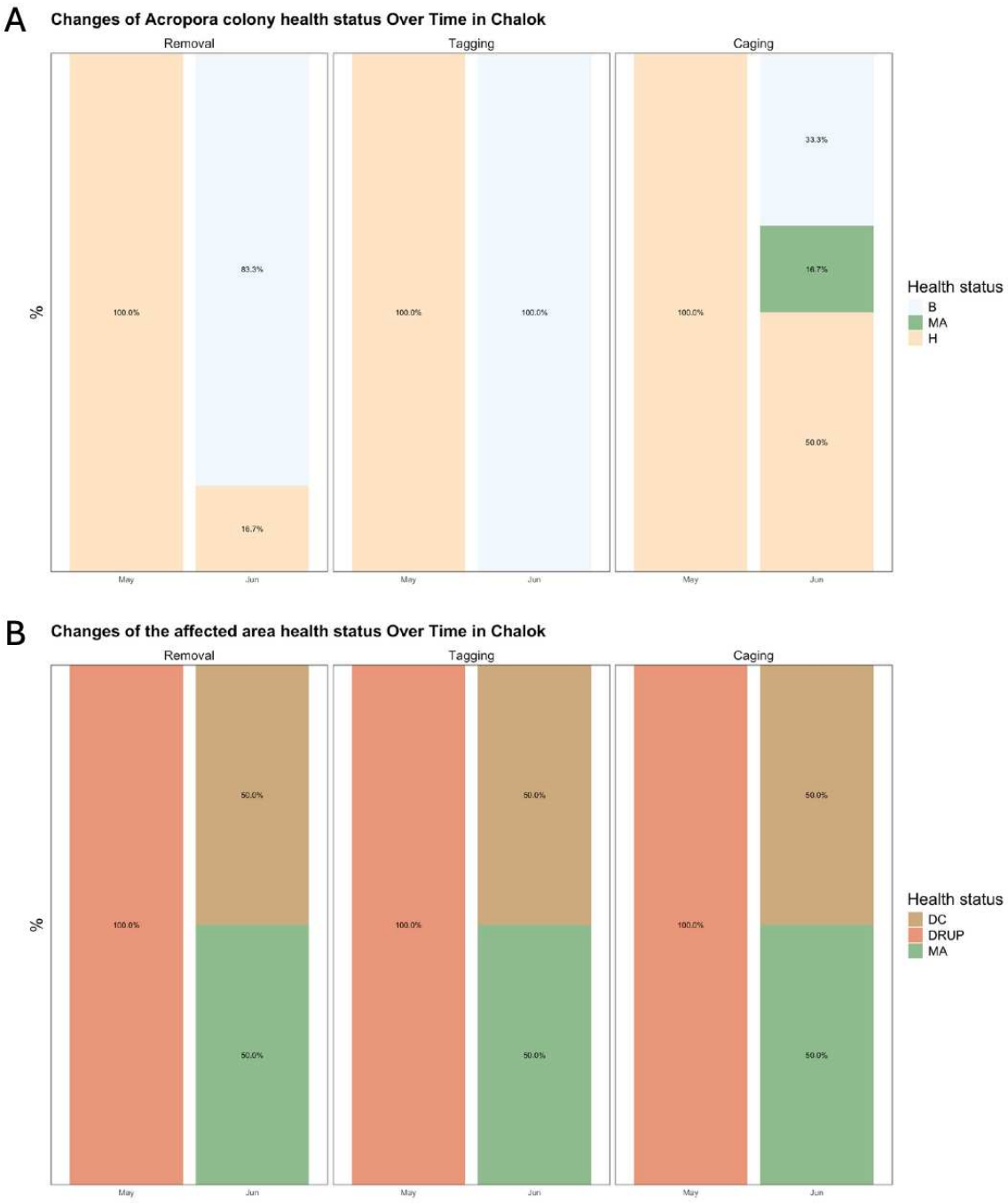
The substrate characterization conducted at the surveyed sites highlighted the conditions observed in areas with a high density of *Acropora sp*. As can be seen

in graph 2 The Chalok site, showed the highest percentage of healthy corals (36.1%), and a moderate presence of macroalgae-covered colonies (33%). Additionally, in Chalok the highest percentage of colonies predated by *Drupella* was recorded. In the patchy area of Chalok, the substrate was dominated by dead coral (64.5%) and macroalgae (21.2%); in contrast, Taa Cha was mainly dominated by macroalgae growing on top of the coral colonies (53.6%), with minimal evidence of bleached corals or *Drupella* predation. In the patchy area of Taa Cha, healthy coral colonies represent 26.1%, while the dead ones were 56.4%. Finally, Laem Thian showed a similar percentage of dead coral in both the *Acropora* dense area (56.9%) and the patchy area (61.2%). The percentage of colonies affected by macroalgae overgrowth was more than twice as high in the dense *Acropora* area (20.3%) compared to the patchy area. Colonies preyed upon by *Drupella* accounted for 2.6% of the total. Additionally, coral bleaching was more prevalent in the patchy area of Laem Thian, where 3.4% of colonies were bleached—double the percentage observed in the dense *Acropora* area (1.7%).



Graph 3: Average percentage of fish and invertebrates observed in three different bays (Chalok, Laem Thian and Taa Cha), comparing two substrate types: high-density *Acropora* and patchy *Acropor*a (rubble dominated).

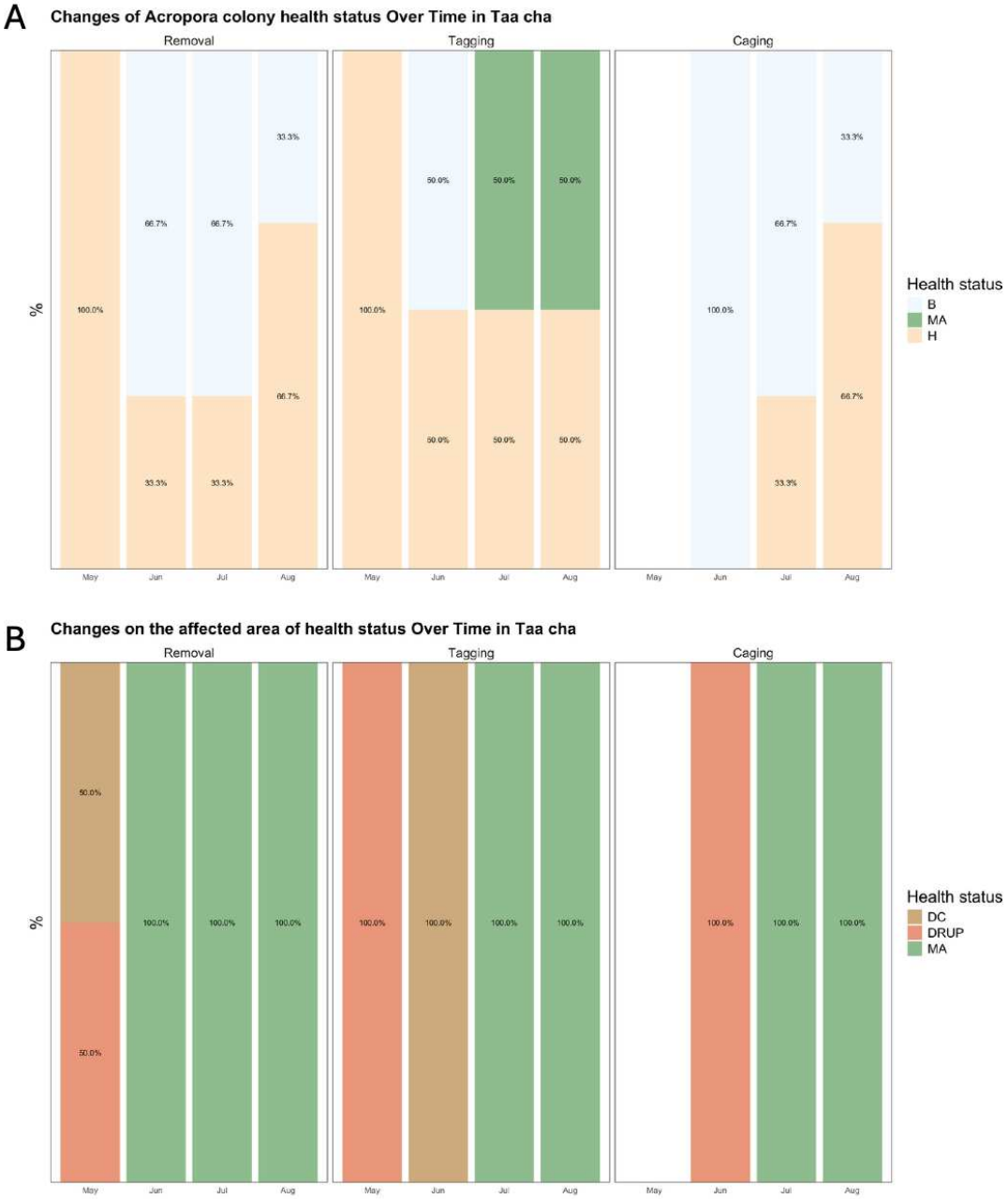
The percentage of fish and invertebrates in Chalok, Laem Thian and Taa Cha Bays (graph 3) are generally higher in areas with dense *Acropora* presence than in areas covered by rubbles, even if the differences are marked only in Laem Thian both for fish and invertebrates and in Chalok for invertebrates only.



Graph 4: Changes in the health status of *Acropora* colony (removal, tagging and caging) in Chalok bay between May and June. A: Assessment of *Acropora* spp colony health status. The

health condition of the colonies was classified into three categories; H=hard coral, MA=algae-covered by damselfish, B=bleached. B: Assessment of the affected area health status. The affected area status was classified into three categories: DRUP= *Drupella* scar, MA =overgrown with damselfish algae, DC=dead coral.

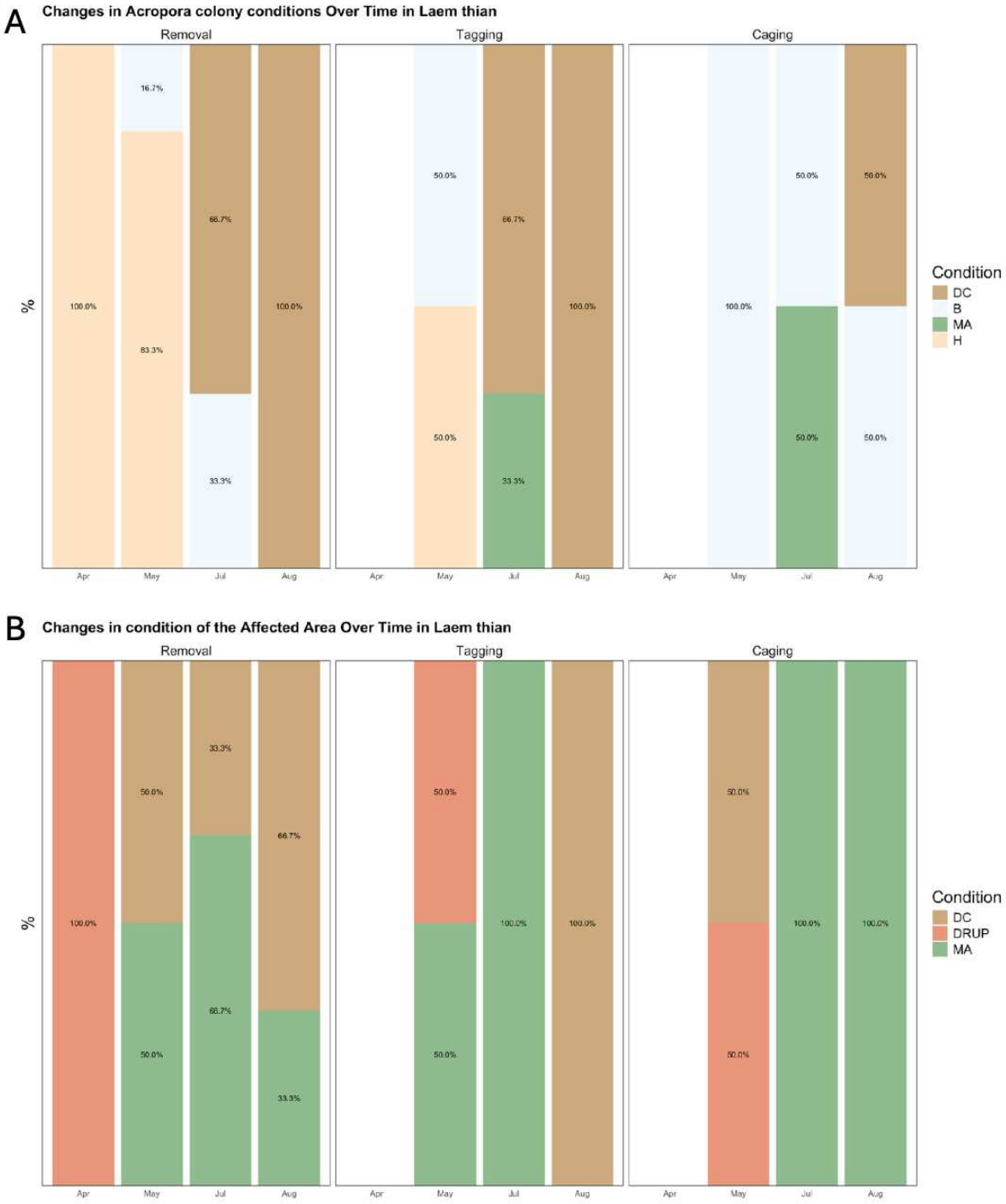
Measurements taken in the Chalok bay during the months of May and June 2024 (graph 4), illustrates the change in health status of *Acropora* colonies (A) and portions of these preyed on by *Drupella* (B) observed in the months of May and June. In May, all colonies were healthy and showed scars caused by *Drupella*. However, in June, colonies bleached and half of the scars were observed to be covered with macroalgae, due to the activity of damselfish, while the other half were dead. A different situation was observed in colonies where cages were placed, where 50% showed signs of recovery, 33.3% bleached and the remaining part was covered with macroalgae.



Graph 5: Changes in the health status of *Acropora* colony (removal, tagging and caging) in Taa Cha bay between may and august. A: Assessment of *Acropora spp* colony health status. The health condition of the colonies was classified into three categories; H=hard coral, MA=algae-covered by damselfish, B=bleached. B: Assessment of the affected area health status. The

affected area status was classified into three categories: DRUP= *Drupella* scar, MA =overgrown with damselfish algae, DC=dead coral

Measurements taken in the Taa cha bay during the months from April to August 2024 (graph 5), illustrates the changes in the health status of *Acropora* colonies (A) and areas damaged by *Drupella* predation (B) between May and August. In May, all colonies from which *Drupella* had been removed were healthy and showed scars. In the following months, colonies tended to bleach, but showed improvement in August, while the scars were progressively covered by macroalgae. In colonies where *Drupella* had not been removed (tagged), the situation was similar: healthy in May, half of the colonies experienced bleaching in the following months, followed by the growth of macroalgae. The scars on these colonies, however, showed necrotic tissue already in June and were covered by macroalgae in the following months. Finally, in colonies where cages were installed, evident bleaching accompanied by scars caused by *Drupella* was observed in June. In the following months, these colonies recovered from bleaching, while all scars were covered by macroalgae.

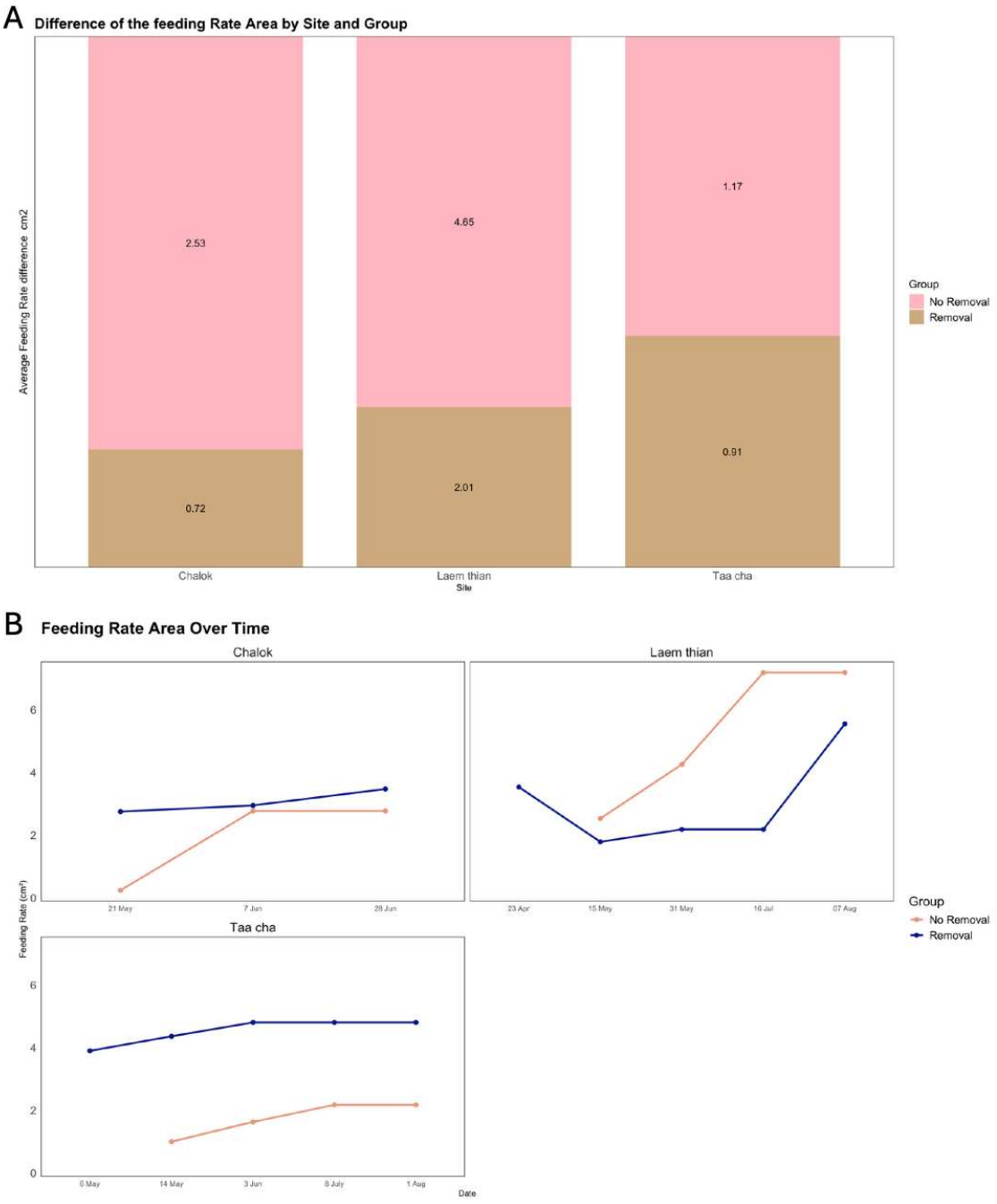


Graph 6: Changes in the health status of *Acropora* colony (removal, tagging and caging) in Laem Thian Bay of April, may, July and august. A: Assessment of *Acropora spp* colony health

status. The health condition of the colonies was classified into three categories: H=hard coral, MA=algae-covered by damselfish, B=bleached. B: Assessment of the affected area health status. The affected area status was classified into three categories: DRUP= *Drupella* scar, MA =overgrown with damselfish algae, DC=dead coral

Measurements taken in the Laem Thian Bay during the months from April to August 2024 (graph 6) show the changes in the health status of *Acropora* colonies (A) and areas damaged by *Drupella* predation (B) in April, May, July and August. As can be seen from graphs A and B, all colonies from which *Drupella* had been removed were healthy and showed scars. In May, half of the colonies were dead, while the other half was covered by macroalgae; the same situation was observed in the scars, where half showed necrotic tissues and half were covered by macroalgae. In July, most of the colonies were dead, the remaining part was bleached, with a parallel growth of macroalgae on the scars. In August, all colonies were dead, and most of the scars showed necrotic tissues. The tagged colonies, on the other hand, were half healthy and half bleached in April, with scars showing active signs of predation on one half, while the other half was already covered by macroalgae. By July, most of the colonies were dead, while the remaining ones were completely covered by macroalgae; at the same time, all scars were colonized by macroalgae. By August, both the colonies and the previously affected scars

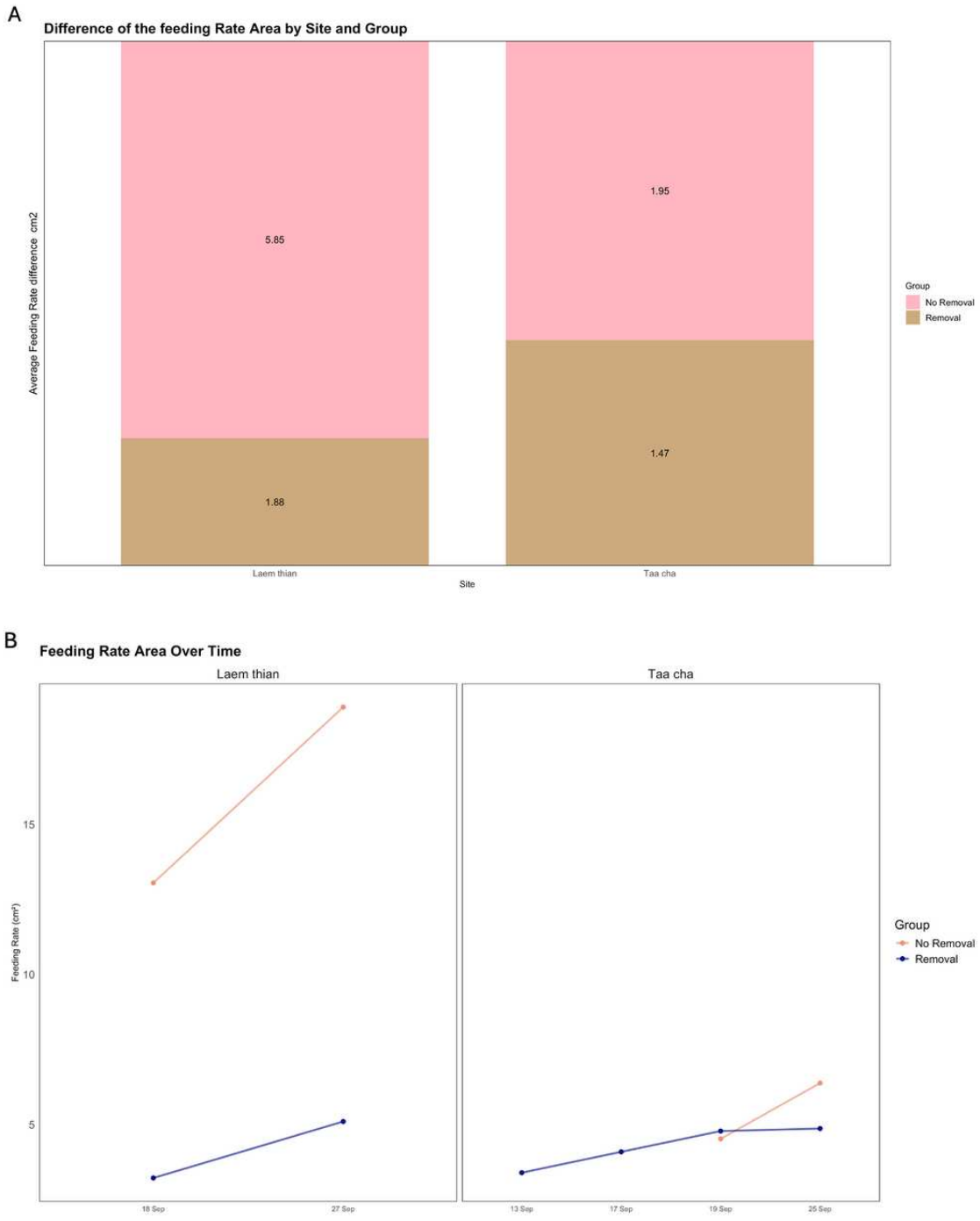
were dead. The caged colonies were completely bleached in May and had scars, half of which showed dead areas, which were completely covered by macroalgae in the following months. By July, half of the colonies became covered by macroalgae, while the other half remained bleached. By August, the half covered by macroalgae died, while the other half maintained its bleached state.



Graph 7: Consumption rates (cm²) of *Acropora spp*. by *Drupell*a. A) Mean difference in feeding rate between colonies with *Drupella* removal (removal) and colonies without removal (no removal) at Chalok, Laem Thian and Taa Cha sites. B) Time course of consumption rate for colonies with removal and without, in three different site Chalok, Laem thina Taa cha

The results obtained from the analysis of the photographs taken during the study shows how the rate of consumption of *Acropora spp*. by *Drupella* changes between the sites of Chalok, Laem Thian and Taa Cha, comparing the colonies from which *Drupella* was manually removed (removal) with those from which no removal was carried out (tagging) (grap 7). From graph a it is possible to observe that in all the locations considered the coral consumption is greater in the colonies without removal, in particular in Chalok Bay the average consumption is 2.53 cm^2 in the colonies without removal and 0.72 cm^2 in those with removal, with a rapid increase between May and June in the former. Laem Thian records the highest rates of feeding rate (4.65 cm^2 in the colonies from which the *Drupella* shells were not removed and 2.01 cm^2 in the colonies from which they were not removed), with a constant increase until July. Taa Cha shows the lowest rates (1.17 cm^2 and 0.91 cm^2) and a stable trend. In graph B it is possible to see consumption rates based on measurements taken on specific days. In Chalok, consumption rates were measured on May 21, June 7 and June 28. Colonies from which *Drupella* was removed had a higher consumption rate in May, but that of colonies without removal increased almost twofold by June 7 and continued to be stable until June 28, while that of colonies with removal remained unchanged for more than two

weeks, with a slight increase between June 7 and June 28. In Laem Thian, measurements were taken on April 23, May 15, May 31, July 16 and August 7. Colonies with removal showed a decrease in consumption rate between April and May, followed by a slight increase until the end of May, and then remained stable until July, with a significant increase only in August. Colonies without removal had a continuous increase in consumption rate until July, remaining stable until August. In Taa Cha, the consumption pattern was similar between colonies with and without removal. Colonies with removal suffered more damage in May, but the consumption rate remained constant until August, while in colonies without removal the rate increased slightly between May and July, then remained stable in August.

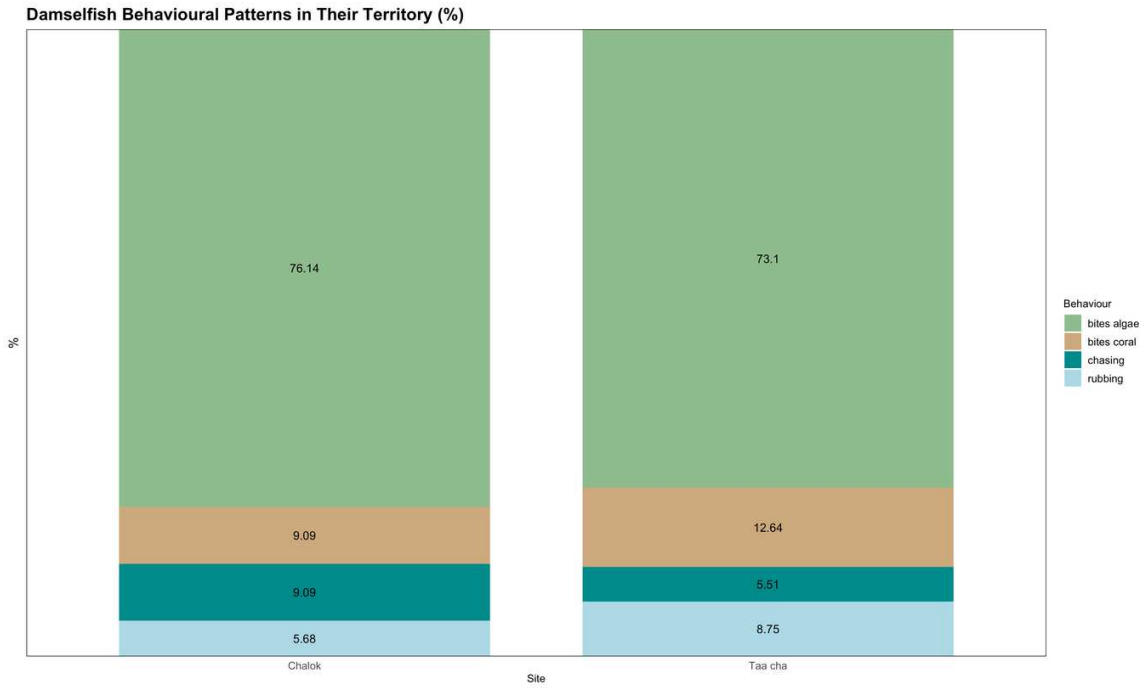


Graph 8: Feeding rates (cm²) of *Acropora spp*. by *Drupella* measured in September. a) Mean difference in feeding rate between colonies with *Drupella* 's removal (removal) and colonies without removal (no

removal) at the Laem Thian and Taa Cha sites. b) Time course of consumption rate for both groups: at Laem Thian on 18 and 27 September, while at Taa Cha, on 13, 17, 19 and 25 September.

The results obtained from the analysis of the photographs taken in September (graph 8) shows the feeding rate (in cm^2) of *Drupella* at the Laem Thian and Taa Cha sites, measured in September, comparing colonies from which *Drupella* was removed (removal)with those from which it was not removed (tagging). From the graph it can be observed that, at the Laem Thian site, colonies from which *Drupella* shells were removed have a significantly lower feeding rate (1.88 cm^2) than that of colonies from which *Drupella* was not removed (5.85 cm^2). At the Taa Cha site, however, the difference is less marked: the consumption rate in colonies from which *Drupella* was removed is equal to 1.47 cm^2, while in colonies from which it was not removed it is slightly higher, with a value of 1.95 cm^2. Graph 8 (b) shows the feeding rates measured on different days. At the Laem Thian site, as previously observed, the difference in the consumption rate of *Drupella* is very marked. In both cases (removal and tagging), the rate tends to increase from 18 to 27 September, but the increase is much more evident in the tagged colonies. At the Taa Cha site, however, measurements were taken on 13, 17, 19 and 25 September. Here it is observed that, although the data of the tagged colonies are only available for 19 and 25 September, their consumption rate increases more significantly than

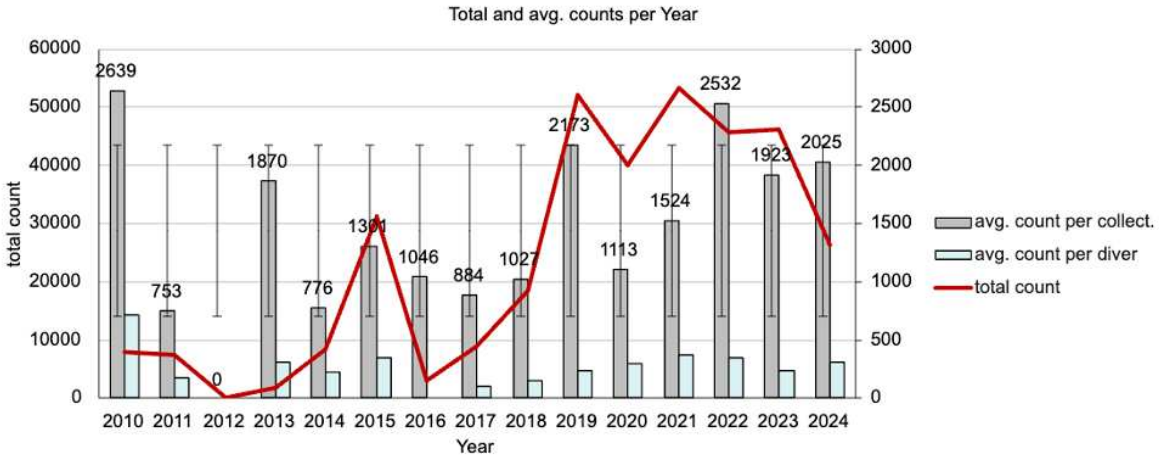
that of the removal colonies, which remains almost stable from 13 to 25 September, showing only a slight increase between 13 and 19 September.



Graph 8: Behaviors of damsel fish in their territory, recorded at the Chalok and Taa Cha sites. Observations were divided into four categories: algae biting, coral biting, chasing and rubbing

Thanks to the monitoring carried out during the month of September in the bays of Chalok and Taa Cha, it was possible to determine the behaviors of damsel fish in their territory (graph 8). As can be seen from the graph, the patterns observed at the two sites are similar: most damsel fish showed a predominant tendency to bite

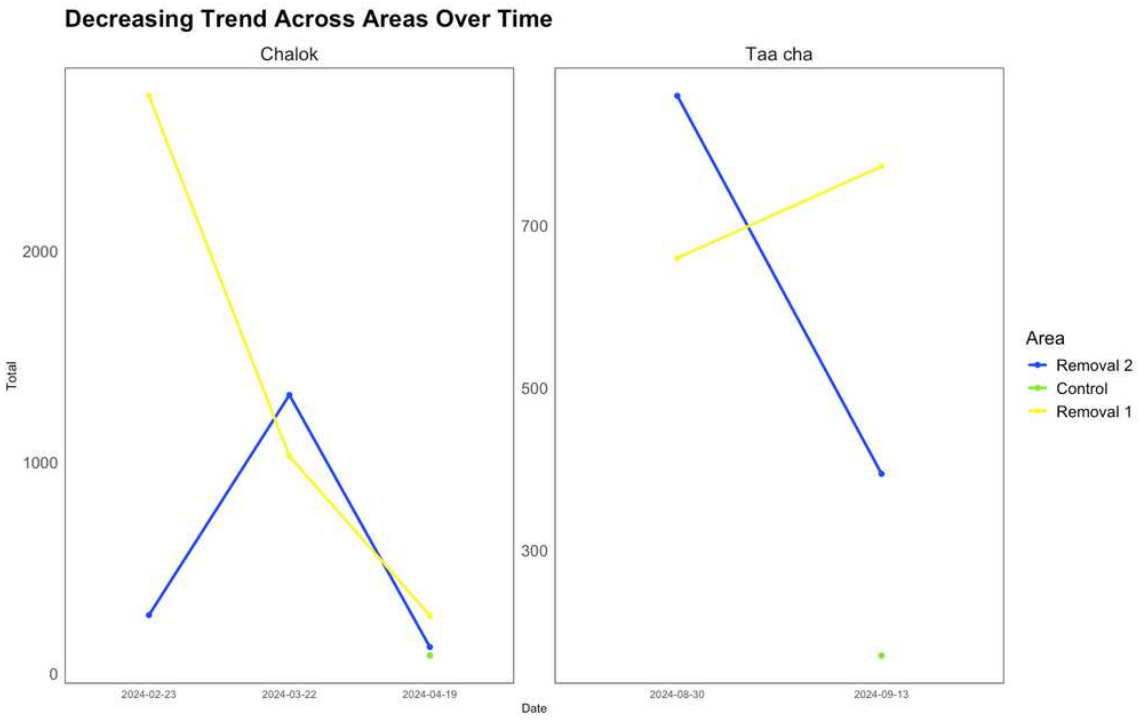
algae, followed by biting corals, chasing other fish, and rubbing against the branches of the colonies.



Graph 10: Total and average of *Drupella spp*. shells collected from 2012 to 2024. Average of shell removed per diver.

The *Drupella* removal activity carried out by the New Heaven center was not focused on a specific area but involved the elimination of all specimens found. Between 2010 and 2024, no clear temporal trend emerged. As shown in graph 10, significant peaks were observed in 2015 (about 30,000 specimens), 2019 (over 50,000) and 2022 (just over 45,000), with overall values that in some years

exceeded the threshold of 50,000. In 2012, since no removal activity was carried out, the count was zero.



Graph 11: Total number of *Drupella* removed over time from the yellow, blue and green areas at the Chalok and Taa Cha sites.

Thanks to the removal activities carried out in the specific areas of Chalok and Taa Cha, some significant differences can be observed (graph 11). At the Chalok site, 2733 *Drupella* were removed from the yellow area on 23/02 and 277 from the blue area. In the following month, removals from the yellow area decreased (1028

shells), while in the blue area they increased (1318 shells) compared to the previous month. On 19/04, a similar number of shells were removed from each site, including the control site (where no removal had ever been performed): 275 in the yellow area, 126 in the blue area and 86 in the control area. At the Taa Cha site, however, 660 shells were collected on an early date and 773 in the yellow area later. In the blue area, 860 *Drupella* were collected on 30/08, while at a later date the number decreased to 394. The only removal performed in the control area dates back to 13/09, with 170 *Drupella* collected.

DISCUSSION

This study highlighted the importance and ecological implications of the *Drupella* removal activity conducted by volunteers at the New Heaven center for over a decade (Canteri 2024). Although this mollusc has been present on Koh Tao since the 1990s (Hoeksema et al. 2013; Scott et al. 2017b), efforts to prevent its proliferation and promote its removal have been intensified in recent years. This activity has been carried out by the "New Heaven Reef Conservation Divers" program founded by Scott Chad in 2007. Between 2010 and 2023, a total of 309,197 *Drupella* specimens were removed (Canteri 2024). Although this is a

significant achievement, the study has provided insight into the impact and ecological consequences of this practice in both the short and long term. While in the short term the removal of *Drupella* may seem like an effective intervention, in the long term it has proven to be counterproductive, causing negative effects on the reef. In particular, it accelerates algal coverage and promotes the subsequent death of corals.

Determination of Acropora and rubbles' densities and substrate characterization

At each site, an analysis of the density of *Acropora* present was carried out, as it is considered the coral type favored by *Drupella* (Chad et al. 2017b). These data highlight the similar morphology of these bays that are dominated by *Acropora*, a species known for its fast growth and strong susceptibility to environmental stress, wave motion, diseases etc. During the year *Acropora* dies and breaks, cyclically transforming into rubble that stratify. This process creates a different environment on which the larval recruitment of other scleractine species is difficult (Fox et al. 2003). Therefore, the high percentage of rubble in the study area indicates a highly degraded habitat, probably subject to disturbances such as coral bleaching, sedimentation and phenomena so far documented only in Chalok Bay (Chad et al.

2017b). Furthermore, the Chalok site appears to be the one with the highest number of colonies preyed by *Drupella* (Scott et al. 2017a)(graph 2); this is probably because the Chalok site has a higher coverage of live *Acropora* (graph 1). The Laem Thian site, on the other hand, is the one with the lowest coverage of *Acropora* and the highest coverage of dead *Acropora*, characterized by turfing algae; this is probably due to the fact that being a shallow and therefore warmer bay, makes the corals more vulnerable and subject to bleaching. An interesting fact concerns the high presence of macroalgae on the colonies in all three sites but particularly evident in Taa Cha. As highlighted by Scott et al. (2017a), the increase in algal cover on corals seems strictly related to a higher nutrient load given by the expansion of urban development activities, deforestation in the reservoir area (Weterings, 2011) and the abundance of damsel fish. During the study, it emerged that Taa Cha is the bay most compromised by the presence of damsel fish, which show a marked preference for areas with a dense cover of *Acropora* (graph 2). These fish, known for their highly territorial behavior, choose these areas because they offer greater protection. However, this dynamic limits the grazing activity of other herbivores, favoring the proliferation of algae (Sheppard et al. 2024). On the contrary, in the transects characterized by isolated colonies of *Acropora* (patches), corals tend to be in better conditions, probably because they suffer less pressure

from both damsel fish and predation of *Drupella* or for the activity of sea turtles that feed on the algae that grow on rubble, Taa cha is recognized as a foraging area especially for green turtles. In addition, a further analysis was carried out that allowed us to examine the abundance of biodiversity in the different areas of each site. From graph 3 It is possible to observe that in the areas dense with *Acropora* corals, moreover, a greater biodiversity was observed compared to that found in areas dominated mainly by rubble, and this can be attributed to the structural complexity offered by corals, which provide shelter, spaces for reproduction and a greater availability of food resources for invertebrates and fish (Seraphim MJ et al. 2020). In particular, however, in the sites of Chalok and Laem Thian, a greater abundance of invertebrates was verified in the areas rich in *Acropora*. The invertebrates that dominate the area colonized by damselfish (*Acropora*) are hermit crabs that use the shells of dead *Drupella* and feed on debris in the territories of the damselfish.

From this last analysis, it was also possible to observe a significant difference in the distribution of fish species between the areas rich in *Acropora cervicornis* and those characterized by patchy *Acropora* and rubble. In the areas with a high density of *Acropora cervicornis*, damsel fishes are dominant, while in the fragmented and debris-rich areas a significant abundance of *Siganus doliatus*

(commonly known as rabbitfish) is observed, a herbivorous species absent in the areas dominated by healthy corals. This pattern could be attributed to the territorial behavior of damsel fishes, which, as suggested by Sheppard et al. (2024), tend to aggressively defend the coral-rich areas, discouraging the presence of other fish species. This territoriality could also be explained by the fact that damsel fishes spawn in their territory (Fig.15), more precisely above the rubble that are found at the base of the healthy *A. cervicornis* colonies. Another aspect that has emerged concerns the ability of damsel fish to manage macroalgae; According to Schopmeyer & Lirman (2015), when algal meadows exceed a certain extent, damsel fish may no longer be able to control their growth, especially in the case of more invasive macroalgae. This phenomenon can lead to a reduction in the available space between coral branches, limiting the shelter for damsel fish and favoring their movement towards new territories. Consequently, other herbivorous species, such as rabbitfish, can colonize these now free areas, grazing on the algae that cover dead or damaged corals.

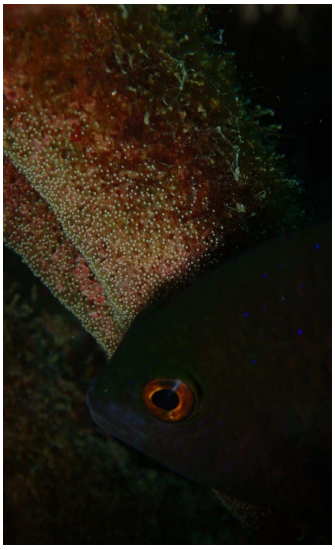
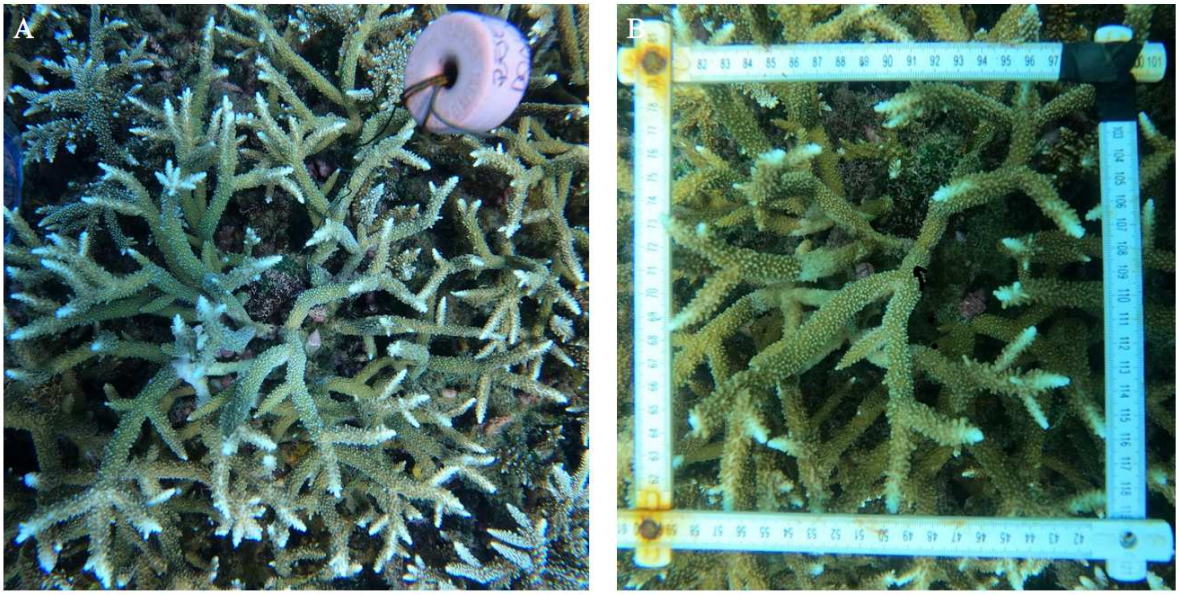


Figure 15: *Plectroglyphidodon lacrymatus* eggs laid on rubble at the base of an *Acropora cervicornis* colony. Photo taken with Olympus TG6 digital camera.

Behaviour of Drupella spp. and effects on the predated corals

The study highlighted that, as previously stated (Scott et al., 2017b; Zhang et al., 2024), *Acropora cervicornis* is the coral favored by *Drupella* and that its removal from colonies produces positive effects in the short term; after removal, in fact, in the first weeks these molluscs do not return to occupy the same colony, thus interrupting their harmful impact on the coral. Even if new *Drupella* could arrive, the time needed to re-establish themselves is sufficient to temporarily stop the consumption of the coral. However, analyses (graph 4,5,6) have shown that the removal of *Drupella* accelerates a problematic natural process (Fig.16): the

portion of coral preyed on dies, leaving a scar (Fig.16a) that is rapidly colonized by filamentous algae (Schopmeyer & Lirman 2015) (Fig.17c) including *Polysiphonia sp.2* (red algae), specifically associated with the damsel fish *Plectroglyphidodon lacrymatus* (Hata & Kato 2006), able to expand their territory using the white scars as springboards (Hata et al. 2020). This leads the coral to succumb to the competition with the algae, aggravating the degradation of the ecosystem. In summary, if initially the removal of *Drupella* seems to offer positive results (Canteri 2024), in the bays examined this manual practice conducted by volunteers ends up increasing the availability of coral surfaces for damsel fish, inadvertently contributing to the loss of coral.



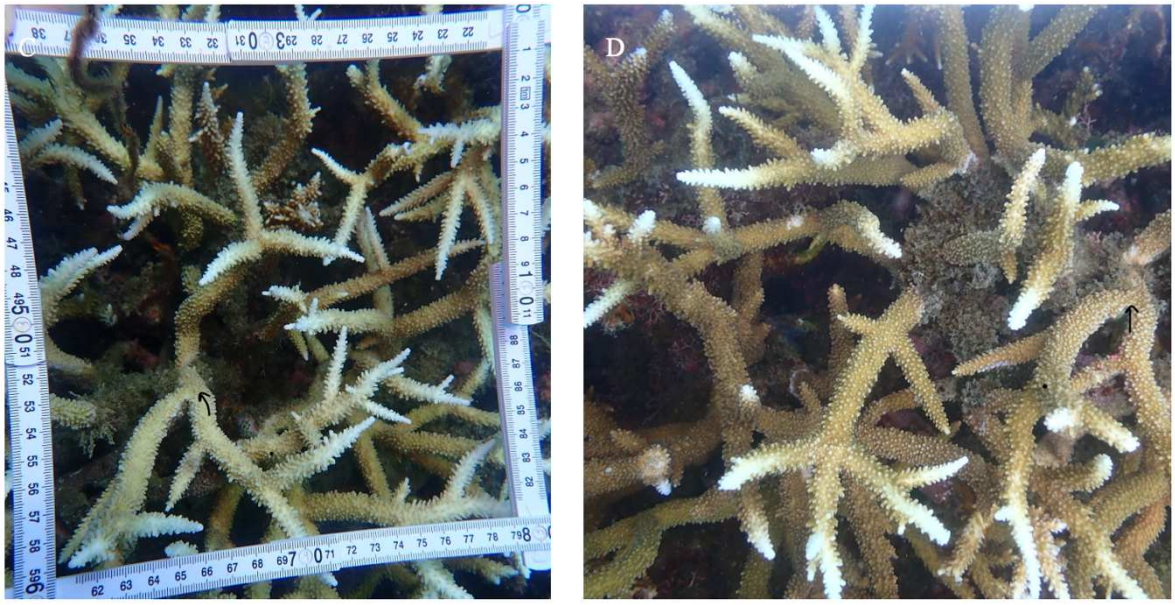


Figure 16: Colony of *Acropora cervicornis* from which the removal was performed, with the evolution of the scar caused by *Drupella rugosa*, in the colony 3A of Taa Cha. The photo of 6/05 shows the presence of *D. rugosa* and a white scar. On 14/05 the scar appears darker, a sign of the death of the coral tissue. On 8/07 the scar is invisible, covered by algae released by the damselfish, while on 1/08 it is completely covered by algae

On the contrary, in colonies where the removal was not performed, *Drupella* snails in addition to remaining longer on the colony and therefore continuing to consume portions of tissue, they stop on the area already eaten considered a resting time, as they are not able to avoid being constantly stung by the nematocysts, (Hsieh et al. 2011). Possible explanation for the aggregation behavior when they eat. In any case, the scars will become covered with *Polyshonia sp.2* macroalgae, but with longer times because the damsel fish does not immediately find the space to

cultivate them. Furthermore, as will be explored later, what has been observed in graphs 4b,5b,6b is that the expansion of the macroalgae increases with time; therefore, after being positioned in a specific area by the damsel fish, this tends to colonize a large part of the central part of the colony (Schopmeyer & Lirman 2015). For these colonies, a tagging method for *Drupella* shells has been developed that does not impede their movement. This allowed us to find some shells on the same colony or at distances between 20 cm and 2.30 meters. Many *Drupella* specimens were no longer identified due to the nature of the substrate present in the bays, characterized by rubble accumulated over time, which made it impossible to recover the fallen shells (Fig.17a). As reported in literature (Bessey et al. 2018; Cumming 2009), this phenomenon is explained by the fact that by preying at night, during the day *Drupella* tends to take refuge in protected areas, in this case offered by the rubble layers. Furthermore, during the study a gregarious behavior was observed (Fig. 17b), already described in literature as a result of the attraction between conspecifics, the presence of compounds released by damaged corals and the settlement histories shared between individuals of the same cohort (Schoepf et al. 2010).

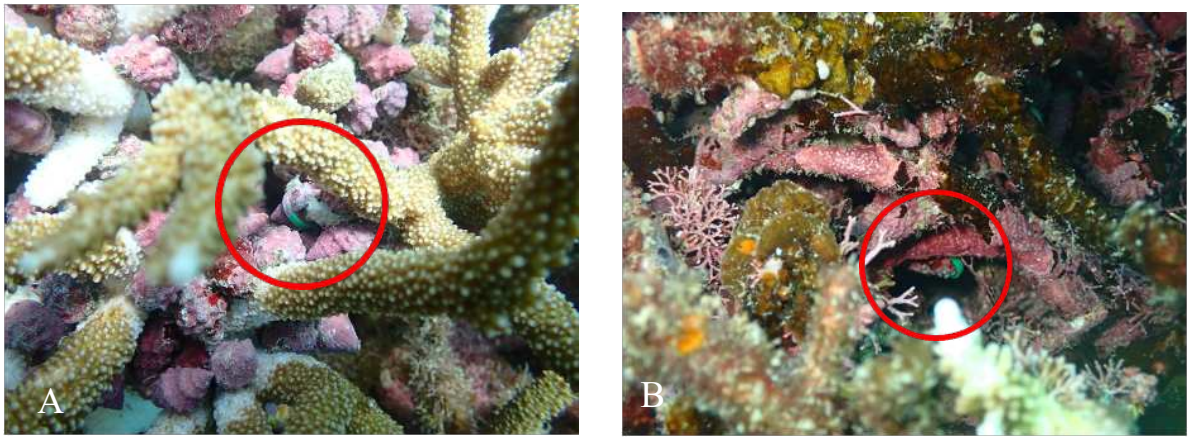


Figure 17: *Drupella rugos*a on a colony of *A. cervicornis*; A: gregarious behavior of *Drupella rugosa* during predation activity. B: tagged *Drupella rugosa* (green cable ties) under some rubble at the base of an *Acropora cervicornis* colony. Photos taken with Olympus TG6 digital camera.

The dives and the analysis of the photographs of the colonies allowed us to evaluate their health, which in most cases did not correspond to that of the scars left by the *Drupella*. In June, almost all the sites had partially bleached colonies. In the Chalok and Taa Cha sites, an improvement in conditions was observed, while in the Laem Thian site the colonies tended to die or be covered by macroalgae. This phenomenon could have been influenced by the increase in water temperature in the months of April and May, when it reached values between 31°C and 32°C. In the following months, however, bad weather and frequent rains lowered the water temperature by 2-3°C, favoring the recovery of some colonies. The recovery process was particularly evident in the Taa Cha and Chalok colonies,

where the shells were removed and cages were positioned. This improvement could be attributed to either a decrease in temperature or a reduction in pressure exerted by *Drupella rugosa* and damsel fish, respectively. In contrast, in Laem Thian bays all colonies died in July. This could also be explained by the data highlighted in graph 6, according to which the colonies in Laem Thian had the highest feeding rate, resulting in being more stressed by *Drupella*. Colonies marked with the letter C are those from which shells were initially removed, followed by the installation of cages to exclude damsel fish. This approach allowed us to evaluate the influence of *Plectroglyphidodon lacrymatus* on colonies previously subjected to *Drupella* predation. Unfortunately, it was not possible to obtain results in all colonies. The difficulties related to the construction of the cages, the high compactness of the colonies and the way in which damsel fish transfer algae exclusively by mouth led to the widespread presence of algae on all scars. It has often been observed that, unable to reach the branches protected by the cages, damsel fish cultivated algae directly on the structures themselves (Fig.18a,b), limiting the exposure to light necessary for the survival of the branches. In contrast, the rest of the Taa Cha and Chalok colonies showed signs of recovery, despite the cages being completely covered with algae. This could be due to the fact that damsel fish concentrated their territory on the cage and the

surrounding branch, leaving the rest of the colony undisturbed. Furthermore, as argued by Weil et al. (2020) the overall recovery of *Acropora* colonies seems to be site-specific and strongly influenced by environmental variability.

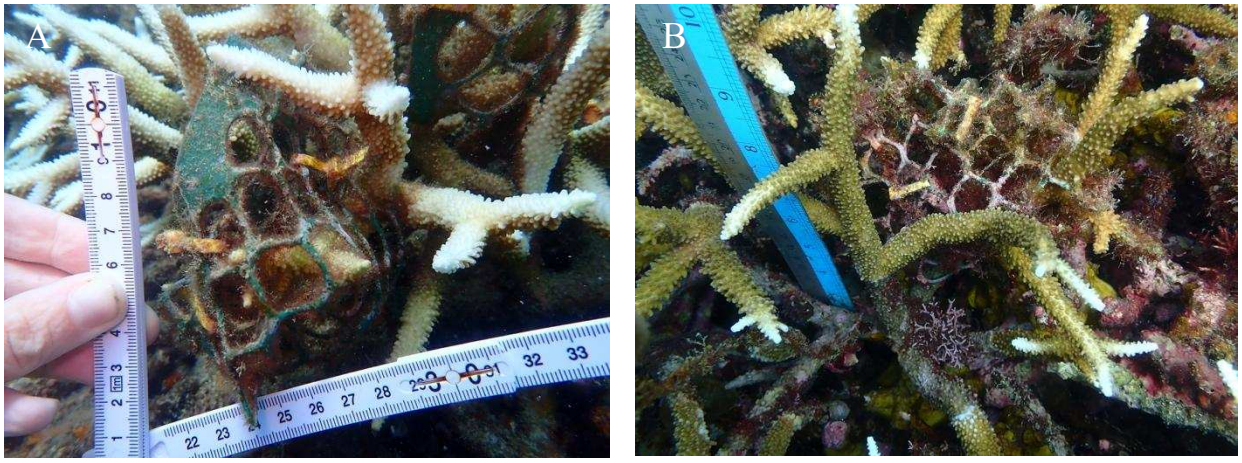


Figure 18: Algae placed by damlsefish on cages positioned on colonies 1C(a) and 3C(b) of Taa Cha Bay, taken on 01/08.

Feeding rate

Analysis of the images collected during the study allowed us to calculate the feeding rate of *Drupella* on *Acropora cervicornis* branches. As shown in graphs 7, at each site, removal activity appears to reduce the feeding rate (Scott et al., 2017b) to approximately 1.21 cm^2/day, compared to 2.78 cm^2/day observed in colonies not subjected to removal. These values differ from what has been reported

in the literature, where D. rugosa consumes coral tissue at a rate of 1.81 ± 0.95 cm^2/day (Zhang et al., 2024). This suggests that the predation activity of D. rugosa at Koh Tao is more intense than at other documented locations. The study also found that, although shell removal initially appears to reduce damage by temporarily blocking predation, this activity tends to recur over time. In colonies from which *Drupella* is removed, the consumption rate remains stable, while in colonies not subjected to removal the rate increases significantly, in the short term to stabilize secondarily.

At the Chalok site, in the area where the shells were not removed, an initial peak is observed followed by a stabilization, probably because *Drupella* move, perhaps attracted by the colonies subjected to removal, or remain on the branches reducing their predatory activity. In contrast, in the areas where the removal was carried out, the predation rate increases subsequently, presumably because *Drupella* move towards colonies stressed by the intervention. This phenomenon is even more marked at the Laem Thian site, where the dynamics are amplified. At Taa Cha, however, the trend is more uniform, perhaps due to the high presence of damselfish, which could influence both the movement and the predatory behavior of *Drupella*. Regardless of the intervention on the colony, predation by *Drupella* persists over time, albeit with different evolutionary times. This phenomenon

could be explained, at least in part, by the activity of damsel fish, which take advantage of damaged colonies to cultivate algae. Contrary to the claim by Osborne and Williams (1992), according to which the manual removal of *Drupella* seemed to permanently reduce their presence, preventing a subsequent recolonization of the colonies, the present study found that, after a few days/weeks, specimens of *Drupella rugosa* reappeared on the same colonies from which they had been removed. This result supports the idea that removal represents only a temporary solution. Since it was not possible to establish the exact time of their return, future more in-depth studies could provide further confirmation of this hypothesis.

Considering that the growth rate of *Acropora cervicornis* is 3.1 ± 0.44 cm per month, or about 0.1 cm^2 per day (Weil et al. 2020), and that the consumption rate of *Drupella spp*. is 1.81 ± 0.95 cm^2 per day (Zhang et al., 2024), it could be assumed that a colony of *Acropora cervicornis* could be consumed within a few hours if subjected to the attack of one or more individuals of *Drupella*. Furthermore, the growth of this coral is influenced by various factors, including occupation by damsel fishes (Schopmeyer & Lirman, 2015), diseases, predation by marine organisms and adverse environmental conditions (Bonin, 2012),

including rising ocean temperatures (Weil, 2004), making A. cervicornis particularly vulnerable

Damselfish behaviour

One of the most interesting aspects that emerged during this study concerns *Plectroglyphidodon lacrymatus*, a damsel fish that is particularly abundant in the bays examined. As already observed in previous research (Bonin 2012; Schopmeyer & Lirman 2015; Weil et al. 2020), this species seems to prefer the microhabitat offered by *Acropora cervicornis*. Also known as "whitespotted devil", *P. lacrymatus* is an extremely territorial fish, which aggressively defends its algal territory (Frédéric & Parmentier 2016). This behavior reduces the pressure of herbivory from other organisms, allowing algae to grow within its territory (Schopmeyer & Lirman 2015). Furthermore, *P. lacrymatus* has been observed to have a low amount of digestive enzymes (Hata et al. 2010), which limits its diet to a few algal species, including the red alga (rhodophyte) *Polysphonia sp*., also identified in the present study, and some cyanophytes (Gibson et al. 2001). A particularly interesting aspect is the mutualistic relationship between *P. lacrymatus* and the rhodophyte *Polysphonia sp*. This “cultivation mutualism” is

favored by the fact that *Polysphonia sp*. is less competitive than other less edible algae for damselfish (Hata & Kato 2006). By defending their territory from vertebrate and invertebrate herbivores and other competitive algal species (Hata et al. 2010), damsel fish promote their expansion range by maintaining algal turf. In return, damsel fish obtain food, mainly by feeding on the vertical axes of filamentous rhodophytes (Hata & Kato 2002). During the surveys carried out in this study, *P. lacrymatus* was found to "bite" the algae present on the branches of *Acropora cervicornis*; Weil et al. (2020) pointed out that algae rarely colonize healthy coral tissues, but factors that damage coral colonies can facilitate excessive algal growth. This supports the initial hypothesis of the study, according to which the removal of *Drupella* shells makes the tissue-free portions of coral vulnerable, favoring the cultivation of algae by damsel fish and thus accelerating algal cover and coral death.

Furthermore, in graph 9 it is possible to observe that the second most practiced behavior by damsel fish was that of biting corals, probably to remove unwanted algae or to damage coral tissues, thus favoring the growth of favored algae (Schopmeyer & Lirman, 2015). The low percentage of this activity could be explained by the fact that due to the high predation on *Acropora* carried out by various organisms (including *Drupella*), damsel fish do not have the need to create

new cultivation areas as they are already present. Furthermore, *P. lacrymatus* has been observed chasing other fish, a behavior that could be related to its high aggressiveness and territoriality (Frédéric & Parmentier, 2016) and rubbing against the branches of coral colonies. This last action, already documented by Verwey (1930) in relation to sea anemones, has been interpreted to improve the conditions of the territory. The behavioral patterns observed in the two study sites, Chalok and Taa Cha, were very similar, indicating that these behaviors are intrinsic to the species and are not significantly influenced by local conditions. In light of the analyses conducted and the information from the literature, it can be stated that the activity of damsel fish has a negative impact on coral restoration, hindering the settlement of larvae and the attachment of *Acropora* fragments (Schopmeyer & Lirman, 2015; Bowden-Kerby 2022). According to some authors, the best solution to address this problem would be to reduce the abundance of damselfish, whose proliferation seems to be linked to the scarcity of natural predators (Weil et al. 2020) and the high availability of branching corals (Cole et al. 2008). This goal could be achieved through a more effective management of their predators, such as groupers and snappers, promoting a balanced trophic cascade that favors the improvement of the general health of the coral reef. In support of this, surveys conducted by the “Conservation Divers” program have highlighted a reduction in

the abundance of fish (Appendix 1) including groupers, probably due to fishing practiced by locals. Despite some contrasting hypotheses regarding the management of the damsel fish population (Schopmeyer & Lirman 2015), mitigating their impact through the restoration of predator populations seems to be the most viable solution.

Determination of the density of Drupella spp. on branching corals spp. and the effect of Drupella removal

Manual removal of *Drupella rugosa* has been adopted in several locations, including the Maldives, Ningaloo Reef and Koh Tao, although its ecological consequences have not been adequately studied. Analysis of data collected by the New Heaven centre between 2010 and 2024 (graph 10), subsequently reviewed by Canteri (2024), highlighted that this practice has not produced a significant improvement. The number of specimens removed in 2010, in fact, is comparable to that of 2022, and over the course of more than a decade no significant reduction or lasting positive effect has been observed. The study also showed that although removal temporarily reduces coral consumption by *Drupella*, the absence of these molluscs can expose the scars left on the colonies to rapid colonization by

filamentous algae such as *Polysiphonia sp.*. These algae, often associated with damsel fish (*Plectroglyphidodon lacrymatus*) (Hata & Kato 2006), hinder the recovery of the coral and contribute to its further degradation. Contrary to Osborne and Williams (1992), who observed a permanent reduction in *Drupella* after removal on Ningaloo Reef, the study revealed that in the Koh Tao colonies the molluscs reappeared within a few weeks of their removal.

Another critical issue that emerged concerns the use of untrained volunteers. This choice has often led to the manual removal of similar organisms, such as hermit crabs, which use the shell of *Drupella* when it dies. Inexperienced use of tools has also caused collateral damage, such as the abandonment of removed shells among coral debris or their movement to other colonies, paradoxically favoring the spread of the parasite. In summary, although manual removal may initially seem an effective solution, it has proven not only ineffective in the long term, but even harmful to the health of coral reefs. These results highlight the urgency of developing more sustainable management strategies, based on solid scientific evidence.

Determination of the density of Drupella spp. on branching corals and comparison of Acropora gardens with and without Drupella spp.

Thanks to the removal activity conducted in March and April at the Chalok site and in August and September at the Taa Cha site, it was possible to examine three different areas marked by the colors yellow, blue and green. The green area represented the control zone, from which *Drupella* were not removed. The areas were selected based on similar characteristics and environmental conditions. This analysis allowed to calculate the density of shells per square meter using the formula: number of *Drupella* removed/25 m^2 (with areas of 5 m x 5 m). The results showed an average density of 52.78 individuals per square meter, with the highest values detected at Chalok (46.9 ind/m^2), in sharp contrast to what reported by Scott et al. (2017b), who estimated a density of 7.9 individuals per square meter. At Taa Cha, however, the density was 30.4 ind/m^2. These data highlight the presence of a real outbreak, considered as such when densities higher than 3 individuals per square meter are recorded, as indicated by Moerland et al. (2016). From graph 11 it is possible to note that although systematic and repeated interventions were carried out in the areas of Chalok and Taa Cha, the number of

Drupella snails removed was still in some cases higher than in the control area, where removals occurred only on the final date. This data suggests that the simple removal activity may not be sufficient to contain or stably reduce *Drupella* population. This observation suggests that the effectiveness of control measures, such as manual removal, must be integrated with more comprehensive management strategies to obtain more lasting results.

Personal observation

In parallel with the monitoring study, some specimens of *Drupella rugosa* were observed in a controlled environment (aquarium). Observations on feeding behavior confirmed what has been reported in literature, that is, that these molluscs seem to be influenced by the presence of coral nematocysts. When a live fragment of *Acropora cervicornis* was placed in the center of the aquarium, no *Drupella* specimen approached(Fig.19a). However, if a piece of substrate (rubble) was placed next to the live fragment, it was used as a support base for feeding (Fig.19b). If the fragment of substrate was placed far from the live coral, but near a wall of the aquarium, *Drupella* climbed along the wall, extending its proboscis towards the coral polyps. Furthermore, in the absence of food, a curious behavior was often observed: smaller specimens tend to remain attached to the shell of larger *Drupella*, sometimes forming aggregations of three individuals(Fig.19 c,d).

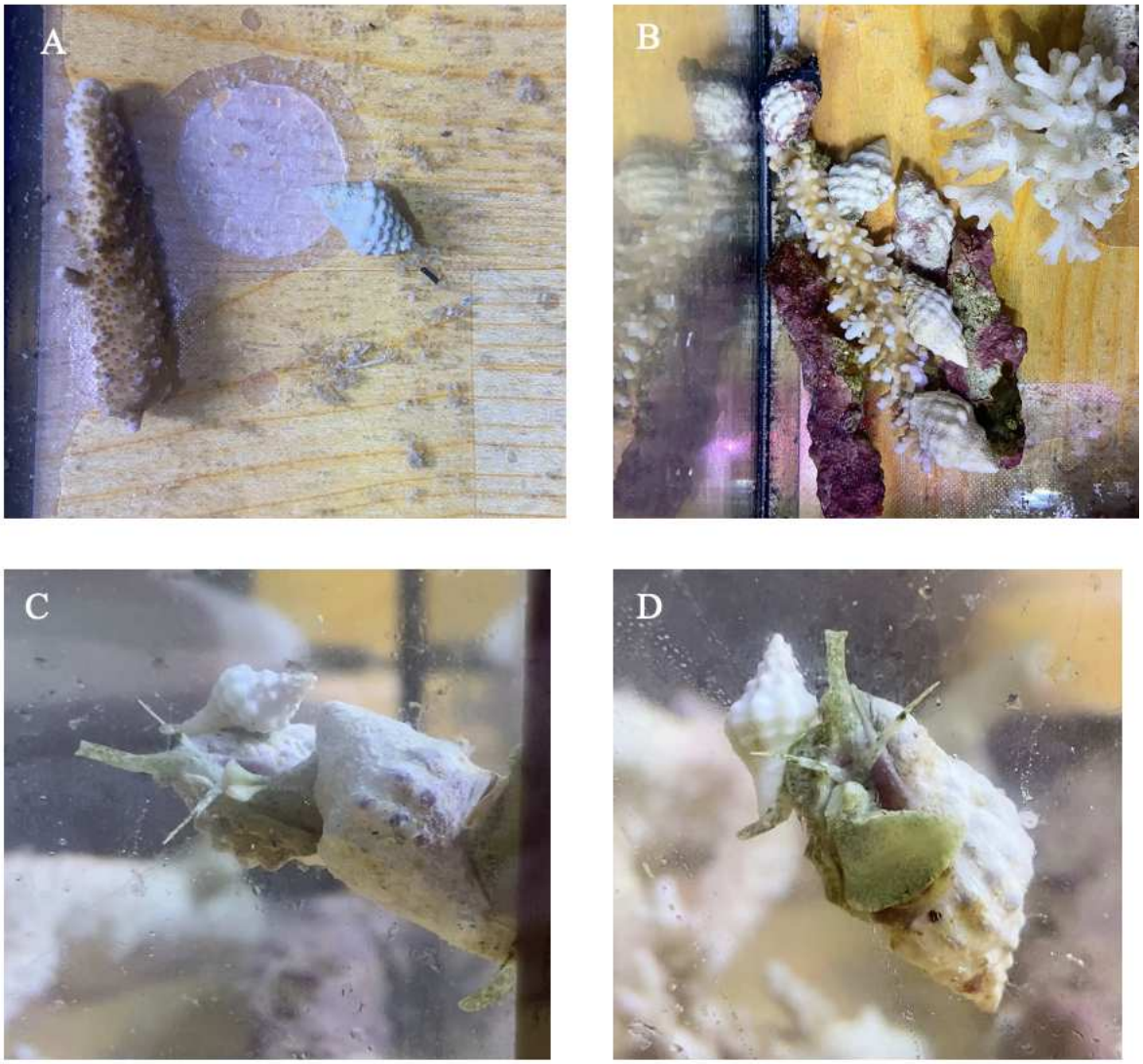


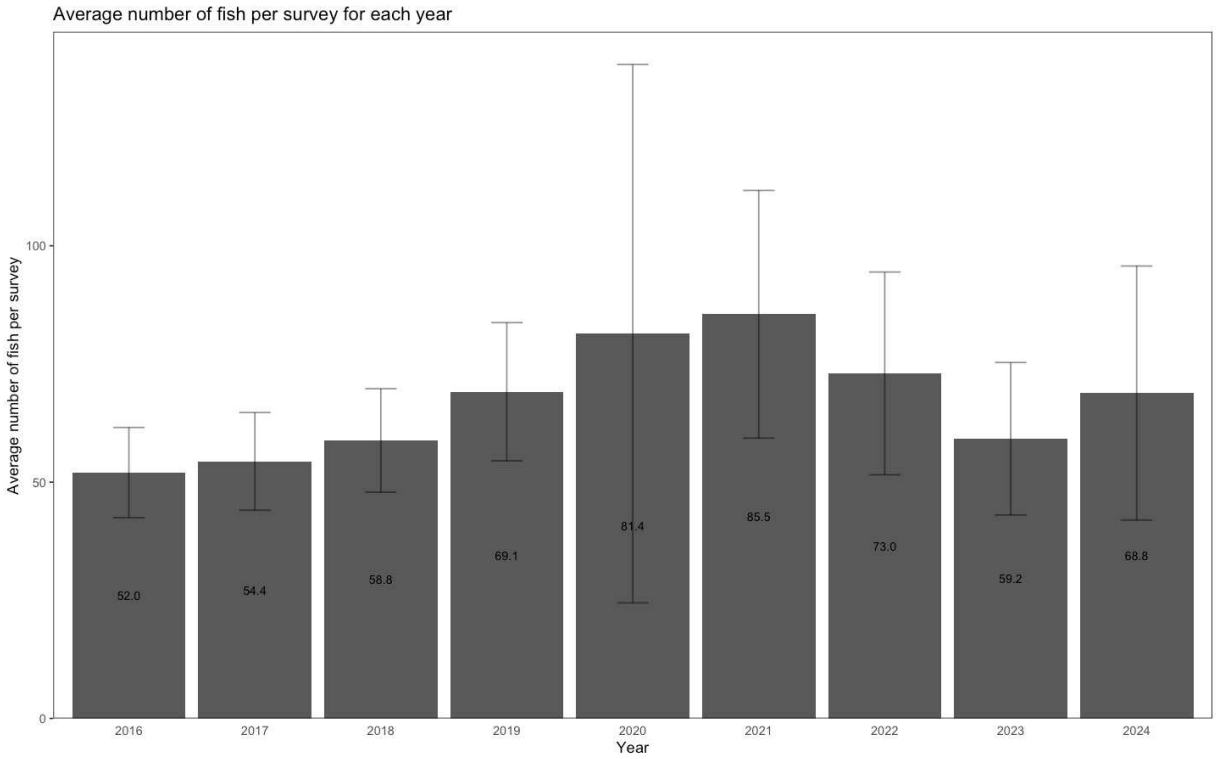
Figure 19: *Drupella rugosa* in aquarium: a: *D. rugosa* moving away from the fragment of *A. cervicornis*; B: several *D. rugosa* feeding on a fragment of *A. cervcornis* next to rubble; C,D: aggregation of two or more *D. rugosa* one above the other.

CONCLUSION

In conclusion, this study investigated the effectiveness and implications of manual removal of *Drupella spp.* shells, an activity promoted by the "New Heaven Conservation Divers" program, founded in 2007 by Chad Scott. Thanks to the implementation of a specific sampling design, factors relevant to future management strategies for *Drupella* outbreaks were identified. The research, conducted in Chalok, Laem Thian and Taa Cha bays of Koh Tao island between April and September 2024, highlighted several critical issues related to this practice. The entrustment of coral reef management to unqualified volunteers led to the involuntary removal of other organisms, (such as hermit crabs), due to the similarity of the shells. Furthermore, the incorrect use of tools caused collateral damage, such as the abandonment of the removed shells among the rubble or the transfer to other colonies, favoring the spread of the parasite. This demonstrates that the proposed manual removal is not only ineffective, but can also further damage coral reefs. A significant contribution of this research is to have explored, for the first time, the relationship between the presence of damsel fishes and the impact of *Drupella*. Furthermore, the data suggest that any management strategy for *Drupella* will be incomplete if the ecological role of these fishes is not

considered. In light of these evidences, it is recommended to integrate the monitoring of damsel fishes as indicator species, assessing their abundance to develop more targeted and effective approaches to combat *Drupella* outbreaks. Further investigations will allow to better understand the reproductive strategy and in particular the spawning patterns and the behavior of juveniles, essential elements to conduct a correct management of the mollusc outbreaks. In summary, this work provides an original contribution to the understanding of the ecological dynamics related to *Drupella rugos*a and highlights the need to adopt more sustainable and evidence-based management strategies. The results obtained pave the way for further research, with the aim of preserving coral ecosystems and mitigating the impact of parasitic species such as *Drupella*.

APPENDIX



Appendix 1: Average number of fish per survey carried out from 2016 to 2024

Thanks to the surveys carried out by the New Heaven center from 2016 to 2024, a peak in the average number of fish observed is observed in 2020, which decreases until 2023, and then recovers the following year.

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