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Short- and long-term effects of culling invasive corallivorous gastropods

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Eradicating invasive species and maintaining their populations at acceptable densities is both costly and challenging in marine environments, primarily due to the open water connectivity between culled and non-culled areas. This research aims to evaluate the short- and long-term effects of culling invasive species, considering the invasive gastropod *Drupella rugosa* (Born, 1778) from the coral reefs of Koh Tao (Gulf of Thailand) as a case study. Ecological, logistical, and behavioural factors that influenced the removal efforts were identified, highlighting key components that can inform future strategies aimed at managing outbreak events. Specific objectives included: (1) estimating gastropod densities and to study the behaviour of *D. rugosa* on *Acropora*-dominated reefs; (2) assessing short-term effects of *D. rugosa* removal by monitoring the fate of grazed corals; (3) examining the long-term impact of culling by analysing data from a removal campaign spanning over a decade, including an evaluation of the effort in terms of time and diver involvement. The relationship between damselfish and the feeding activity of corallivorous gastropods was also investigated. A key finding of this study is that poorly planned culling is ineffective in controlling outbreaks of invasive species such as those belonging to the genus *Drupella*. Long-term data from culling campaigns conducted between 2010 and 2024 revealed that the number of removed specimens remained relatively constant, despite significant differences in effort. This disparity underscores the lack of strategic coordination in the implementation of removal activities. Following a critical comparison with cases reported in the literature, common issues and transferable strategies were identified and thoroughly analyzed. Directions for management were provided, with the understanding that future actions should be grounded in a thorough knowledge of the species' ecological traits, the biotic and abiotic drivers of outbreak events, a quantitative assessment of its impact on *Acropora* reefs, and integration into with well-established international removal and prevention programs.

Keywords Biological invasions, Removal, Muricidae, Control of pests, Surge

Global change is rapidly reshaping key biotic interactions among corals and reef-associated species, potentially triggering irruptions of invasive coral consumers[1,2] that further impact coral growth, fitness, and coral community dynamics[3,4]. Through their feeding activities, invasive corallivores damage coral tissue and mucus layers, compromising natural defences and facilitating microbe entry[5], contributing to the recurrence and spatial spread of coral diseases[6].

Among corallivorous gastropods that feed on hard corals, the Muricidae *Drupella* spp., although representing only a fraction of all corallivorous mollusks, can degrade coral reefs on a large scale[7]. With outbreaks involving millions of individuals[8], *Drupella* spp. can lead to coral cover declines of up to 86%[1,9].

Molecular analyses have identified at least four obligate corallivorous *Drupella* species distributed across Indo-Pacific reefs and the Red Sea—*D. cornus* (Röding, 1798), *D. eburnea* (Küster, 1862), *D. fragum* (Blainville, 1832), and *D. rugosa* (Born, 1778)—as well as one species complex that exhibits opportunistic corallivory, *D. margariticola* (Broderip, 1833)[10–12].

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Population explosions have been documented since the mid-1970s[13], with more recent ones reported in Mandu reef, Ningaloo Marine Park, Western Australia[14] in the Red Sea[15] Thailand[16,17], Taiwan[18], Mauritius[19] and the Maldives[20].

When feeding, *Drupella* spp. remove the living coral tissue (i.e., coenosarc), exposing the underlying white skeleton, by using its specialized mouthparts, an externally cuticularized proboscis and lateral teeth on the radula, which protect against coral nematocysts and facilitate rapid feeding[21].

Rapid *Drupella* population outbreaks remain poorly understood but may be linked to their attraction to freshly damaged corals, which are more common in shallow reefs exposed to natural stressors and human impacts[15,20,22,23]. Despite their preference for Acroporidae (mainly *Acropora* spp.) and Pocilloporidae corals[16], *Drupella* species are characterized by high dietary plasticity, selecting coral prey based on availability, nutritional content, and local environmental conditions[24,25]. Individual snails consume approximately 1.8 cm² of coral tissue per day, with maximum feeding rates reaching up to 6.5 cm²[8,14].

Drupella snails follow an r-selected reproductive strategy, characterized by high fecundity and rapid population growth with minimal resource investment in each offspring[26]. They typically have high offspring mortality, short life spans, small body sizes, and little to no parental care[8]. Under natural conditions, biological barriers help regulate *Drupella* populations at each life stage. Fertilization barriers can limit initial reproduction[27], while pelagic larvae face challenges such as dispersal, starvation, and predation[28]. Settlement is another critical bottleneck[29], as only a few individuals successfully complete metamorphosis due to disease and predation, and ultimately, only a small percentage reach sexual maturity. When these regulatory processes are disrupted, adult populations can grow uncontrollably[30]. One key factor increasing survival rates is food availability—especially phytoplankton—which can enhance larval survival, settlement success, and recruitment[8].

To control outbreaks, manual collection and culling of *Drupella* spp. have been implemented in various regions[30]. Nonetheless, no long-term studies have yet assessed the sustained effectiveness of repeated snail culling efforts.

Despite numerous and regular removal campaigns since 2010, the density of *Drupella rugosa* remains high in Koh Tao Island in the Gulf of Thailand[31]. Since the 1990s, Koh Tao has experienced multiple outbreaks of this corallivorous gastropod, with impacts comparable to those of the crown-of-thorns starfish *Acanthaster planci* (Linnaeus, 1758)[16,24,31]. These outbreaks, combined with bleaching events and other stressors, have contributed to significant coral decline, posing threats to reef health and dive tourism[31]. The largest outbreaks occurred in 2010 and 2013–2014 following severe bleaching episodes, with *D. rugosa* densities reaching up to 7.9 individuals per m² in 2010, later reduced to 5.6 individuals per m² in 2011[31]. Despite the removal of approximately 26,000 individuals by 2014, *D. rugosa* populations doubled in several areas, particularly in Chalok Bay, where *Acropora* and free-living mushroom corals dominate[17,32]. In 2010, *Acropora* cover declined by 60% at depths of 3–6 m due to predation and bleaching[24], prompting *D. rugosa* to shift its diet toward deeper-dwelling mushroom corals[24,31].

Controlling invasive species or maintaining their populations at acceptable densities is both costly[33] and challenging in marine environments, primarily due to open water connectivity between culled and non-culled areas[34,35]. As a result, successful cases of long-term control have been limited to situations where the invasive species was present at low densities, confined to a restricted area, and detected during the early stages of invasion[36].

One of the key priorities in developing effective management strategies for controlling marine invaders is to address knowledge gaps in their dispersal mechanisms and behavioural patterns[8,34]. To this end, studies on *Drupella* behaviour, combined with a critical evaluation of long-term removal efforts, can provide valuable insights for designing effective management plans aimed at controlling gastropod outbreaks.

Therefore, the aim of this research is to evaluate the short- and long-term effects of culling the invasive gastropod *D. rugosa* on tropical reef ecosystems, using the reefs of Koh Tao as a case study. Specific objectives were: (1) to estimate gastropod densities and to study the behaviour of *D. rugosa* on *Acropora*-dominated reefs; (2) to evaluate the short-term effects of *D. rugosa* removal by monitoring the fate of grazed corals, and (3) to examine long-term effects of culling by analysing data from previous removal campaigns and evaluating the effort of these actions.

It was also hypothesized that the activity of algal-gardening damselfish was linked to the predation of *D. rugosa*.

The results of this study will contribute to assessing the effectiveness of culling in controlling the spread of the native invasive species, while also identifying methodological limitations, and essential elements to be considered in future efforts to design a management plan for these overabundant and voracious predators.

Materials and methods

Sampling activity

Field activities were conducted by SCUBA diving (ARA) from February to September 2024 in Chalok Bay (10°04'04"N, 99°49'29"E) on Koh Tao Island (see[37] for site location and description). Although *Drupella rugosa* can also feed on corals of the Fungiidae family, it exhibits a pronounced preference for branching staghorn corals[24]. All samplings were therefore conducted on the *Acropora*-dominated reef of at 3–7 m depth. where *Acropora* spp. colonies generally thrive in the area. Underwater photos were taken with a GoPro Hero9 and Olympus TG6 digital camera. Each experiment is detailed in the next paragraphs and synthesized in Table 1.

Population structure and density over time of *Drupella rugosa*

To determine the population density (i.e., number of individuals/m²) and structure of *D. rugosa*, four permanent plots measuring 5 × 5 m were randomly established on Chalok reef, each positioned at least five meters apart. From February to May 2024, monthly surveys were conducted during which all *D. rugosa* individuals within

Objective	Methods
Assessment of *Drupella rugosa* (Born, 1778) population density and structure	Four 5 × 5 m permanent plots randomly placed in Chalok reef; all *Drupella rugosa* individuals counted and measured monthly (Feb–May 2024), classified into juveniles, intermediates, and adults (after[38]). Divers trained to remove *D. rugosa* using 30-cm tongs and 3-L bottles along 60 × 10 m transects
Determination of *Drupella rugosa* movement patterns and potential migration among coral colonies	Mark–recapture experiment. Tagged 54 *D. rugosa* individuals on nine *Acropora* colonies using plastic cable ties; monitored every two months (Apr–Aug 2024) within a 5 m radius
Short- and middle-term effects of *Drupella rugosa* removal on coral health status	Compared two groups of nine tagged colonies: R (with removal) vs. NR (without removal). Monitored changes in scar length and condition (May–Aug 2024). Lower and upper margin of predation scars marked with cable ties. Photographs of predation scars taken periodically; scar length measured using ImageJ; scars classified as MA (algae-covered), DRUP (presence of *Drupella*), or DC (newly dead coral)
Long-term effects of culling (2010–2024)	Analysis of 14 years of removal campaign data (*D. rugosa* abundance, removal effort, and culling effectiveness) from the New Heaven Reef Conservation Divers Program
Behaviour of *Stegastes lacrymatus* (Quoy and Gaimard, 1825) exploiting feeding scars caused by *Drupella rugosa*	Fifteen *Acropora* colonies inhabited by damselfish observed for 15 min each to monitor the use of feeding scars by the fish, as well as biting, chasing, and rubbing behaviours

Table 1. Summary of specific objectives and used methodologies.

each plot were counted and measured. Individuals were then classified into three size categories, following Saponari et al.[38]: juveniles (< 1 cm), intermediates (from 1 to 2 cm) and adults (> 2 cm).

To check for changes in the density of *D. rugosa* adult individuals over time (random, 4 levels: February, March, April, May), data were firstly checked for normality, homoscedasticity and sphericity using the Shapiro-Wilk, Levene and Mauchly tests, respectively. Because these assumptions were not met, a non-parametric Friedman test was used. Due to the very low number of intermediate and juvenile individuals recorded, no statistical analyses were run for these categories.

Data visualization was performed using box plots generated with the *ggplot2* package, while statistical tests on the adult individuals were conducted with the g R packages *car* and *rstatix* in the R version 4.0.4[39–42].

Behaviour of *Drupella rugosa*: the mark-recapture experiment

To assess the feeding behaviour and movement patterns of *D. rugosa* among coral colonies, a mark-recapture experiment was conducted tagging individual snails with plastic cable ties[43]. Prior to field application, preliminary trials were conducted in aquaria to ensure that the tagging procedure did not affect snail mobility or behaviour. Since no adverse effects were observed from the use of cable ties, a field experiment was subsequently implemented. Nine *Acropora* colonies were randomly selected and tagged with small red buoys attached to dead colony sections using metal wire, ensuring no contact with healthy tissues. Plastic tags of different colours were used to distinguish the replicates. In situ, *D. rugosa* individuals were marked using plastic cable ties (3 mm in width and 100 mm in length), secured around the widest part of each shell. The excess length of each tie was trimmed to avoid interferences with snails' natural movement. From 5 to 9 individuals were marked per colony, for a total of 54 tagged snails. After tagging, each individual was immediately returned to its original position to minimize handling disturbance. Monitoring surveys were conducted every two months, from April to August 2024, to record whether the marked snails: (i) remained on the same *Acropora* colonies, (ii) moved onto nearby rubble, or (iii) dispersed to other areas within approximately 5 m of the colony.

Short-, middle-term and decadal effects of *Drupella rugosa* removal

Considering that small scars (≤ 8 cm^2) caused by corallivores may undergo partial or complete healing[44], *D. rugosa* feeding scars were monitored to assess potential coral tissue regeneration. Hereafter, the term 'scar' refers to the bare, white skeletal areas exposed after tissue loss, which have not yet been colonized by other organisms [45].

To evaluate the short and middle-term effects of the *D. rugosa* removal, the extent of coral damage and the health status of predated coral branches were compared between two experimental groups, each consisting of nine tagged *Acropora* colonies: (i) R (Removal): colonies from which gastropods were manually removed and, (ii) NR (No Removal) control colonies where gastropods were left undisturbed.

On each colony, the lower and upper margins of three predation scars were marked using cable ties (Fig. 1) to delineate the boundaries of the scars at the start of the experiment. Photographic surveys of each scar were performed using an Olympus TG6 digital camera: (i) on the day of the start of the experiment (May-T0) and six days after (May-T1), to detect any short-term changes or enlargement of the scar, and then (ii) monthly until the end of the experiment (June-T2, July-T3, August-T4), to quantify middle-term damage progression. A reference scale was placed beside each scar during photography to enable subsequent measurement of scar lengths using ImageJ software[46]. Additionally, for each photo, the fate of the scars left by *D. rugosa* was recorded across the same time intervals, classifying their condition into three categories: covered with algae (MA), presence of *D. rugosa* (DRUP), and recent scars, intended as newly dead coral (DC).

Any potential change in scar size was evaluated over two-time scales: short-term (six days) - (random factor, 2 levels: May-T0 and May-T1) and the middle-term (four months) - (random factor, 4 levels: May-T0, June-T2, July-T3, August-T4) considering the two treatments (fixed factor, 2 levels: R colonies and NR colonies).

Because the tagged branches varied in size, the initial scar length (measured at May-T0) was included as a covariate to account for its potential influence on subsequent damage rates in both control and treatment colonies. Accordingly, a first one-way Analysis of Covariance (ANCOVA) was conducted for both the short- and middle-term periods, using the increment in scar length between May-T0 and May-T1 and between May-T0 and August T4 respectively.

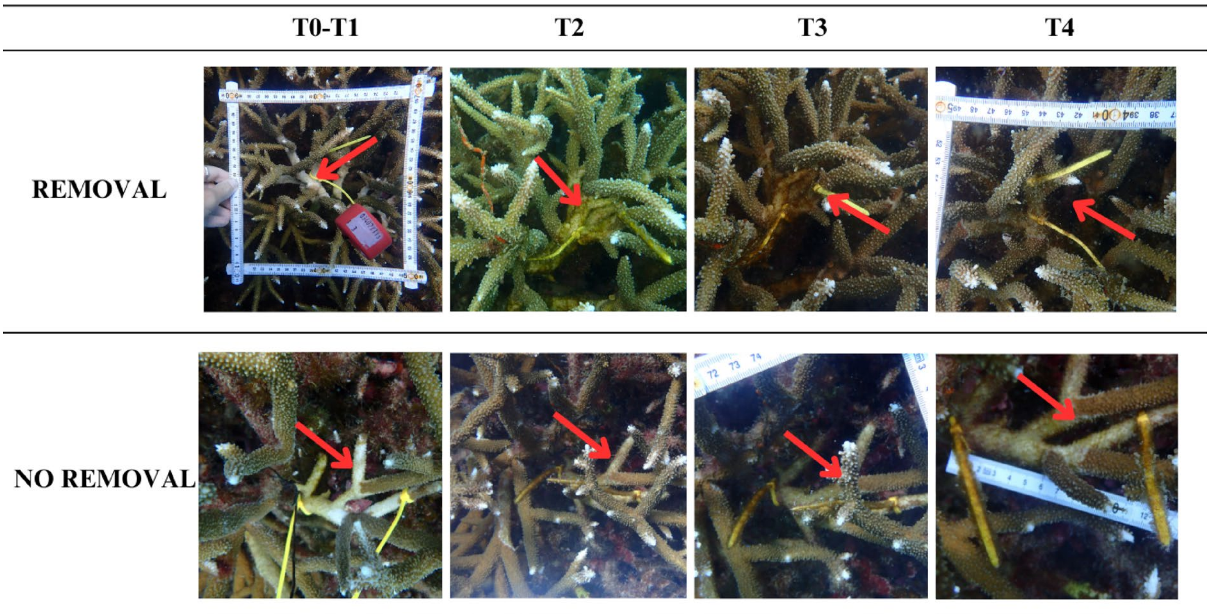

Fig. 1. Progressive development of *Drupella rugosa* predation scars in *Acropora cervicornis* (Lamarck, 1816) in Removal and in control colonies (No Removal) from May (T0-T1) to August (T4). The images show the transition from freshly exposed dead coral tissue (T0) to areas later colonized by filamentous algae (T3), which are more abundant in the Removal colonies.

Then, two-way repeated measures Analysis of Variances (RM-ANOVA) were performed to evaluate differences between treatments across time. When significant effects were detected, post hoc pairwise comparisons were carried out to identify specific differences.

Prior to all analyses, data were checked for normality, homoscedasticity, sphericity, and parallelism (using linear regressions). Statistical tests were performed using R packages *car*, *rstatix* and *gglot2*.

To evaluate the long-term effectiveness of *D. rugosa* removal over a 14-year period (2010–2024), data from culling campaigns conducted during this time were analyzed. The interventions were carried out at haphazardly chosen sites in the Chalok Bay as part of the New Heaven Reef Conservation Divers Program established by Scott Chad in 2007.

The removal technique, described in Saponari et al.[38], was performed by trained volunteers to ensure consistent collection procedures and to minimize coral damage. Gastropods were collected using 30-cm steel tongs and 3-L plastic bottles with no lids, which were used both to capture and contain the snails underwater. Each culling session lasted approximately 1.5 h and covered an area of about 600 m². The number of divers involved varied annually, ranging from 6 to 171 participants per year. Inside this area, all *D. rugosa* individuals visible to the naked eye were removed.

For each year, the average number of snails removed (± standard deviation, SD) and the effort (number of divers × dive duration in minutes) were calculated. To assess whether the culling effort was related to the number of collected *D. rugosa*, data were first checked for normality and homoscedasticity. Since these assumptions were not met, a non-parametric Spearman rank correlation was used. To determine the effectiveness of removal campaigns over time (random factor: 12 levels, representing sampling years), data expressed as number of *D. rugosa* removed per collector per minute were analysed using a Kruskal–Wallis test. When significant differences were detected, Dunn's post hoc tests with Bonferroni-adjusted p-values were applied. Additionally, differences between the beginning (2010) and the latest available data (2024) were specifically compared to identify long-term trends.

All statistical analyses were performed using the R packages *car*, *rstatix* and *ggstatsplot*.

Behaviour of the damselfish *Stegastes lacrymatus* living in *Acropora* colonies

The damselfish *Stegastes lacrymatus* (Quoy and Gaimard, 1825) is known to cultivate gardens of filamentous algae on *Acropora* spp.[47]. At Koh Tao, this species was frequently observed establishing algal gardens on coral colonies previously affected by *D. rugosa* predation. To assess whether scars left by *D. rugosa* predation on corals were utilized by algal-gardening damselfish for algae attachment, the predated colonies were monitored, and fish behaviour was recorded. Fifteen coral colonies hosting the damselfish were selected for behavioural observations. Fieldwork was conducted with the assistance of trained volunteer scuba divers, who were instructed to avoid contact with corals and to minimize disturbance to alter fish behaviour.

For each selected colony, divers defined the boundaries of the damselfish territory using a tank banger to gently approach the coral until the fish stopped displaying aggressive defence behaviour. Once the territory was established, a 15-minute observation period was initiated[45,48]. During this time, observers recorded: (i) bites on farmed algae, (ii) chasing behaviour directed toward other damselfish, grazers, or corallivorous fish intruding into the territory and (iii) rubbing behaviour on the corals (i.e., some territorial damselfish have been observed to rub their bodies against coral branches to remove ectoparasites when cleaner fish are absent[49]).

Results

Density and population structure of *Drupella rugosa*

Inside the four permanent 5 × 5 m plots, adult individuals dominated the population, while juvenile and intermediate stages were comparatively rare (Fig. 2).

For adults, a marked decrease in density was observed over the four-month monitoring period, with the highest abundance densities recorded in February (60 ± 69 individuals/m^2) and the lowest in April (13 ± 7 individuals/m^2). The Friedman test, nevertheless, revealed no significant temporal variation ($p = 0.112$), likely due to the high variances recorded among plots, especially in February (Fig. 2A). Regarding the other two size classes, juveniles were recorded with very low densities only in February and March (0.02 ± 0.03 individuals/m^2 and 0.01 ± 0.02 individuals/m^2, respectively), while intermediate individuals were found at slightly higher densities in all months (0.2 ± 0.2 individuals/m^2 in February, 0.1 ± 0.2 individuals/m^2 in March and April), while were absent in May. No consistent temporal pattern was observed for either class (Fig. 2B).

Behaviour of *Drupella rugosa*: the mark-recapture experiment

The mark-recapture experiment started in April, with the first monitoring conducted two months later on the tagged colonies (Fig. 3). At that time, more than half of the marked *D. rugosa* individuals (58.5 ± 36.9%) were no longer detected. Among the remaining individuals, 17.9 ± 18.1% were observed on the surrounding rubble, 19.1 ± 25.4% remained on their original colonies, and only 4.4 ± 13.3% had moved to a nearby colony. The distance of displaced individuals from their original colony ranged between 30 cm and 90 cm. By the end of the experiment in August, no tagged *D. rugosa* individuals were observed in the area.

Short-, middle-term and decadal effects of *Drupella rugosa* removal

The analysis of sequential photographs of control (No Removal, NR) and treatment (Removal, R) colonies revealed temporal changes in scar size over both short- and middle-term periods (Fig. 4A).

After only six days (May-T0 to May-T1), both NR and R colonies showed an increase in scar size, reaching 2.37 ± 2.39 cm and 0.48 ± 0.31 cm, respectively. Although the increase in NR colonies was more than twice that of R ones, no significant differences in the scar size were detected between treatments over time, and the variation was independent of the initial scar length (Table 2B). A similar pattern emerged over the middle-term period (May-T0 to August-T4), where the overall increase in scar size was again independent of the initial scar length and not statistically significant (Table 2C). Even though the increment in NR colonies exhibited higher increases than R colonies (166.9 ± 90.2% and 129.7 ± 56.9%, respectively), considering the two treatments across the entire study period, a significant temporal effect was detected ($p < 0.05$; Table 2D), with notably larger scar sizes recorded in July-T3 and August-T4, particularly in NR colonies (pairwise comparisons, $p < 0.05$), (Fig. 4A).

The photographic analysis further clarified the fate of the predated branches (Fig. 4B). At the initial time point (May-T0), all colonies, in both NR and R groups, showed clear evidence of *D. rugosa* predation, with 100% of coral colonies exhibiting at least one feeding scar.

By May-T1, over half of the scars on R colonies remained unrecovered, and *D. rugosa* snails were still grazing some branches. In contrast, 71.4% of scars on NR colonies stayed uncolonized by other organisms, while the remaining were overgrown by filamentous (among which *Polysiphonia* sp.) and turf algae. At June-T2, more than half of all scars were covered by algae in both NR and R colonies, while the remaining injuries showed no signs of recovery (Fig. 4B). By July-T3, extensive algal overgrowth persisted, with 80% of the scars colonized by algae. Notably, by August-T4, 20% of the R coral colonies were recolonized by *D. rugosa*, with individuals feeding along old scars and extending damage to adjacent healthy branches.

Regarding the long-term effects of the removal activities (Fig. 5 A), the culling effort, expressed as the number of diver-minutes, showed a general increasing trend from 2010 (220 ± 139 n diver x min) to 2019 (1,066 ± 519 n diver x min), followed by a sharp decrease during the COVID-19 years (371 ± 289 n diver x min in 2020, and

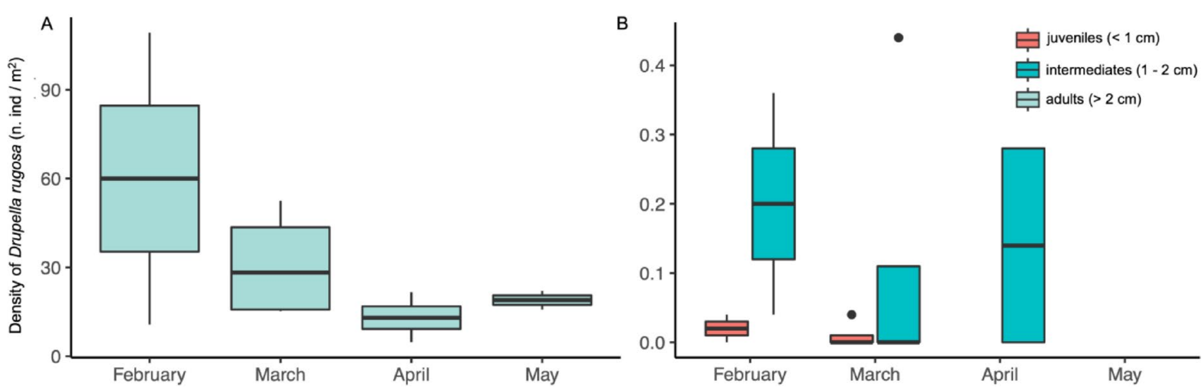

Fig. 2. Box plot displaying the density (expressed as number of individuals/m^2) of *Drupella rugosa* individuals in their adult (> 2 cm) (**A**), intermediate (from 1 to 2 cm), and juveniles (< 1 cm) (**B**) phases.

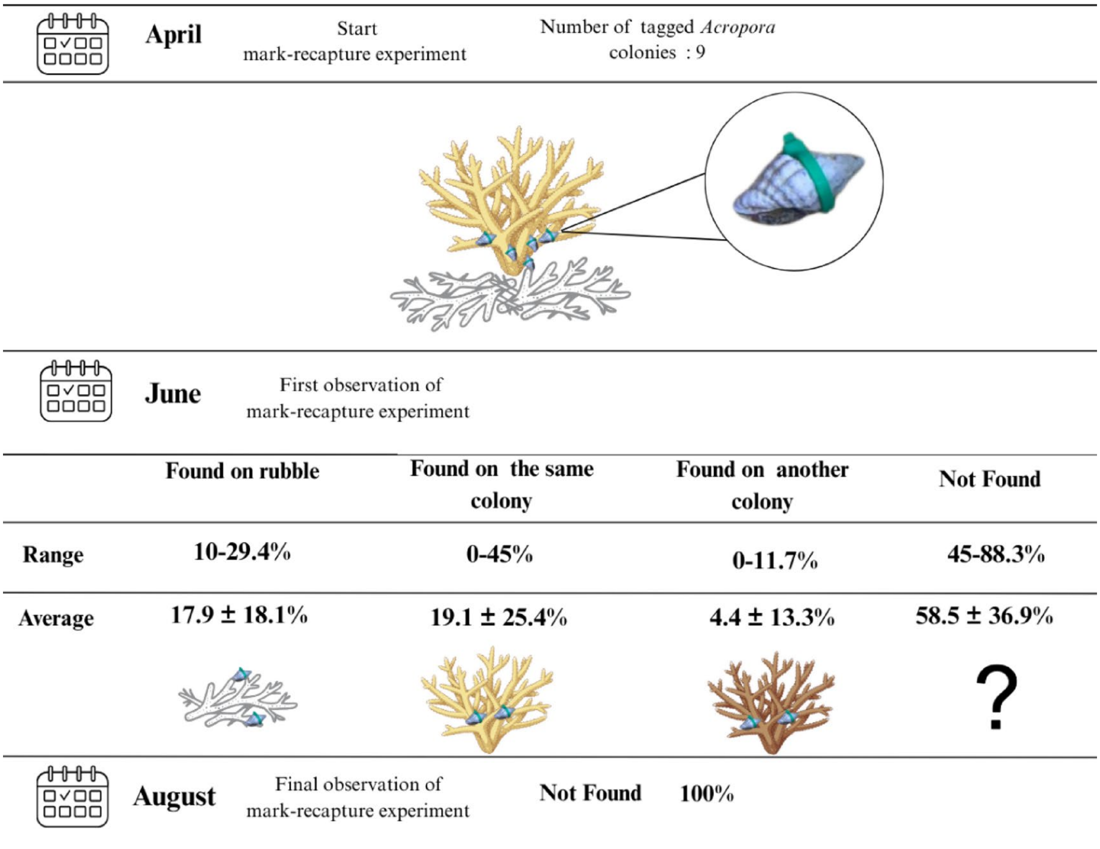

Fig. 3. Mark-recapture experiment. *Drupella rugosa* individuals were marked in April using cable ties and surveyed after two months the first time (June) and four months later (August). After the first monitoring activity in June, some individuals were found in rubble, others on the same marked colony, and some on different colonies (indicated in dark brown). The majority, nevertheless, were no longer visible (indicated by a question mark in the scheme). Marked snails were not observed during the August survey.

474 ± 343 n diver x min in 2021). From 2022 onward, the effort rose again (894 ± 343 n diver x min), stabilizing in 2023 (659 ± 208 n diver x min) and 2024 (680 ± 452 n diver x min).

In contrast, the number of *D. rugosa* removed per diver-minute did not follow this trend, instead showing an inverse relationship with effort (Fig. 3A). The Kruskal-Wallis test revealed significant differences in the standardized number of *D. rugosa* collected among years ($p < 0.001$), notably between 2017, and 2018–2019, which displayed the lowest values (1.7 ± 0.8, 2.3 ± 1.3, 2.5 ± 1.1 ind/(n diver x min), respectively) and the years 2014 (7.5 ± 4.0 ind/(n diver x min)), 2015 (6.4 ± 2.7 ind/(n diver x min)) and 2021 (7.0 ± 2.9 ind/(n diver x min)) (Dunn's post-hoc, $p < 0.05$). No significant difference was detected between the initial year (2010) and the last available data (2024) (Kruskal-Wallis, $p > 0.05$).

When analyzing each dive separately, a quite strong linear correlation emerged between the total number of *D. rugosa* collected and the culling effort per dive (Spearman rank correlation: $p < 0.001$, $\rho = 0.69$) (Fig. 3B).

Relationship between the damselfish *Stegastes lacrymatus* and predated *Acropora* colonies

The monitoring activities revealed distinct territorial behaviours of the damselfish *Stegastes lacrymatus* within their defended areas (Fig. 6).

Most individuals primarily grazed on their farmed filamentous algae (*Polysiphonia* sp.), while occasionally biting healthy coral branches, chasing away herbivore organisms, or rubbing their bodies against coral branches. The monitored damselfish fixed their algae both on coral patches previously bitten by the fish themselves and on areas damaged by *Drupella rugosa* predation, taking advantage of the exposed skeletal surfaces left by feeding scars. Their pronounced territoriality effectively prevented other herbivores from entering these areas, thereby promoting the persistence and expansion of their algal farms. Notably, no further *D. rugosa* predation was observed in coral colonies defended by *S. lacrymatus*.

Discussion

Overview

This study provides insights into outbreaks of muricid gastropods *Drupella rugosa* preying on *Acropora* coral gardens. The population dynamics of *D. rugosa* on Koh Tao reefs appear closely linked to the presence of *Acropora* rubbles (Fig. 7). Seasonal wave action frequently causes breakage of *Acropora* colonies[37], leading to the gradual

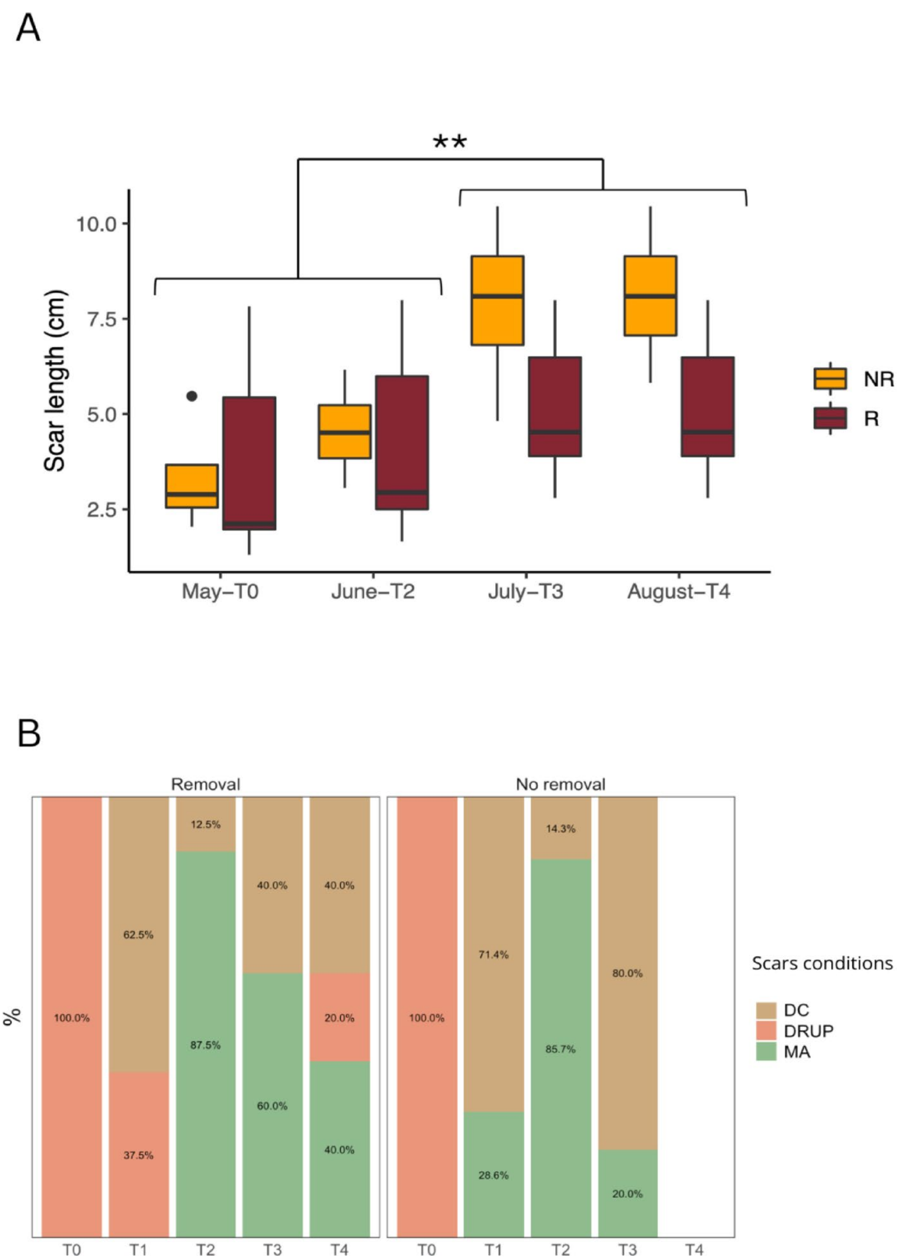

Fig. 4. Scar length (**A**). Box plot displaying the length of the scars left by *Drupella rugosa* in time in Removal (R, i.e., colonies from which gastropods were removed) and No Removal (NR, i.e., colonies from which gastropods were not removed) colonies. ** indicates significant differences ($p < 0.05$) highlighted by the pairwise comparisons. Fate of *Acropora* scars (**B**). The conditions of the predated branches have been classified as: *MA* covered with algae, *DRUP* presence of *Drupella*, *DC* recent scars (newly dead coral).

accumulation of coral rubble on the seabed. These layers of dead coral fragments create cryptic micro habitats likely used by *D. rugosa* for settlement and shelter[31,50,51] (Fig. 7, phases 1). In the absence of known predators in Koh Tao, *D. rugosa* may use this rubble 'subway' to move between coral colonies, potentially as a strategy to avoid wave action, exposure during low tides, or direct contact with coral nematocysts (Fig. 7, phases 2, 3).

The gastropods typically invade *Acropora* colonies from the basal region, crawling over dead branches—including old feeding scars— to reach the central parts of the colony. Here, they form dense aggregations (Fig. 7, phases 4, 5, 7), while avoiding branch tips that likely host higher densities of nematocysts and stronger toxicity[52]. Once the tissue at the centre of the coral colony is depleted, the snails cease feeding and migrate to adjacent colonies (Fig. 5, phase 7).

In the short- and mid-term, removal of *D. rugosa* and the reduction in predation pressure did not promote coral healing. Damaged branches were rapidly overgrown by turf algae or appropriated by algal-gardening damselfish (Fig. 7, phases 5, 6). The damselfishes (e.g., *Stegastes* spp.) establish algal lawns on bare coral skeletons[53,54], including the feeding scars left by *D. rugosa* (present work). These fishes aggressively defend their

		DFn	DFd	F	*p*
A					
	Treatment (T)	1	7	1.422	0.272
	Covariate	1	7	1.066	0.336
B					
	Treatment (T)	1	16	0.214	0.65
	Time (Ti)	1	16	1.037	0.324
	T x Ti	1	16	0.285	0.601
C					
	Treatment (T)	1	7	1.422	0.272
	Covariate	1	7	1.066	0.336
D					
	Treatment (T)	1	32	3.672	0.066
	Time (Ti)	3	32	3.949	**0.018**
	T x Ti	3	32	1.328	0.285

Table 2. Results of the: (A) one-way Analysis of Covariance (ANCOVA) to test differences in the increment of the scar length between treatments (R and NR colonies) in the short-term period (May-T0 vs. May-T1), using the initial scar length as covariate; (B) two-way repeated measures Analysis of Variances (RM-ANOVA) to test differences in the scar length in the short-term period (May-T0 and May-T1) between treatments; (C) one-way ANCOVA to test differences in the increment of the scar length between treatments in the middle-term period (May-T0 vs. August-T4), using the initial scar length as covariate; (D) two-way RM-ANOVA o test differences in the scar length in the middle-term period (May-T0, June-T2, July-T3 and August-T4) between treatments.

territories, driving away other coral visitors, including *Drupella*. The highest abundance of algae-colonized scars occurred in the "Removal" colonies, suggesting that culling *D. rugosa* may enhance the algal-farming activity of *Stegastes lacrymatus*. This effect could be reinforced by the scarcity of pomacentrid predators such as groupers (Fig. 7, phases 6, 8). Compared to other *Drupella* species, *D. rugosa* produces smaller egg capsules and fewer per clutch, but the relatively large size of the veligers increases survival and the likelihood of reaching metamorphosis[8,51]. Since no egg capsules were observed during the surveys, they were likely deposited within the intricate rubble matrix, where they remained concealed (Fig. 7, phases 4). Alternatively, eggs may have been laid in other microhabitats, such as shallow areas or artificial substrates (approximately 3,000 concrete cubic frames have been deployed around Koh Tao[55].

Why culling of *Drupella rugosa* was unsuccessful

Based on the analyzed data, poorly planned culling does not represent an effective strategy for controlling outbreaks of native invasive gastropods of the genus *Drupella*. Since the 1990 s, extensive corallivory of *D. rugosa* in Koh Tao[24,31] has prompted a series of uncoordinated removal campaigns, resulting in the culling of almost 300,000 specimens between 2010 and 2024. Within the permanent plots, though, the density of *D. rugosa* remained around 60 individuals/m^2, suggesting that approximately 3 million adults could inhabit a single bay of about 500 m x 100 m.

Most culled snails belonged to the largest size class (adult, > 2 cm), while juveniles (< 1 cm) likely occupied coral rubble, and thus remained inaccessible for collection[38] and undetected[56]. In addition, repeated removal of exposed individuals may have favoured the spread of snails exhibiting concealment behaviour, at least during daytime, as reported for other culled invasive species[57].

Although the high number of culled specimens provides an estimate of adult abundance, the actual population size of *D. rugosa* in Koh Tao, including juveniles, is likely much higher than that estimated, rendering the culling effort inadequate for outbreak control.

The culling effort also varied considerably among years, influenced by volunteer availability, the tourism halt during the COVID-19 pandemic (2020–2021), and logistical constraints linked to differing organizational goals. The absence of baseline data on natural *D. rugosa* population further complicated interpretation of temporal fluctuations in removal numbers.

Regarding environmental factors, the persistence of *D. rugosa* populations in Koh Tao may depend on high larval density supported by nutrient enrichment[32,37,58], lack of natural predators of early developmental stages, and elevated temperatures that enhance both larval dispersal[59], and adult fecundity[8]. Outbreaks of aquatic species with invasive traits (i.e., physiological plasticity, high fecundity, long-lived larvae[60,61]), are notoriously difficult to control[62]. Historically, pest management has often relied on large scale removal without strategic planning, often resulting in only temporary success, at the best[63,64]. This has been described as a "slippery slope towards management failure"[63].

Table 3 shows some examples of short- and long-term outcomes of culling across several invasive taxa from temperate and tropical regions. Manual removal of *D. rugosa* has been implemented in locations such as the Maldives, Ningaloo Reef, and Koh Tao, but its long-term effectiveness has never been assessed[8,65]. Most studies in Table 3 report temporary reduction in invader numbers within two years of initial culling, yet substantial and lasting declines have been observed only for the mollusc *Coralliophila erosa* from the Florida Keys[66]. In that case,

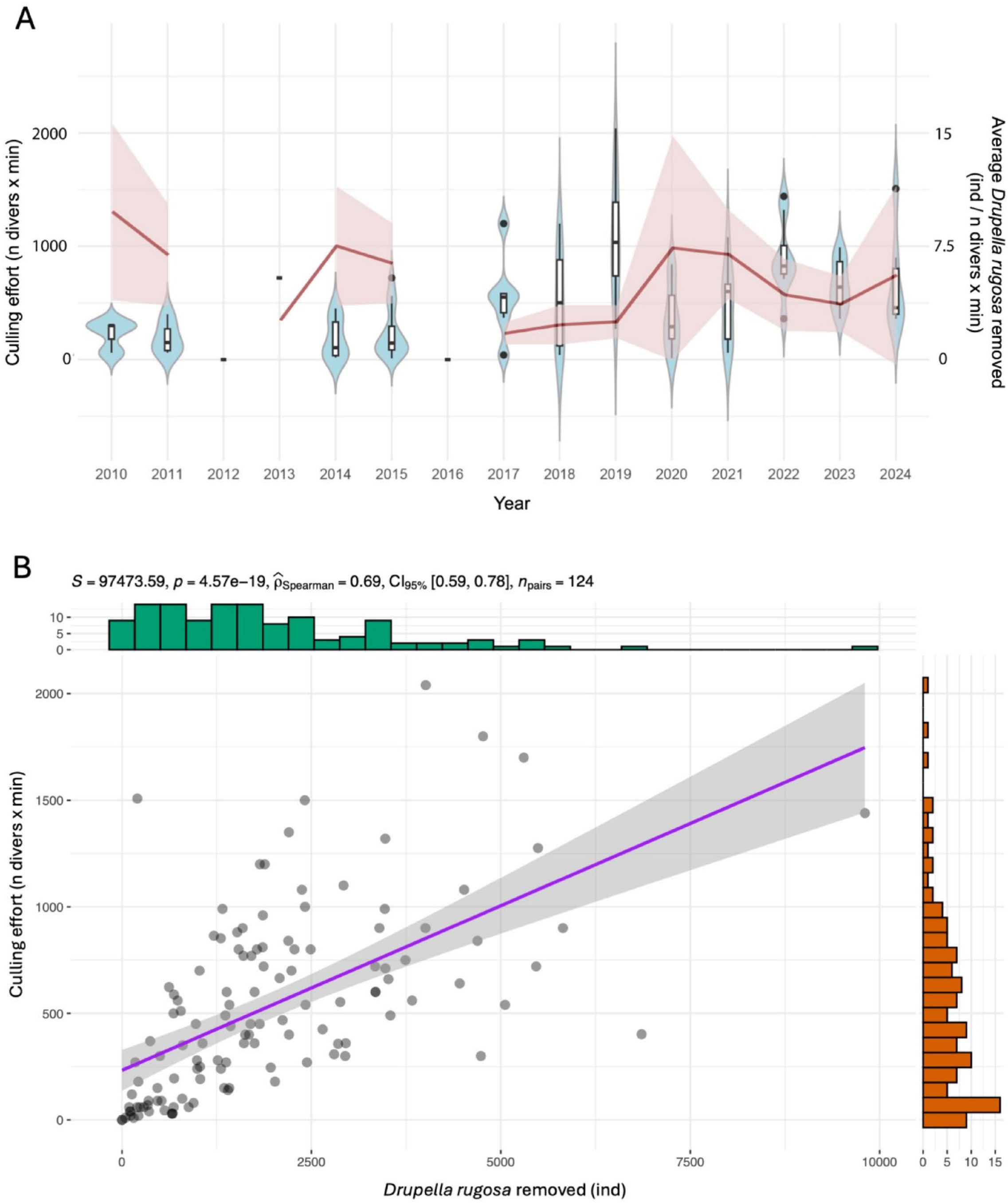

Fig. 5. Decadal effects of culling *Drupella*. **A** Violin plot representing the culling effort per year and line plot displaying the average number of *Drupella rugosa* removed each year with standard deviation (reddish area). **B** Spearman rank correlation between the cumulative number of *D. rugosa* removed in each dive and the collection effort; the bar plots represent the number of dives per point.

fewer than 500 gastropods were removed in 1800 m^2, suggesting that the density of the muricid was quite low in the culled area. A reduction in mean snail size was also recorded, likely reflecting a shift in sex ratio.

The larger the invaded area and the greater the dispersal capacity of the invader, the more challenging effective population control becomes[67,68]. Despite major investment in culling *Acanthaster* spp. in Australia and globally, few cases have demonstrated lasting ecological benefits. In Japan, chronic infestations of *A. solaris* destroyed over 90% of coral cover across extensive fringing reefs, despite more than a decade of removal efforts[69]. Similarly, the removal of invasive lionfish has shown limited success, as culled populations quickly adapted to evade human hunters, complicating further control[57].

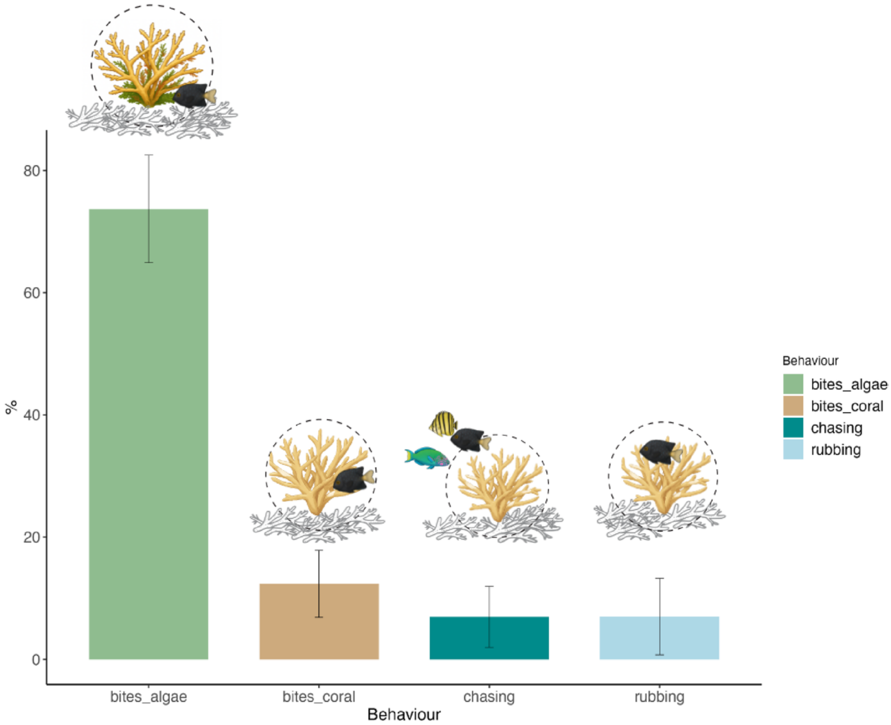

Fig. 6. Behavioural frequencies (%) of *Stegastes lacrymatus*. The most frequent activity was algal biting, followed by coral biting associated with algal garden maintenance, as well as rubbing against coral branches for self-cleaning, and chasing of intruding fishes and gastropods as a territorial defence behaviour. Error bars represent standard deviation.

Biological control methods, such as introducing predators or pathogens, or using biocides[45,70–73], are largely ineffective and pose significant risks to non-target organisms[34]. Therefore, such approaches should be avoided for *Drupella* management.

Future directions for the management of *Drupella rugosa* outbreaks in the Koh Tao island

Before implementing any management strategy, priority should be given to understanding the distribution and biology of *D. rugosa* across the *Acropora* gardens surrounding Koh Tao, with particular focus on its early developmental stages. Key processes influencing larval supply, metamorphosis, and post-settlement mortality must be thoroughly examined[80]. These investigations should be complemented by phytoplankton sampling and measurements of physical and nutrient parameters to better assess how abiotic factors and food availability influence veliger dynamics. A year-long monitoring program of *D. rugosa* population dynamics would help quantify true population density and identify temporal fluctuations in abundance and size structure. Further studies on gametogenesis would be valuable to determine the timing of egg deposition and improve understanding of larval dispersion development and dispersal. Conducting night dives could also reveal critical information on diel activity patterns, offering a more complete perspective on the ecological behaviour and population dynamics of this species.

As a native-invasive species, the recurrent population booms of *D. rugosa* in Koh Tao likely reflect shifts in reef ecosystem dynamics. Although long-term environmental data for the area are lacking, the cumulative impacts of urban expansion, overfishing, marine traffic, and intensive tourism activities have plausibly caused significant deterioration of reef water quality and to ecological imbalance[37,81], thereby facilitating *D. rugosa* proliferation. In this context, extensive involvement of all local stakeholders is indispensable to mitigate anthropogenic pressures and improve overall water quality. Considering the aggregation behaviour of *D. rugosa*, which is stimulated by chemical cues released by conspecifics and damaged corals[23], the development of attracting devices may represent an innovative control strategy[8]. Such devices could promote gastropod aggregation and thereby facilitate removal actions.

Another crucial step will be to investigate the distribution and dynamics of *Acropora* spp. The declines of *Acropora* gardens[37] may have resulted in gastropod clustering in the few areas where *Acropora* colonies persist. Further research should aim to: (1) determine the level of predation that can be compensated by the coral's natural regeneration rate, (2) clarify the role of rubble in facilitating gastropods spread, and (3) design coral restoration strategies that use utilizes natural rubble, rather than artificial substrates, to promote coral settlement and growth while limiting *D. rugosa* mobility within the rubble network. Finally, assessing the resilience of predated *Acropora* colonies will be crucial, particularly by testing fecundity of branch tips, the only portions that typically escape predation. Once this baseline is established, a coordinated approach among communities in Koh Tao and other reef systems worldwide could facilitate the exchange of knowledge on the dynamics of

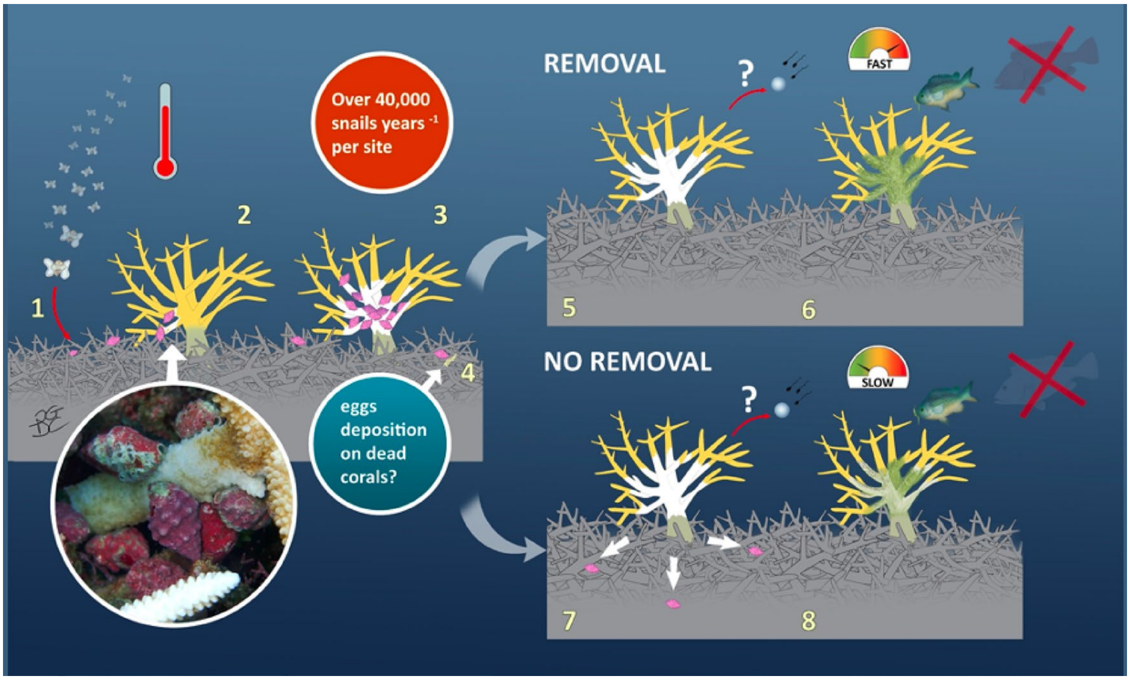

Fig. 7. Dynamics of *Drupella rugosa* in Koh Tao. Larval production and survival are likely enhanced by increased nutrients and water warming (1). Juveniles and adults likely move from rubble to *Acropora* spp. (2) to feed on live coral tissue (3). *D. rugosa* likely returns to rubble to reproduce (4) or to move towards other corals (arrows). The gastropods devour all the colony except the branch tips (5, 7), whose reproductive biology is unknown. Neither the coral colonies from which snails were removed, nor those left untouched showed signs of recovery; instead, both were colonized by turf algae or algal-farming damselfish (6, 8). In contrast, damselfish colonization—potentially facilitated by the depletion of pomacentrid predators—occurred more rapidly in the Removal colonies.

invasive corallivorous gastropods. Such collaboration would strengthen the potential to secure funding from diverse sources by presenting policymakers with a robust and well-structured program of control measures. Artificial Intelligence (AI) could also be employed[82] to develop predictive models capable of forecasting using both existing and future datasets.

Several management strategies have been implemented to prevent and control invasive alien species (IAS) in European waters[83]. This approach could serve as a useful framework for designing an ad hoc program targeting both native and non-native marine invaders.

Citizen science initiatives should be promoted to track outbreaks and support researchers in studying gastropod behaviour[84]. The commercial utilization of the invader[85] could also help raise public interest and generate financial resources to plan coordinated removal campaigns[83]. Current initiatives exploring the extraction of Tyrian blue pigment from this muricid gastropod (newheavenreefconservation.org), could be further developed and scaled up, provided that collection practices remain sustainable and scientifically monitored.

Conclusions

Data collected by the New Heaven Centre from 2010 to 2024 indicate that, although the removal initiatives were driven by good intentions, the culling of *Drupella rugosa* has not produced lasting ecological improvements. This outcome can be attributed to (i) limited understanding of the species' ecological traits and the biotic and abiotic factors that trigger outbreaks, (ii) unclear objectives, and lack of coordinated culling effort, (iii) the absence of a comprehensive prevention plan.

Currently, only about $1.2 billion per year is allocated to ocean protection[81], with most projects prioritizing restoration efforts over a deeper understanding of biodiversity and ecosystem processes. Therefore, we emphasize the importance of continuing to advance knowledge on phenology and behaviour of marine species, as well as on the environmental conditions influencing their populations, prior implementing any management strategy.

Ultimately, the long-term success in managing *D. rugosa* should be grounded in well-structured international guidelines that are carefully refined and adapted to local contexts. The numerous conservation initiatives in Koh Tao should align with broader programs to enhance visibility among scientists and policymakers, increase the likelihood of securing funding, and strengthen the potential for implementing effective, evidence-based control campaigns.

Authors, locality and threaten habitat	Invasive taxa	Methods	Shot-term effects (< 2 years)	Long-term effects	Side effects/difficulties
[65] Australia Coral reef	*Drupella cornus* (Röding, 1798) Gastropoda Native	Repeated manual removal activities in two 25 m x 25 m plots conducted within 35 weeks	No changes in live coral cover. The repeated removal resulted in a reduction in snail number within the plots; no significant recolonization from the extern. Reduction in snail size more evident in removal plots.	-	High effort, shift in the snail size classes, no evidence of long-term success
[8] Indo-Pacific (e.g., Ningaloo, Japan) Coral reef	*Drupella* spp. Gastropoda Native	Manual removal, biocontrol	Manual removal most direct effective short-term method	Limited information; removal helpful locally but not strategic population control	Research fragmented; manual removal extremely laborious; not widely documented
[74] Caribbean Coral reef	*Coralliophila erosa* (Röding, 1798) Gastropoda Native	After manual removal of the snails, scars on the coral colonies were tagged and photographed to verify and quantify coral tissue loss	Removal (at small scale) reduced snail incidence by an average of 81% during the two-month experiment.	-	The experiment utilized a small set of replicates aimed at evaluating the short-term impact of snail removal on coral health
[66] Florida Keys, USA Coral reef	*Coralliophila erosa* (Röding, 1798) Gastropoda Native	Three manual removal activities within 8 months, BACI (Before-After-Control-Impact) design to assess the effectiveness of removing corallivorous snails from 12 plots of 150 m^2. Five follow-up surveys were conducted over the next 19 months.	Corallivorous snail removal effectively and significantly reduced both snail abundance and the prevalence of scars over the 19 months following the interventions	The time required for snail recolonization (time to return to baseline conditions) was estimated to range from 1 to 6 years, with an average of approximately 4 years	At the final survey, reduction in size was observed; males 2–3× higher proportion than females. Probable shift in sex ratio, as larger snails are known to be female in this protandrous species.
[33]Australia Coral reef	*Acanthaster planci* (Linnaeus, 1758) Asteroidea Native	Manual collection followed by transfer to land or lethal injections with sodium bisulphate or bile salts	A few evidence of effectiveness of culling programs	Culling efforts failed due to inadequate control and prevention programs targeting water quality and fishery restrictions	Low feasibility of the methods, difficult in extracting the starfish from the reef, limited detectability of smaller individuals, the starfish suffer a slow death, culling is costly and it requires a huge effort
[70] Australia Coral reef	*Acanthaster planci* (Linnaeus, 1758) Asteroidea Native	Diver use of a bile salt solution injected in the stars (aquaria and field-based tests; the latter conducted on 50 starfish)	All *A. planci* injected with bile salts and sodium bisulphate) died within 24 h of being injected. By day 4 there were only left over of *A. planci* were small piles of spines and skeletal elements. The rapid decomposition of sea stars injected with bile salts, is likely due to free-living marine bacteria	–	No negative effects at experimental scale. No data about large-scale culling (possible negative effects on scavengers feeding on the starfish rests and high biomass of dead starfish)
[67] Australia Coral reef	*Acanthaster planci* (Linnaeus, 1758) Asteroidea Native	Diver manual removal via injection (vinegar, bile salts) or hand collections and disposal on shore; improvement of water quality	Hard coral cover improved by ~ 1–3% at local sites	Repeated interventions led to improve coral cover; however, sustaining long-term benefits would require ongoing culling efforts, albeit at a reduced frequency compared to initial activities	Highly labour-intensive; variation by sites; only local scale feasible; water quality enhancement was not enough to reduce larval supply
[72,73], Norway Kelp forests	*Strongylocentrotus droebachiensis* (O.F. Müller, 1776) Echinoidea Native	Underwater use of quicklime (CaO)	High sea urchin mortality and kelp recovery within a year	Harvesting and predation by crabs facilitated the control of the sea urchins and the recovery of the forests	Although there were no significant effects of CaO on other taxa, the treatment proved ineffective in areas where sea urchins managed to hide and escape exposure
[75] Tasmania Kelp forests	*Centrostephanus rodgersii* (A. Agassiz, 1864) Echinoidea Alien	Underwater extermination by crushing the sea urchin test	Highly effective in significantly reducing sea urchin density for at least 12 months	A report of 2018 ([76]) stated that the population of the sea urchin was increasing	High costs and logistical difficulties hinder the implementation of the program on a large scale
[77] Tasmania Kelp forests	*Centrostephanus rodgersii (A. Agassiz, 1864)* Echinoidea Alien	Underwater culling from abalone fishermen by creating a hole of at least 10 mm diameter in the sea urchin test using an iron tool	Regrowth of seaweeds in barrens in the culled patches	A report of 2018[76] stated that the population of the sea urching was increasing	Culling urchins while fishing abalones does not reduce sea urchin densities at scales ≥ 10 m^2. Culling was preferentially performed in abalone sites and not in relation to sea urchin density. The duration of dives was also influenced by abalone's density. Fishermen were poorly motivated for culling sea urchins.
Continued					

Authors, locality and threaten habitat	Invasive taxa	Methods	Shot-term effects (< 2 years)	Long-term effects	Side effects/difficulties
[57] Bahamas Coral reef	*Pterois volitans* (Linnaeus, 1758); *Pterois miles* (Bennett, 1828) Fish Alien	SCUBA measures to assess lionfish wariness: (1) extent of concealment at first sighting; (2) tendency towards crepuscular activity; and (3) alert distance	Lionfish on culled reefs were less active and hide deeper within the reef during the day than lionfish on patches where no culling had occurred.	Lionfish on culled reefs also adopted an alert posture at a greater distance from divers than lionfish on unculled reefs.	Change in the fish behaviourdue to hunting pressure: fish flee from humans more readily in culled areas or change the areal or timing of their activities
[78] and[79] Caribbean Coral reef	*Pterois volitans* (Linnaeus, 1758); *Pterois miles* (Bennett, 1828) Fish Alien	Diver harvesting (spearing, traps), lionfish derbies	Removal reduces local lionfish density; some behavioural changes observed	To maintain control, ~ 27% adult removal monthly needed; sustained effort required	High effort; diver safety; behavioural shifts in fish (more wary); limited scalability

Table 3. Examples of short- and long-term outcomes of culling of tropical and temperate marine invasive species.

Data availability

Data available on request by contacting both the correspondent Author (c.dicamillo@staff.univpm.it) and the New Heaven Reef Conservation Program (conservation-team@newheavendiveschool.com).

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Author contributions
Di Camillo CG and Baruffaldi M contributed to the study conception and design. Baruffaldi M and Di Camillo CG wrote the first draft of the paper and provided figures. Baruffaldi M and Tonolini R performed samplings and collected data. Roveta C, Baruffaldi M, Pulido Mantas T analyzed data. All authors contributed to improve and revise the manuscript.

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Declarations

Competing interests
The authors declare no competing interests.

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