Occurrence, distribution, and linear progression of a coral-killing sponge Haliclona (Chalinula) nematifera on coral reefs in the Nusa Penida Marine Protected Area, Indonesia

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Occurrence, distribution, and linear progression of a coral-killing sponge *Haliclona (Chalinula) nematifera* on coral reefs in the Nusa Penida Marine Protected Area, Indonesia.

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Abstract

Coral reefs worldwide face increasing threats from climate change, overfishing, and other human pressures. These stressors are often associated with pollution and habitat degradation, which may facilitate biological invasions, including coral-killing sponges that can overgrow and kill live coral tissue, altering reef structure and function. This study investigates the occurrence and distribution of *Haliclona (Chalinula) nematifera* in the Nusa Penida Marine Protected Area (MPA), Indonesia, a tourism destination experiencing growing pressures from urbanization and nutrient pollution. Field surveys, photographic analysis, and linear progression monitoring were conducted across multiple reef sites to assess sponge occurrence frequency, coral host range, and linear progression rates on coral hosts. The sponge was recorded at six of the 12 surveyed sites, occurring primarily in the northern and eastern regions, with limited presence at one western site and complete absence from all surveyed southern sites. These occurrences were predominantly observed at reefs situated near developed coastlines and areas influenced by land-based inputs such as wastewater discharge, sediment runoff, and coastal construction. Targeted surveys and long-term monitoring consistently showed higher occurrence frequencies in the northern and eastern regions. *H. nematifera* was observed on 45 coral species belonging to 23 coral genera, as well as on dead coral, rock, sponges, corallimorphs, zoanthids, and artificial substrates, with no consistent depth-related pattern detected. Linear progression rates varied significantly, with the sponge proliferating fastest on *Echinopora* (1.15 ± 0.55 mm day^{-1}), approximately 1.8 times faster than on *Porites* (0.63 ± 0.44 mm day^{-1}). The capacity of *H. nematifera* to spread across diverse hosts and habitats signals a broader conservation concern, underscoring the importance of incorporating invasive species management into broader conservation strategies.

Keywords: *sponge–coral interactions; host susceptibility; reef resilience; coral reef degradation; invasive sponge; Southeast Asia.*

Highlights:

- *Haliclona (Chalinula) nematifera* recorded at half of the studied sites in Nusa Penida MPA, Bali, Indonesia.
- Sponge occurrence was highest at northern and eastern sites exposed to greater coastal development
- Species colonized 23 coral genera with no consistent pattern in host use or depth distribution

- Linear progression rate on *Echinopora* was 1.8× faster than on *Porites*.

1. Introduction

Coral reefs occupy only a small fraction of the seafloor yet sustain extraordinary biodiversity and provide critical ecosystem services (Burke et al., 2011; Costanza et al., 2014). Nearly one billion people live within 100 km of reefs and depend on them for food, income, and coastal protection (Burke et al., 2011), while their global economic contribution is estimated at US$ 482,428 km^{-2} annually (Spalding et al., 2017). Despite this importance, reefs are declining under climate pressures such as bleaching and acidification (Hoegh-Guldberg et al., 2007; Hughes et al., 2018), compounded by local stressors including nutrient enrichment, sedimentation, and overfishing (Bell et al., 2013; Vega Thurber et al., 2014). These stressors restructure benthic communities toward opportunistic taxa and reduce reef resilience, creating ecological space for invasive or fast-spreading organisms.

Sponges play important ecological roles on coral reefs, contributing to nutrient cycling, habitat complexity, benthic-pelagic coupling, and bioerosion processes (Wulff, 2006; Bell, 2008). However, some opportunistic and space-competing species can aggressively overgrow living corals, particularly under environmentally degraded conditions. Coral-killing sponges exemplify this interaction, competing directly with reef-building corals by overgrowing tissue, driving bioerosion, and altering the physical structure of reefs (Rützler, 2002; López-Victoria et al., 2006; Thinesh et al., 2020). Their success has been linked to degraded water quality, including nutrient enrichment, as well as thermal stress, both of which weaken coral physiological resistance and favor space-occupying, encrusting organisms such as coral-killing sponges that can overgrow and smother live coral tissue (Shi et al., 2012; Bell et al., 2013; Schönberg et al., 2017). Consumer pressure can also play a role. In the Caribbean, spongivory has been shown to regulate sponge assemblages, with reduced predation leading to the proliferation of opportunistic and chemically defended species (Loh & Pawlik, 2014).

Few specialist predators are known. Generalist spongivores such as angelfishes (*Pomacanthus* spp.), parrotfishes (*Scarus* spp.), puffers (*Arothron* spp.), and filefishes (*Cantherhines* spp.), as well as the hawksbill turtle (*Eretmochelys imbricata*), can contribute to sponge control where they remain abundant (Meylan, 1988; Pawlik, 2011). Although no direct evidence links these predators specifically to the control of coral-killing sponges, their broad dietary range suggests they may influence sponge–coral competitive dynamics. Declines in *Scarus* spp. abundance have been reported at monitored reef sites in Indonesia, decreasing from 13 to three individuals per transect between 2000 and 2006 (Habibi et al., 2007), reflecting broader changes in reef fish communities. Many demosponges reproduce via larvae, while some species also propagate through fragments that readily colonize new substrates (Maldonado, 2006), and dispersal can be accelerated through maritime traffic via hull fouling and ballast water (Carlton & Geller, 1993; Molnar et al., 2008; Geburzi & McCarthy, 2018). Consequently, in reef systems exposed to multiple local stressors and chronic human pressures, sponge outbreaks are increasingly reported, particularly in areas influenced by coastal development, ports, and urban runoff (Shi et al., 2012; Schönberg et al., 2017; Thinesh et al., 2017; Turicchia et al., 2018). These local disturbances may interact with global climate drivers, notably ocean warming and acidification, in ways that further weaken coral physiological conditions (Bell et al., 2013; Schönberg et al., 2017; Bell et al., 2018). Thermal anomalies and bleaching events reduce coral immune capacity and competitive ability, increasing susceptibility to overgrowth by opportunistic benthic organisms such as sponges (Bell et al., 2013; Schönberg et al., 2017; Thinesh et al., 2020). Rising seawater temperatures and altered carbonate chemistry can further enhance microbial activity and organic matter availability, conditions that favor sponge metabolism, growth, and competitive performance relative to reef-building corals (Carballo & Bell, 2017; Bell et al., 2018). Collectively, these interacting pressures are predicted to increase the likelihood of phase shifts from coral- to sponge-dominated reef states under future climate scenarios (Bell et al., 2013; Bell et al., 2018), with cascading effects on reef structural complexity, biodiversity, fish assemblages, and ecosystem services that support coastal fisheries and human livelihoods (Chaijaroen, 2022; Mortimer et al., 2023).

Coral-killing sponges comprise a diverse group of ecologically competitive taxa, including *Terpios hoshinota*, *Clathria* spp., and *Cliona* spp., that have been associated with coral overgrowth, tissue mortality, and reef degradation (Rützler & Muzik, 1993; Ashok et al., 2020; Chaves-Fonnegra & Zea, 2011; Yamashiro et al., 2023). Within this group, *Haliclona (Chalinula) nematifera* (de Laubenfels, 1954) (formerly reported as *Chalinula nematifera*; hereafter *H. nematifera*) exhibits several traits that may enhance its competitive performance on coral reefs, including rapid linear progression of approximately 50 mm month^{-1} on *Acropora* (Rossi et al., 2015). This rate falls within the range reported for *T. hoshinota*, which spans from about 19 mm month^{-1} on *Favites*, *Platygyra*, and *Acropora* (Thinesh et al., 2017) to seasonal peaks of approximately 66 mm month^{-1} during summer conditions in Okinawa (Aini et al., 2021). Evidence also suggests that *H. nematifera* may produce allelopathic compounds that contribute to coral tissue necrosis and skeletal erosion (Rossi et al., 2015; Elliott et al., 2016; Turicchia et al., 2018; Quang, 2020). In addition, it acts as a substrate generalist, colonizing both live and dead corals across a wide range of morphologies and genera (Ávila & Carballo, 2009; Rossi et al., 2015; Turicchia et al., 2018; Quang, 2020). First described from the central Pacific (de Laubenfels, 1954), the species has since been reported in Australia (Hooper, 2008), Indonesia (Rossi et al., 2015; Turicchia et al., 2018), Malaysia (Muhammad-Hisham & Azman, 2024), the Philippines (Tan et al., 2018), Vietnam (Quang, 2020), Japan (Reimer et al., 2022; Albelda et al., 2024), and Mexico (Ávila & Carballo, 2009). The sponge is distinguished by its purple pigmentation and symbiotic fungal filaments and has been observed from shallow reef flats to at least 40 m across its range (Turicchia et al., 2018; Quang, 2020; Albelda et al., 2024). Across its distribution it has been recorded on more than 20 coral genera, including massive, foliose, laminar, encrusting, and branching forms, yet no consistent host preference has been identified despite site-specific associations such as *Pavona* and *Pectinia* in Vietnam or *Pocillopora* in Mexico (Ávila & Carballo, 2009; Rossi et al., 2015; Turicchia et al., 2018; Quang, 2020). These regional associations may partly reflect differences in local coral community composition rather than intrinsic host specificity.

Within the Coral Triangle, where Indonesia hosts the highest global diversity of reef-building corals, the emergence of coral-killing and competitive sponges represents a growing concern for reef persistence (Veron et al., 2009; Hadi et al., 2020). Recent evidence from southern Bali Province underscores this risk: surveys at Nusa Dua reef documented active coral–sponge interactions involving two coral-killing sponges (*Mycale* sp., *Neopetrosia* sp.) and competitive encrusting sponges such as *Lamellodysidea herbacea*, all contributing to coral overgrowth and mortality in reefs subject to intense tourism and coastal use (Haryanti et al., 2024). Located immediately southeast of Bali, Nusa Penida Marine Protected Area (MPA) represents a comparable regional setting where exceptionally high conservation value coincides with rapidly increasing human activity (Yunitawati and Clifton, 2021). The MPA supports at least 296 species of scleractinian corals and diverse megafauna assemblages (Turak and DeVantier, 2013), yet has experienced substantial tourism-driven development, with more than 300 accommodations, 160 land-based enterprises, and 30 marine transport operators established between 2003 and 2018 (Sudipa et al., 2020), despite the island's limited land area of approximately 203 km^2 (BPS, 2022) and the protected area encompassing roughly 200 km^2 of surrounding waters (Yunitawati and Clifton, 2021). In light of documented sponge-driven coral mortality in nearby Bali and the escalating local pressures within the Nusa Penida MPA, the occurrence of *H. nematifera* in this MPA warrants targeted investigation, particularly given the absence of prior systematic data on its distribution, host range, and lateral expansion within the area.

To address this gap, the present study provides a formal assessment of *H. nematifera* in the Nusa Penida MPA. Specifically, it aims to (1) quantify the prevalence of *H. nematifera* across depth gradients using targeted field surveys, (2) document host range and interaction types with reef-building corals, and (3) evaluate linear progression rates of *H. nematifera* and patterns of sponge-coral interactions across coral genera. In addition, to place these observations within a broader temporal context, the study incorporates a secondary long-term benthic monitoring dataset to examine temporal variation in *H. nematifera* occurrence over a 14-month period. Taken collectively, these complementary datasets provide initial insight into the spatial and temporal patterns of *H. nematifera* within a high-use MPA of the Coral Triangle, offering an evidence base to support reef health assessments and management strategies in systems increasingly shaped by local and climate-driven stressors.

2. Materials and methods

2.1 Study sites and monitoring schedule

The study was conducted at 12 sites around the Nusa Penida MPA, which includes Nusa Penida, Nusa Lembongan, and Nusa Ceningan (Fig. 1). The waters around the Nusa Penida MPA are characterized by high energy with strong, predominantly unidirectional currents and seasonal upwelling driven by the Indonesian Throughflow (ITF) and the tidal cycle (Turak and Devantier, 2013; Varela et al., 2016; Wen et al., 2023). The ITF transports warm, lower salinity water from the Pacific Ocean to the Indian Ocean through the Lombok Strait, located east of Bali, where water depths exceed 1,000 meters in some areas. While the predominant flow moves from north to south, there is some limited water movement in the reverse direction, further contributing to the dynamic oceanographic conditions around the Nusa Penida MPA (Taniguchi et al., 2019). The area encompasses approximately 1,419 hectares of coral reefs and supports high coral diversity, with 296 species of scleractinian corals recorded (Darmawan and Wen, 2010).

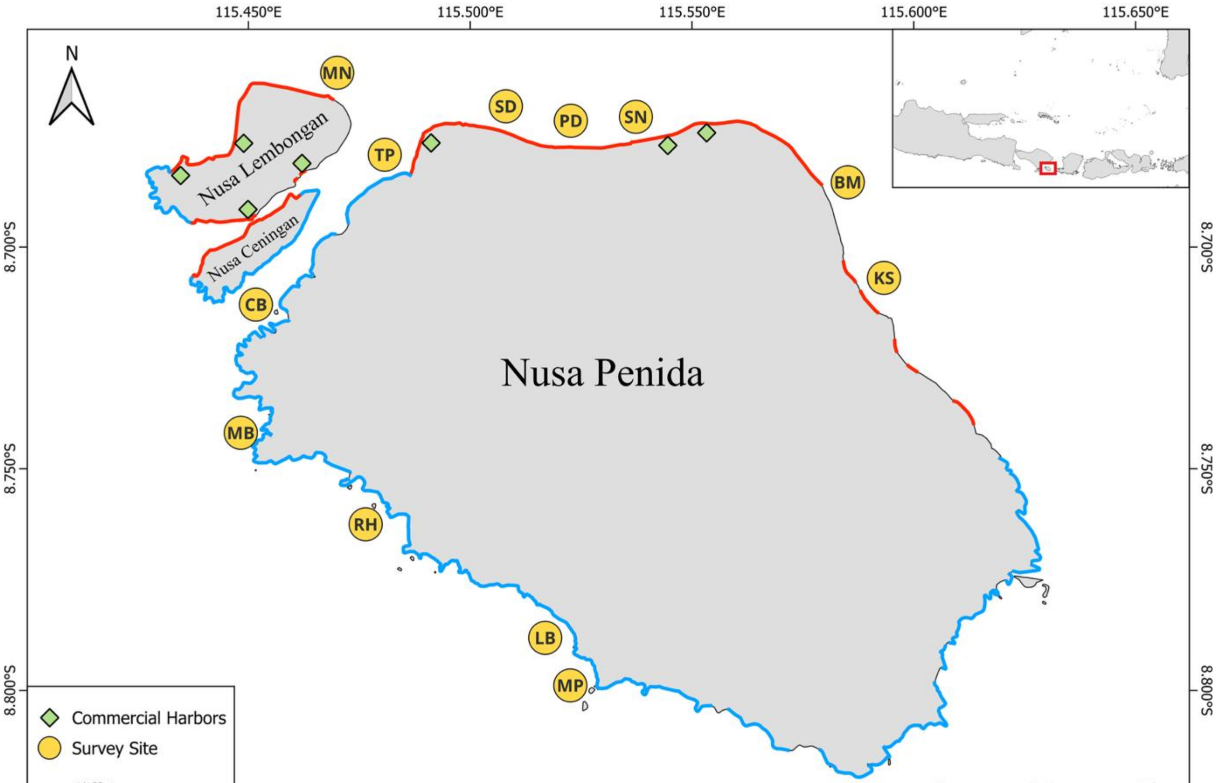

Figure 1. Map of the Nusa Penida Marine Protected Area, Indonesia, which includes three islands (Nusa Penida, Nusa Lembongan, Nusa Ceningan), showing survey sites, commercial harbors, cliff zones, and urbanized areas (delineated from satellite imagery in QGIS 3.43.3 as zones with high building density within 50 m of the coastline; Quiros et al., 2017; Marty-Gastaldi et al., 2025). Site codes: BM = Batumulapan, KS = Karang Sari, MN = Mangrove, PD = Ped, SD = SD Point (Sekolah Dasar Point), SN = Sental, TP = Toyapakeh, CB = Crystal Bay, MB = Manta Bay, RH = Rabbit Hole, LB = Labyrinth, MP = Manta Point.

The substratum across these sites primarily consists of reef slopes, ranging from coral-dominated areas with steep vertical relief to regions showing evidence of swell-driven physical disturbance, including fractured coral colonies and unstable coral rubble. High cliffs border the south and west coasts, while the north and east coasts, along with the northwest coastline of Nusa Lembongan, are more heavily influenced by tourism and infrastructure, including three commercial harbors in Nusa Penida and four in Nusa Lembongan (Fig. 1).

The data collection took place between April and July 2024 and aimed to quantify the occurrence frequency, host interaction patterns, and linear progression rate of *Haliclona (Chalinula) nematifera*. The sponge was identified in situ based on external morphology, including its purple coloration and characteristic white filamentous structures, consistent with previously published descriptions from the Indo-Pacific region (Rossi et al., 2015; Turicchia et al., 2018). All dives were conducted by two scientific SCUBA divers. For the occurrence frequency and host interaction assessment, 12 dives of approximately one hour each were conducted, with a single survey performed at each site to document sponge presence and host interactions across the MPA. Surveys were conducted at nominal depths of 5, 10, 15, 20, and 25 m; each depth category includes observations within a ±2.5 m range to account for natural depth variation during timed swims. In contrast, sponge linear progression rates were assessed during five dives conducted at the SD Point (Sekolah Dasar Point) site, selected for its high *H. nematifera* abundance, safe access, and the presence of multiple clearly defined sponge–coral interfaces suitable for marking and repeated measurements. Details of individual survey dives are provided in Appendix A.1.

2.2 Occurrence frequency of coral-killing sponge

The occurrence frequency of *H. nematifera* was assessed using photoquadrat surveys. During each dive, an eight-minute timed swim was conducted at each depth, covering approximately

120 m at a constant speed of 15 m min^{-1}. Along each transect, 37 photographs were taken at fixed intervals of approximately 13 s. An Olympus TG-6 camera was mounted 1 m above the substrate on a custom-built PVC frame measuring 0.5 m × 0.5 m (Appendix B.1), ensuring a constant image footprint. The resulting photographs were analyzed to determine the occurrence frequency of *H. nematifera*, defined as the percentage of photoquadrats containing at least one colony of the sponge. A secondary long-term benthic monitoring dataset collected between January 2023, and March 2024 was analysed separately to place observed patterns of *H. nematifera* occurrence within a broader temporal context. These surveys followed the same photoquadrat protocol described above, including eight-minute timed swims per depth and 37 images per transect using the same camera setup and frame dimensions. This monitoring was conducted as part of an ongoing reef assessment program, with four replicate surveys per site per year.

2.3 Host Interaction Assessment

Host interaction data were collected concurrently with the occurrence-frequency surveys during the same depth-stratified dives. A second diver conducted a standardized survey at the same depth and duration to actively locate and document all visible *H. nematifera* occurrences. For each occurrence of *H. nematifera*, the depth and interaction characteristics were recorded in situ. Each observation was photographed using an Olympus TG-6 camera, and overgrown substrates were subsequently identified post-dive, to species level where possible, based on photographic records. In cases where the sponge occurred on non-coral substrates, such as rock, dead coral, other key benthic taxa, or artificial structures, these were recorded accordingly. Each observation was categorized into one of three interaction types: (1) Peripheral, where the sponge grew along the coral edge (Fig. 6B, 6D); (2) Overgrowth, where it colonized live coral tissue (Fig. 6A, 6C); or (3) a combination of both (Fig. 5F), following established approaches for sponge–coral interactions (Turicchia et al., 2018).

2.4 Linear progression determination

To determine the linear progression rate of *H. nematifera*, colonies from three coral genera were tagged and monitored between April 17th and June 19th, 2024. The monitoring schedule followed tagging and remeasurement intervals used in a previous study of *H. nematifera* expansion (Rossi et al., 2015). Tagging was conducted on two occasions: on April 17th, nine colonies of *Pocillopora* spp. and nine colonies of *Echinopora* spp. were tagged, and on May 18th, seven colonies of *Porites* spp. and eight additional colonies of *Echinopora* spp. were tagged. Each colony was marked with a zip tie and a numbered tag placed at the interface between the sponge and the adjacent healthy coral tissue. All tagged colonies were located at SD Point within a depth range of 2.5–7 m, chosen for its accessibility and the high occurrence of *H. nematifera*-infected colonies that enabled consistent monitoring.

Colonies tagged on April 17th were remeasured on May 17th, May 29th, and June 19th, while those tagged on May 18th were remeasured on May 29th and June 19th. Linear progression was measured with calipers from the initial tagging points, and rates were calculated in millimeters per day (mm day^{-1}). Colonies that were broken or detached or that became fully overgrown by the sponge during the study were excluded from further analysis.

2.5 Statistical analysis

To address the study objectives, two complementary datasets were analysed using distinct statistical approaches. The primary survey dataset was used to quantify the occurrence frequency of *H. nematifera* and its interactions with coral hosts across sites and depth strata. These data were analysed descriptively to characterise patterns of infection across space and depth, and to document host-specific interactions observed during surveys.

The secondary long-term benthic monitoring dataset was used to formally test for spatial and temporal variation in *H. nematifera* prevalence using analysis of covariance (ANCOVA), followed by Tukey's honestly significant difference (HSD) post hoc tests to identify significantly different groups. Depth-related differences in occurrence frequency and differences in linear progression rates of *H. nematifera* were analysed using the Kruskal–Wallis rank-sum test, as the data did not meet parametric assumptions. Where significant effects were detected, Dunn's multiple comparison test with p-value adjustment was used for post hoc pairwise contrasts. All statistical analyses were conducted in R version 4.3.3 (R Core Team, 2024), and figures were produced using the ggplot2 package (Wickham, 2016). For comparison with the present study, linear progression rates reported in previous studies were converted from mm month^{-1} to mm day^{-1} assuming a 30-day month.

3. Results

3.1 Spatial distribution and occurrence frequency

Field surveys documented substantial colony-level infection of *Haliclona (Chalinula) nematifera* at several sites, with the largest aggregation recorded in Karang Sari (64 colonies; Fig. 2, Table 1). Other northern sites such as SD Point, Sental, and Ped also exhibited considerable numbers of infected colonies, while Mangrove in the west harbored 18 colonies. In contrast, southern sites and most western sites showed no occurrences of the sponge. *H. nematifera* was observed across a depth range of 2.5–26.5 m (Fig. 2, Table 1), with occurrence frequencies generally higher between 10 and 20 m, spanning multiple reef zones (Appendix C.1). Occurrence frequency differed among depth categories (Kruskal–Wallis test:

$\chi^2_4 = 10.08$, $p = 0.04$), but post-hoc pairwise comparisons did not reveal significant differences between individual depth categories after correction for multiple testing.

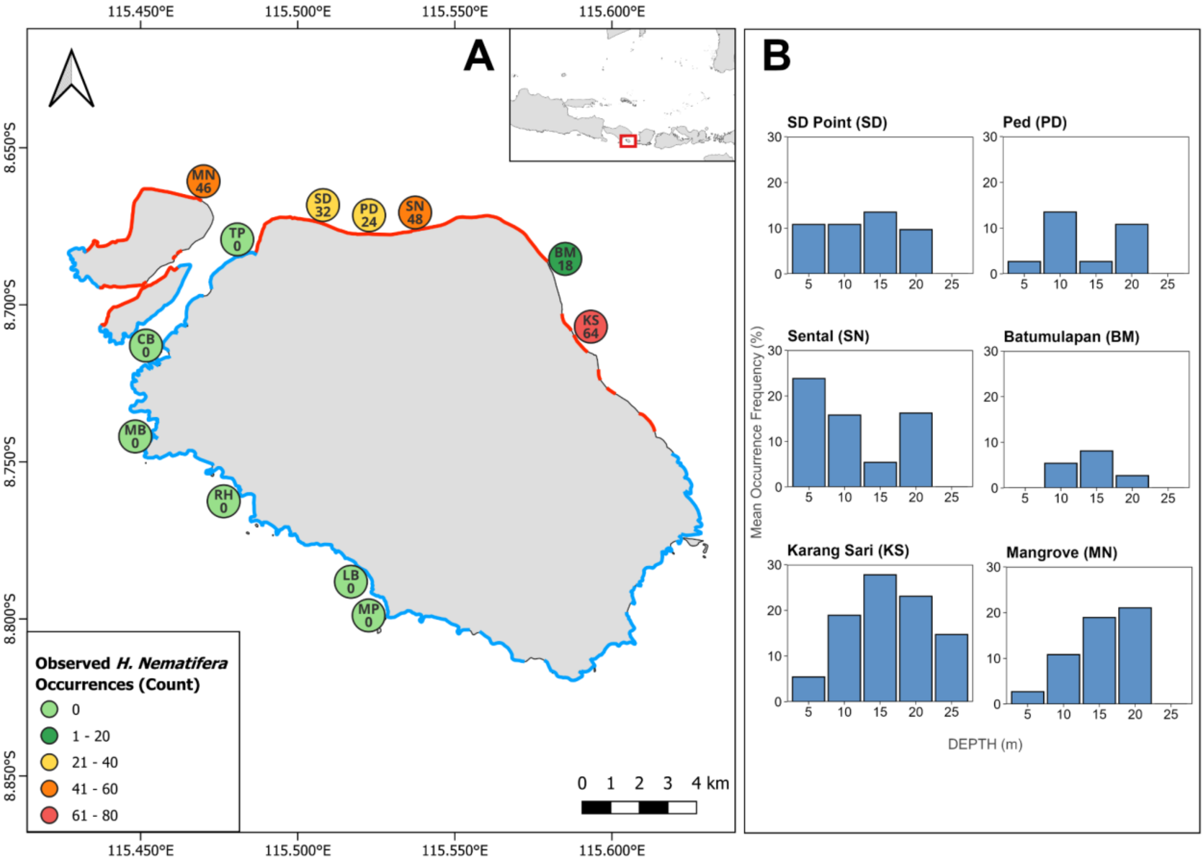

Figure 2. Spatial distribution of *Haliclona (Chalinula) nematifera* and depth-specific occurrence frequency in the Nusa Penida Marine Protected Area. (A) Map of the 12 surveyed sites showing the total number of observed *H. nematifera* occurrences at each site based on primary survey dives. (B) Mean occurrence frequency (%) by depth for the six sites where *H. nematifera* was detected based on long-term photoquadrat monitoring. Site codes: BM = Batumulapan, KS = Karang Sari, MN = Mangrove, PD = Ped, SD = SD Point (Sekolah Dasar Point), SN = Sental, TP = Toyapakeh, CB = Crystal Bay, MB = Manta Bay, RH = Rabbit Hole, LB = Labyrinth, MP = Manta Point.

This pattern is consistent with long-term photoquadrat surveys (January 2023–March 2024; Appendix C.2), which similarly identified Karang Sari in the east as a site with consistently high occurrence frequency. Across the combined dataset (targeted 2024 surveys together with the 2023–2024 long-term photoquadrat records), *H. nematifera* presence was uneven but recurrent, showing significant spatial variation (ANCOVA: $F = 16.45$, $p < 0.05$). Tukey's

HSD post-hoc test confirmed that Karang Sari had markedly higher occurrence frequency than Batumulapan, Mangrove, Ped, Sental, and SD Point (all $p < 0.001$). Full model outputs and Tukey HSD pairwise comparisons are presented in Appendix D.1–D.3.

Temporal patterns in the long-term dataset were less pronounced (Fig. 3). Site-specific ANCOVAs revealed no statistically significant changes in occurrence frequency at any monitored location over the 14-month period.

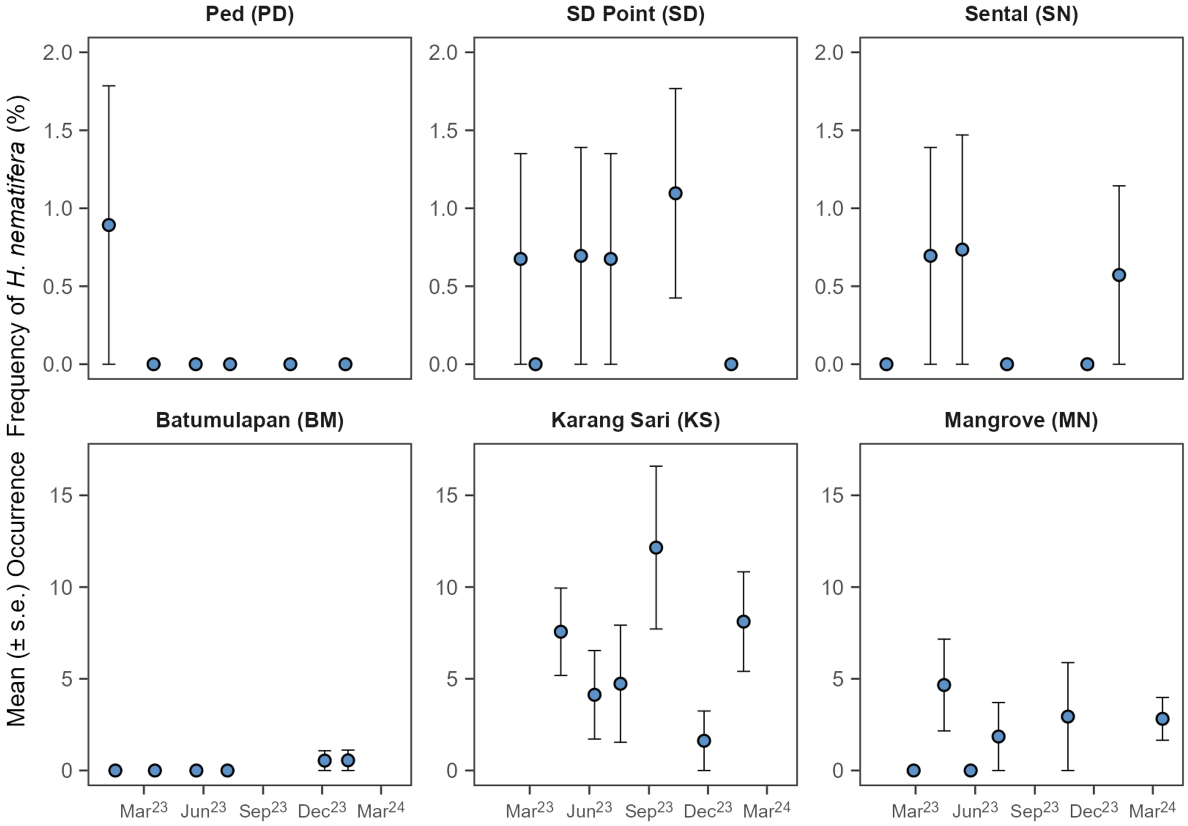

Figure 3. Mean ± s.e. occurrence frequency of *Haliclona (Chalinula) nematifera* (%) over time based on the long-term photoquadrat monitoring (January 2023-March 2024). Data are shown only for the six sites where the sponge was detected (out of 12 monitored).

3.2 Host interaction

Infection by *H. nematifera* exhibited a broad host range across coral taxa, morphologies, and study sites. (Fig. 4; Table 1; Appendix C.5). The sponge was found predominantly on hard corals, comprising 86.6% of all recorded sponge occurrences (201 out of 232; Fig. 4A). Among infected genera, *Acropora* was the most frequently affected (30.4%), followed by *Echinopora* and *Porites* (each 16.4%) (Fig. 4B). In total, *H. nematifera* was documented on 45 hard coral species representing 23 genera and a range of morphologies, including branching (44.8%), massive (21.1%), foliose (17.7%), laminar (7.2%), submassive (5.2%), and encrusting (4%). However, this broad host range was not consistent across sites. Karang Sari and Sental exhibited the greatest diversity of infected corals, with infections found in 15 coral genera each, whereas Batumulapan and Ped showed lower diversity, with infections found in five and seven genera, respectively.

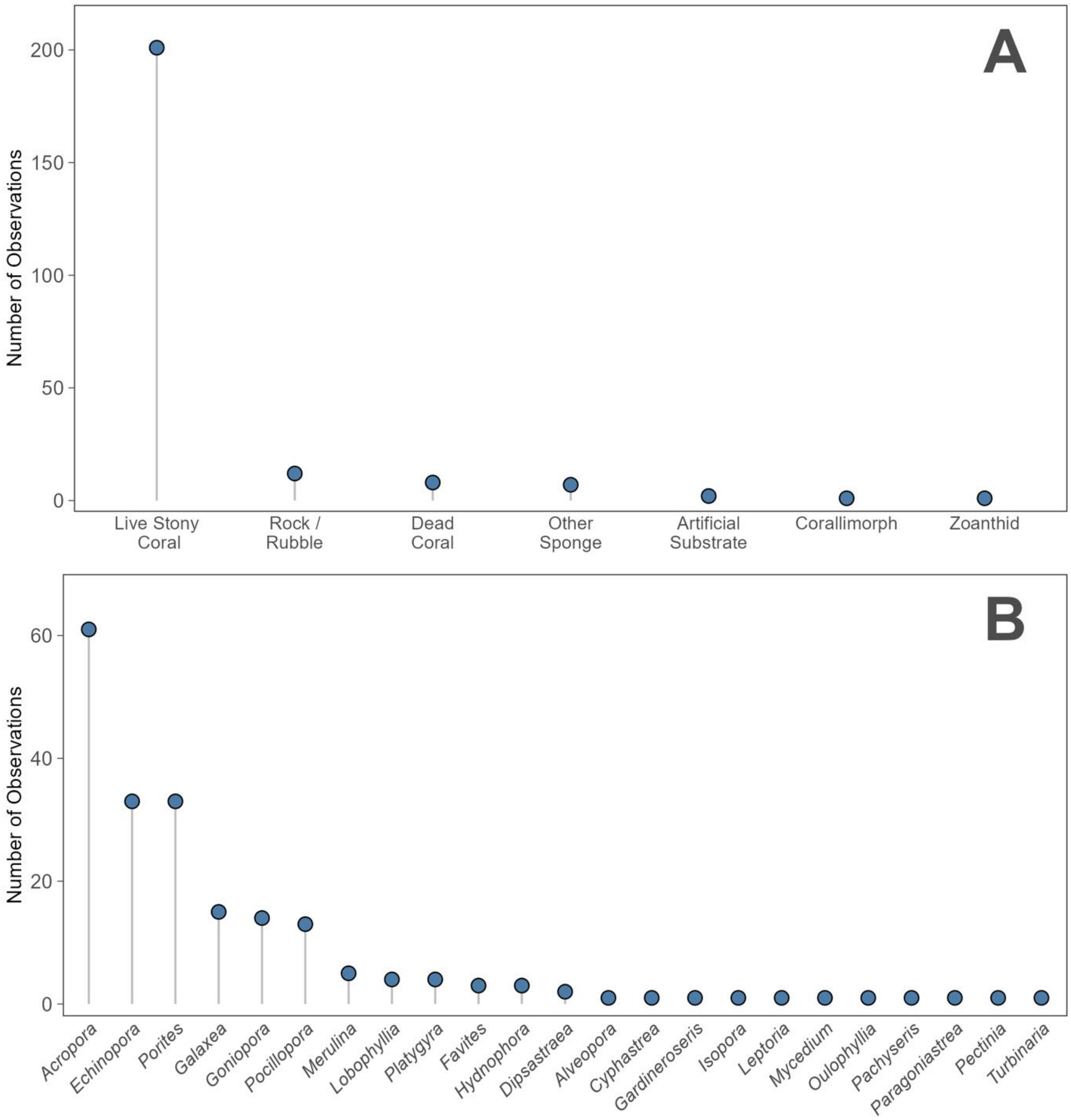

Figure 4. Distribution of *Haliclona (Chalinula) nematifera* observations across (A) substrate types (total observations = 232); (B) live stony coral genera (total observations = 201).

H. nematifera often spreads between adjacent coral colonies, irrespective of species (Fig. 5A, 5B), and overgrew other benthic organisms such as corallimorphs, zoanthids, and sponges (Fig. 5C–5E). It also colonized artificial materials such as ropes and steel rebars on coral restoration structures (Fig. 5F; Appendix C.4). In a few instances, the sponge was itself overgrown by other encrusting sponges (Fig. 5D) or corallimorphs, highlighting the complex and competitive nature of benthic space occupation in the reef environment.

Most interactions between *H. nematifera* and coral hosts involved a combination of peripheral contact along colony margins with concurrent overgrowth of live tissue (74.6%; Table 1; Fig. 6A–6D), whereas strictly peripheral contact and strictly overgrowth were less frequent (20.9% and 4.5%, respectively). The sponge sometimes extended filamentous projections that bridged across to nearby substrates (Fig. 6E). Colonization typically began on compromised coral tissue, particularly areas already affected by turf algal overgrowth, invertebrate competition, or bleaching. Following coral death, parts of the sponge frequently died, while other portions continued to spread (Fig. 6F; Fig. 7). A white necrotic band was commonly observed at the interface between living coral and advancing sponge tissue, indicating localized coral tissue death (Fig. 6A–6C).

Table 1. Substrate type colonized by *Haliclona (Chalinula) nematifera* across 12 surveyed sites in the Nusa Penida Marine Protected Area. Columns report, for each substrate type, the number of observed colonies affected, study site(s), depth range (m), host morphology, and interaction type. Counts represent the number of observed sponge–substrate interactions recorded in the survey dataset.

Substrate type	Number of observed interactions	Study site (no. of observed interactions)	Depth range (m)	Host morphology (no. of observed interactions)	Coral-sponge interaction (no. of observed interactions)
Acropora abrotanoides	1	MN (1)	14.8	Branching (1)	M (1)
Acropora anthocercis	1	MN (1)	15.6	Branching (1)	M (1)
Acropora austera	2	PD (1), SD (1)	5-7.9	Branching (2)	M (2)
Acropora bifaria	1	MN (1)	5.8	Branching (1)	M (1)
Acropora cerealis	2	MN (2)	12.4-17.4	Branching (2)	M (2)
Acropora divaricata	1	MN (1)	17.7	Branching (1)	M (1)
Acropora proximalis	27	BM (3), KS (12), MN (5), PD (1), SD (2), SN (4)	7-21	Branching (27)	M (27)
Acropora pulchra	22	KS (4), MN (11), SN (7)	5.3-15.0	Branching (22)	M (22)
Acropora yongei	4	KS (3), PD (1)	4.9-13.5	Branching (4)	M (4)
Alveopora spongiosa	1	KS (1)	22.5	Submassive (1)	M (1)
Cyphastrea serailia	1	KS (1)	10.6	Encrusting (1)	M (1)
Dipsastraea favus	1	SN (1)	11	Massive (1)	P (1)
Dipsastraea rotumana	1	SN (1)	12	Massive (1)	P (1)
Echinopora lamellosa	33	KS (11), MN (8), PD (3), SD (4), SN (7)	2.5-20.6	Foliose (33)	P (1), M (26), O (6)
Favites halicora	1	SN (1)	9	Submassive (1)	M (1)
Favites valenciennesi	2	KS (1), PD (1)	5.6-10.2	Massive (2)	P (2)
Galaxea fascicularis	15	BM (1), KS (3), MN (1), PD (5), SD (4), SN (1)	7.5-24.4	Massive (15)	P (13), M (2)
Gardineroseris planulata	1	SN (1)	5	Massive (1)	P (1)
Goniopora tenuitens	13	KS (2), PD (2), SD (7), SN (3)	9.5-26.5	Massive (13)	P (8), M (5)
Goniopora sp.	1	KS (1)	26.1	Submassive (1)	M (1)
Hydnophora microconos	1	MN (1)	20	Encrusting (1)	P (1)
Hydnophora rigida	2	BM (1), KS (1)	19.7-19.8	Branching (2)	M (2)
Isopora palifera	1	MN (1)	19.5	Encrusting (1)	M (1)
Leptoria phrygia	1	KS (1)	17.7	Massive (1)	P (1)
Lobophyllia hemprichii	1	SD (1)	20	Massive / Submassive (1)	P (1)

Lobophyllia agaricia	1	SN (1)	23.8	Massive (1)	M (1)
Lobophyllia recta	1	SN (1)	20.9	Massive (1)	M (1)
Lobophyllia robusta	1	SD (1)	16	Massive / Submassive (1)	P (1)
Merulina ampliata	4	KS (1), MN (1), PD (1), SN (1)	8.5-23.2	Laminar (2), Laminar / Foliose (1), Foliose (1)	M (4)
Merulina scabricula	1	SN (1)	11	Laminar (1)	M (1)
Mycedium robokaki	1	KS (1)	22	Laminar (1)	P (1)
Oulophyllia crispa	1	SN (1)	21	Massive (1)	M (1)
Pachyseris speciosa	1	KS (1)	5	Laminar (1)	M (1)
Paragoniastrea australensis	1	SD (1)	5	Massive / Submassive (1)	M (1)
Pectinia lactuca	1	SN (1)	20	Foliose (1)	P (1)
Platygyra crosslandi	2	KS (1), SD (1)	11.4-15.9	Massive (2)	P (2)
Platygyra contorta	1	SN (1)	24	Massive (1)	P (1)
Platygyra carnosus	1	SN (1)	15	Massive (1)	P (1)
Pocillopora eydouxi	2	PD (1), SD (1)	5	Branching (2)	M (2)
Pocillopora verrucosa	11	BM (3), KS (4), MN (1), SD (2), SN (1)	5-21	Branching (11)	P (2), M (8), O (1)
Porites attenuata	2	KS (1), PD (1)	5-10.6	Branching (2)	M (2)
Porites cylindrica	2	BM (1), PD (1)	5-12.5	Branching (2)	M (2)
Porites nigrescens	5	BM (1), PD (1)	5-20.2	Branching (5)	M (5)
Porites rus	24	KS (7), MN (8), SD (2), SN (7)	5.6-23.8	Branching (5), Encrusting (5), Laminar (9), Submassive (5)	P (3), M (19), O (2)
Turbinaria reniformis	1	SN (1)	10	Submassive (1)	M (1)
Rock / Rubble	10	BM (3), KS (2), MN (1), PD (2), SD (1), SN (1)	9.8-20.6	-	-
Dead coral	10	BM (1), KS (3), MN (1), PD (2), SD (3)	10.2-19.7	-	-
Other sponges	7	BM (1), KS (2), MN (1), SD (1), SN (2)	9.4-25.5	-	-
Artificial structure	2	SN (2)	8.5-13.5	-	-
Corallimorph	1	BM (1)	12.1	-	-
Zoanthid	1	KS (1)	11.5	-	-

Notes. Interaction types: P = peripheral contact without overtopping live tissue; O = overgrowth of live tissue; M = mixed (both peripheral contact and overgrowth on the same colony). Site codes: BM = Batumulapan, KS = Karang Sari, MN = Mangrove, PD = Ped, SD = SD Point (Sekolah Dasar Point), SN = Sental.

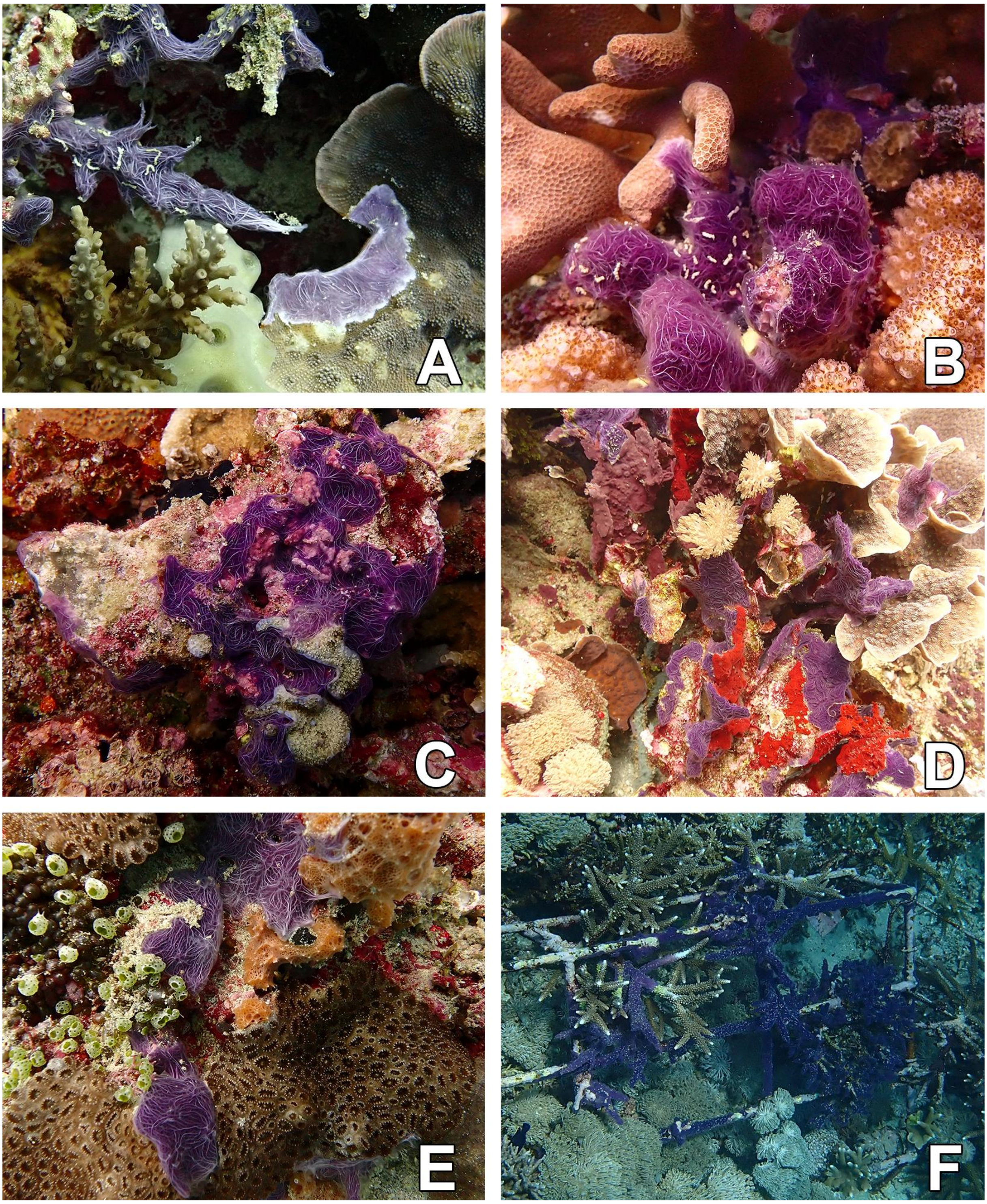

Figure 5. Interactions between *Haliclona (Chalinula) nematifera* and various substrates and organisms. (A, B) *H. nematifera* spreading from one coral colony to an immediately adjacent colony. (C) The sponge overgrowing crustose coralline algae and corallimorphs. (D) Another sponge species (red-colored) overgrowing *H. nematifera*. (E) The sponge overgrowing zoanthids and other sponge species. (F) *H. nematifera* colonizing artificial material at a coral restoration site.

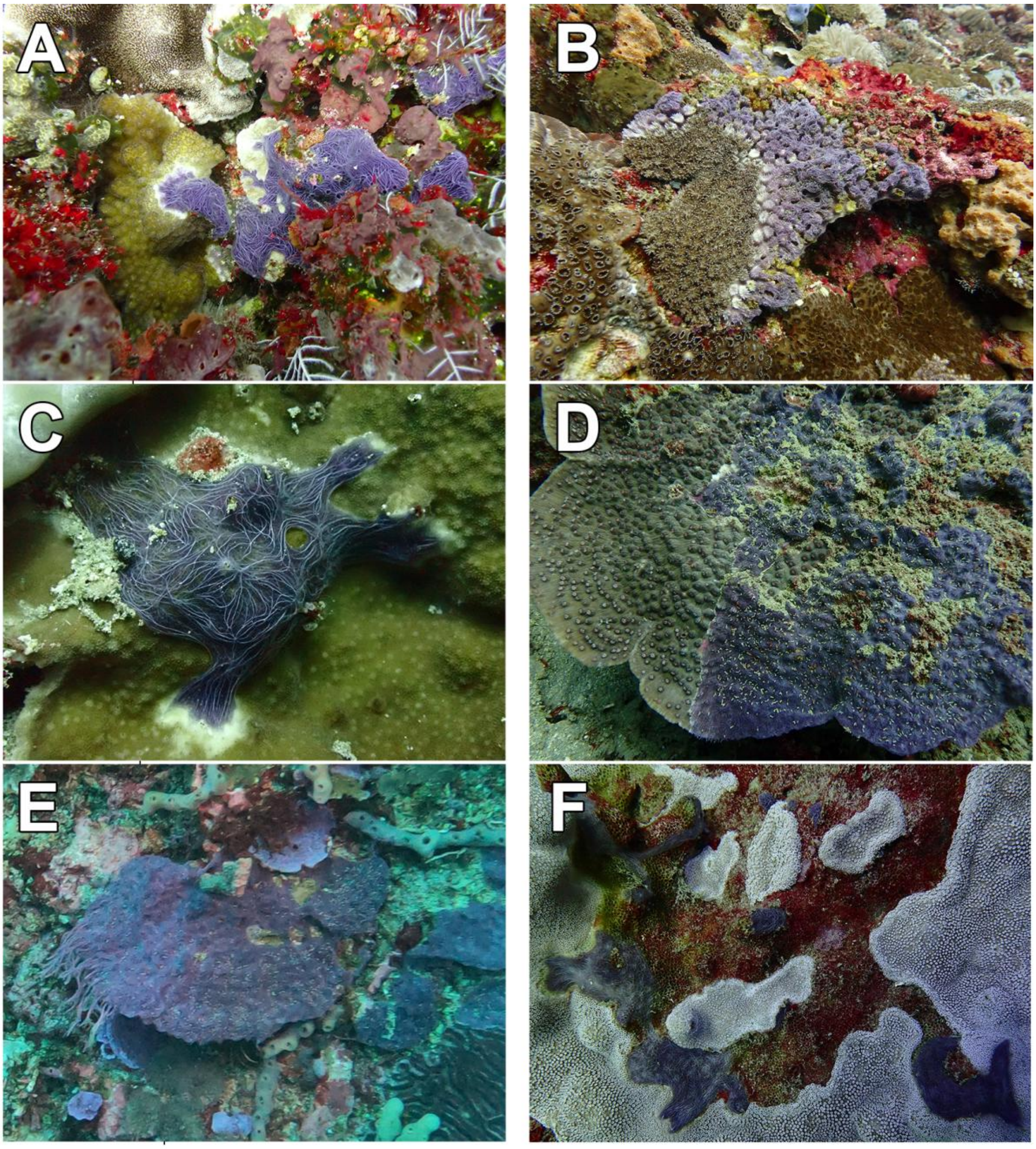

Figure 6. Behaviors and impacts of *Haliclona (Chalinula) nematifera* on coral hosts. (A, C) Coral necrosis in areas of direct contact with the sponge. (B, D) Peripheral contact between the sponge and its host. (C) Sponge overgrowth of living coral tissue. (E) Extension of sponge filaments. (F) Sponge die-off following host tissue mortality.

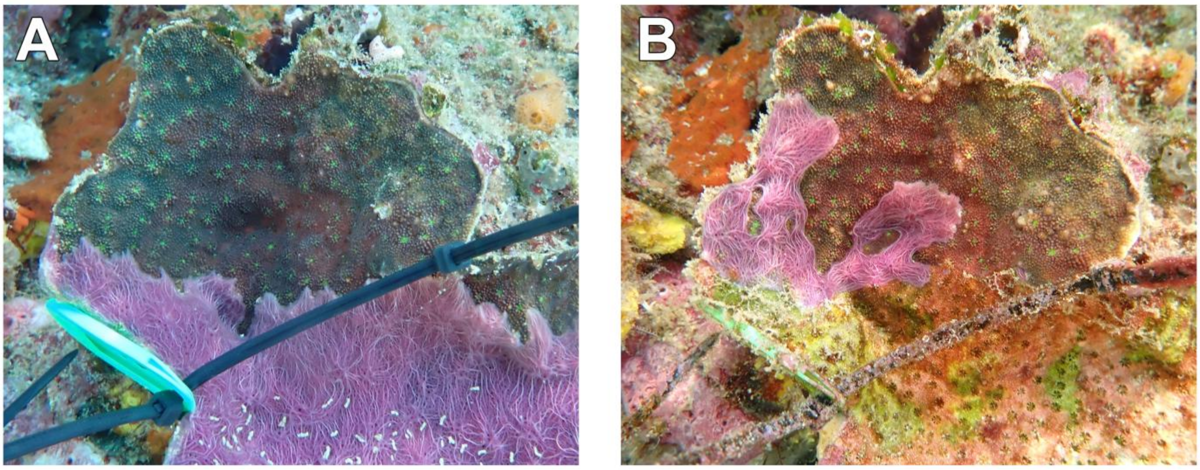

Figure 7. Temporal progression of *Haliclona (Chalinula) nematifera* overgrowth on a tagged coral colony. (A) Tagged *Echinopora* colony at day zero (17.04.2024). (B) The same colony 30 days later (17.05.2024), showing coral tissue mortality followed by sponge die-off.

3.3 Differences in sponge linear progression rates among coral genera

The linear progression rate of *H. nematifera* differed significantly among the three coral genera examined (Kruskal–Wallis; K = 9.32; DF = 2; p = 0.01; Fig. 8). The slowest expansion was observed on branching *Porites* spp., with a mean rate of 0.63 mm day^{-1} (± 0.44 SD). In contrast, growth was significantly faster on foliose *Echinopora* spp. (Dunn's multiple comparison; $p < 0.05$), averaging 1.15 mm day^{-1} (± 0.55 SD), approximately 1.8 times faster than on *Porites* spp. Expansion on *Pocillopora* spp. was intermediate, with a mean rate of 1.05 mm day^{-1} (± 0.54 SD). Individual expansion measurements are available in Appendix C.3; Dunn's post-hoc comparisons are reported in Appendix D.4.

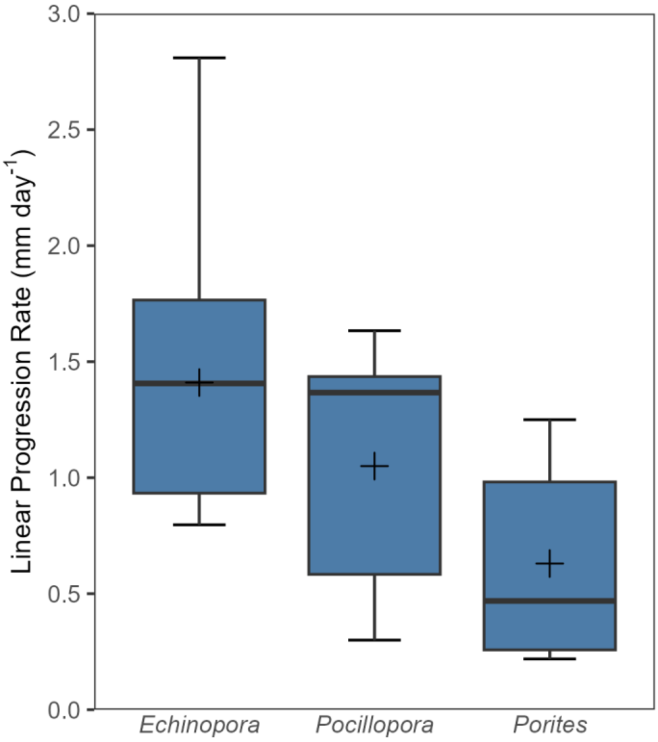

Figure 8. Linear progression rates of *Haliclona (Chalinula) nematifera* (mm day^{-1}) on three coral genera. The boxplots display the median (central line), the 25th and 75th percentiles (lower and upper edges of the box), and the full range of the data (whiskers). The cross indicates the mean.

4. Discussion

4.1. Spatial distribution and anthropogenic influence

The detection of *Haliclona (Chalinula) nematifera* at six of the twelve surveyed sites indicates an uneven distribution within the Nusa Penida MPA, with presence concentrated in the northern and eastern zones. These areas overlap with the island's most developed coastal stretches, where rapid tourism infrastructure growth has been associated with increased land-based inputs of sediment, untreated wastewater, and nutrients (Sudipa et al., 2020). In their assessment of coastal water quality in Nusa Penida, Sudipa et al. (2020) reported that free ammonia concentrations along these coasts ranged from 0.18 to 0.58 mg L^{-1}, with several sites exceeding Indonesia's seawater quality standards. Although turbidity reported in that study had decreased relative to earlier assessments, 2019 values remained moderately elevated (2.8–8.9 NTU), consistent with a persistent but localized influence of coastal development. Comparable patterns have been documented elsewhere, with other sponge outbreaks and coral disease occurring more frequently near disturbed coastlines (Oliver et al., 2018; Aeby et al., 2024). In Komodo National Park, Indonesia, Turicchia et al. (2018) also recorded higher *H. nematifera* occurrence near ports and tourist hubs, indicating that reefs exposed to chronic land-based pressures may be more susceptible to sponge colonization. Although oceanographic connectivity can facilitate the transport of larvae or sponge fragments among reefs (Elmhirst et al., 2009), both previous studies (Turicchia et al., 2018; Quang, 2020) and the present findings show no consistent depth-related pattern in sponge distribution, suggesting an association with land-based pressures rather than reef zonation alone.

The rapid expansion of tourism in the Nusa Penida MPA has likely altered adjacent coastal ecosystems. Land clearing and construction increase sediment runoff and pollutant discharge to nearby reefs (Sudipa et al., 2020), while wastewater management remains limited, with blackwater often treated in poorly maintained septic systems and graywater frequently released untreated (Septiariva et al., 2021). Because the island's porous limestone substrate facilitates rapid groundwater transport to the coast (Ariantana et al., 2023), these inputs can enrich nearshore reefs with nutrients. Such conditions may stimulate microbial proliferation and weaken coral resistance to overgrowth (Fiore et al., 2010; Pawlik et al., 2015), creating ecological opportunities for sponge expansion.

All southern and most western sites surveyed remained free of *H. nematifera*. These regions are characterized by steep limestone cliffs, limited coastal development, and strong oceanographic dynamics, including seasonal upwelling and flushing associated with the Indonesian Throughflow in the Lombok Strait, which varies with El Niño–Southern Oscillation (ENSO) and the Indian Ocean Dipole (IOD) (Sprintall et al., 2014; van Sebille et al., 2014). Such conditions reduce the accumulation of land-based nutrients and promote cooler water temperatures, both of which may enhance reef resilience (Bayraktarov et al., 2013; Fox et al., 2023) and limit the local retention of sponge propagules (Elmhirst et al., 2009). Consistent with studies of upwelling along the southern coast of Bali, the southern portion of Nusa Penida exposed to Indian Ocean forcing experiences recurrent cool-water intrusions, with temperatures often remaining below 28 °C during upwelling periods (Ningsih et al., 2013; Genda et al., 2022). Although absent from these cooler, high-flushing areas, *H. nematifera* persists across a broad thermal range elsewhere, including 18–30 °C in Mexico (Ávila and Carballo, 2009), suggesting that temperature alone does not limit its establishment. Instead, the spatial contrast observed here likely reflects the combined effects of reduced nutrient input, less stressed coral assemblages, and efficient hydrodynamic flushing. Protecting less impacted reefs may therefore be important, as these areas could function as natural buffers against sponge expansion within the MPA.

4.2. Host range, coral morphology, and linear progression dynamics

The broad host range observed in Nusa Penida may partly reflect the composition of local coral assemblages. Genera such as *Acropora* and *Echinopora* were among the most frequently infected, likely because they are also common components of reef communities in the Nusa Penida MPA (Gotama et al., 2025). Similar patterns have been reported elsewhere, where *H. nematifera* primarily colonized dominant coral genera, indicating that high host diversity does not necessarily imply strong selectivity but may instead reflect more frequent contact with abundant taxa (Ávila and Carballo, 2009; Rossi et al., 2015; Quang, 2020).

Host traits nevertheless appear to influence the linear progression rate of the sponge once contact is established. In this study, foliose *Echinopora* supported more rapid progression than branching *Porites*, which showed the slowest rates. A similar pattern was documented in Sulawesi, where *H. nematifera* expanded faster on *Acropora* than on corals with denser skeletons (Rossi et al., 2015). The relative resistance of *Porites* may be related to its compact skeletal architecture, which provides fewer micro-crevices for sponge attachment and may limit the ability of encrusting forms to infiltrate coral tissue (Schönberg and Ortiz, 2008; Chaves-Fonnegra and Zea, 2011). In addition, *Porites* produces mucus with documented antibacterial activity (Geffen and Rosenberg, 2005), similar to *Acropora palmata*, where mucus-associated microbial defenses can inhibit settlement by microbial and opportunistic colonizers (Ritchie, 2006). These mechanisms are consistent with broader findings showing that skeletal structure, tissue defenses, and microbial associations mediate resistance or susceptibility in sponge–coral interactions (Webster et al., 2004; López-Victoria et al., 2006; Chaves-Fonnegra and Zea, 2011; Loh and Pawlik, 2014).

The linear progression patterns observed across coral hosts indicate that *H. nematifera* does not expand uniformly across available substrates. Instead, variation among host taxa suggests that colony-specific characteristics influence how strongly lateral sponge spread is constrained or facilitated, resulting in distinct growth trajectories depending on the host encountered. Progression rates measured in this study were lower than those reported for *H. nematifera* on *Acropora* in Sulawesi (1.67 mm day^{-1}; Rossi et al., 2015), yet they fall within the range documented for other coral-killing sponges. For example, *Terpios hoshinota* exhibits baseline progression rates of 0.63 mm day^{-1} in the Indian Ocean (Thinesh et al., 2017) but can reach seasonal maxima of 2.20 mm day^{-1} under favorable conditions in Okinawa (Aini et al., 2021). This places *H. nematifera* among encrusting sponges capable of ecologically significant overgrowth, even when encountering substrates that slow its advance. Like *T. hoshinota*, *H. nematifera* has an encrusting morphology and lacks a calcareous skeleton, which may reduce energetic demands for calcification and enhance lateral spread (Elliott et al., 2016). These traits are particularly concerning for reef systems in Nusa Penida dominated by branching and foliose corals (Gotama et al., 2025). Because such morphologies contribute disproportionately to three-dimensional reef structure and habitat heterogeneity, faster sponge expansion on these taxa may accelerate the loss of structural complexity and promote localized reef flattening, with cascading consequences for associated reef biodiversity (McManus and Polsenberg, 2004). Given their structural fragility and susceptibility to bleaching, continued expansion of *H. nematifera* could further compromise reef architecture and ecological function within the MPA. Overall, these findings suggest that while host availability influences which corals are encountered, differences in colony morphology shape subsequent progression dynamics once contact occurs.

4.3. Insight into colonization mechanisms and ecosystem consequences

The broad substrate range observed in *H. nematifera* suggests an opportunistic colonization strategy rather than strict substrate specificity. This generalism may arise through at least two non-exclusive mechanisms. First, asexual lateral expansion may allow the sponge to exploit shared substrate traits such as damaged tissue, weakened structural or chemical defenses, or microbial biofilms that facilitate attachment and spread regardless of host identity (López-Victoria et al., 2006; González-Murcia et al., 2023). Second, larval settlement via sexual reproduction may be guided by non-specific microbial or chemical cues, as sponge larvae are known to respond to biofilms and crustose coralline algae (CCA) on reef surfaces (Whalan et al., 2012; Whalan & Webster, 2014). In this study, many infected rubble, rock, and artificial structures were covered by CCA, and the sponge often spread from these substrates to adjacent live corals, suggesting that such surfaces may act as footholds during colonization. In addition, *H. nematifera* was observed extending fine filaments across coral colony surfaces (Fig. 5A, 5B; Fig. 6A), where they projected outward and contacted nearby colonies or surfaces, potentially bridging gaps and enabling spread in areas of patchy or degraded coral cover (López-Victoria et al., 2006; Rossi et al., 2015; Reimer et al., 2022).

The ability of *H. nematifera* to settle on non-coral substrates and subsequently transition to living coral may increase its persistence in reef habitats experiencing declines in live coral cover. In several cases, sponge overgrowth was followed by host coral mortality and subsequent sponge die-off, exposing bare skeletons that were rapidly colonized by turf algae. This sequence aligns with the scenario proposed by Rossi et al. (2015), in which sponge overgrowth is followed by partial sponge die-back, a pattern visually evident in several of our observations. Taken together, these observations suggest that *H. nematifera* may accelerate coral decline and indirectly facilitate algal expansion by clearing live coral surfaces (Rossi et al., 2015). In the Nusa Penida MPA, this pattern was most apparent on northern and eastern reefs already showing signs of degradation, indicating that sponge colonization may interact with local disturbance regimes to influence reef succession processes. Although the longer-term ecological consequences remain uncertain, these observations highlight the need to investigate how benthic competition, coral condition, and substrate availability shape reef trajectories following sponge outbreaks.

5. Conclusion

This study provides a systematic baseline of *H. nematifera* in the Nusa Penida MPA, documenting its distribution, host diversity, and expansion dynamics across multiple reef sites. *H. nematifera* was most abundant in areas exposed to nutrient enrichment, sedimentation, and wastewater from coastal development, underscoring how local degradation can compromise coral health and facilitate opportunistic colonization. In contrast, *H. nematifera* was absent from most southern and western sites, where limited coastal development, stronger flushing, and cooler upwelling conditions likely reduce nutrient retention and inhibit sponge establishment. Its rapid lateral expansion, ability to exploit more than twenty coral genera across multiple morphologies, and persistence on non-coral substrates together signal an ecological flexibility that threatens reef resilience and restoration efforts. In particular, impacts on branching and foliose corals risk loss of structural complexity, with likely reductions in habitat heterogeneity, biodiversity, and ecological function.

The survey design necessarily provided a snapshot of sponge distribution at each site, with one survey conducted per depth. While this approach limited temporal resolution and did not include deeper reef strata, it was effective for detecting spatial patterns of occurrence across the MPA. Importantly, the spatial patterns observed, presence at developed northern and eastern sites and absence along the less-developed southern cliffs, were consistent with those in the long-term monitoring dataset, underscoring the reliability of the baseline established here and its value for future surveillance of sponge expansion. Because surveys in this study were designed to document sponge–substrate interactions rather than quantify colony-level coral availability, host-use patterns reported here represent relative frequencies of observed interactions rather than infestation severity within individual coral taxa. Quantifying infestation severity will require future surveys that explicitly pair interaction records with measures of total coral abundance.

Building on this ecological insight, conservation and restoration strategies should prioritize improving wastewater treatment, regulating coastal development, and reducing land-based inputs to address the root causes of reef degradation. Restoration efforts will also benefit from careful site selection, integration of resistant taxa such as *Porites*, and explicit evaluation of invasive species risks before transplantation. In addition, maintaining populations of generalist sponge predators through sustainable fisheries management may help preserve natural biotic controls on sponge abundance (Loh & Pawlik, 2014; Wooster et al., 2017). Building early detection systems and practical removal guidelines will strengthen the capacity of managers to respond rapidly to outbreaks, safeguarding reef integrity in Nusa Penida and across the Coral Triangle.

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Statements & Declarations

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Competing interests

The authors declare that they have no competing interests.

Author contributions

Anna Plucińska: conceptualization; methodology; investigation (fieldwork); formal analysis (statistics); writing, original draft; writing, review and editing.

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Rinaldi Gotama: writing, review and editing; validation; methodology; investigation; formal analysis; data curation.

Boyd A. McKew: supervision; writing, review and editing.

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Pascal Sebastian: conceptualization; methodology; investigation (fieldwork); resources and logistical support; writing, review and editing.

All authors read and approved the final manuscript.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request. Access to raw images and geo-referenced site metadata is subject to permission from IndoOcean Project and local authorities under research permit 500.16.7.4/086/RP/DPMPTSP/2024. Analysis code and derived summary tables will be deposited in a public repository, and the DOI will be added at proof.

Ethics approval

Not applicable. The study did not involve human participants or regulated vertebrate animals.

Title: Occurrence, distribution, and linear progression of a coral-killing sponge *Haliclona (Chalinula) nematifera* on coral reefs in the Nusa Penida Marine Protected Area, Indonesia.

Appendix A

Table A.1. Details of survey dives conducted between April and July 2024 within the Nusa Penida Marine Protected Area. The first 12 dives addressed objectives (1) occurrence frequency and (2) host assessment; dives 13 to 17 addressed objective (3) linear progression rate determination on three coral host genera (*Porites*, *Pocillopora*, *Echinopora*).

Dive No.	Survey objective	Date	Site	Site code	Reef position around the Island	Depth (m)	Latitude	Longitude
1	1,2	2024-04-27	Karang Sari	KS	East	5,10,15,20,25	-8.707151	115.587722
2	1,2	2024-04-27	SD Point (Sekolah Dasar Point)	SD	North	5,10,15,20,25	-8.673983	115.513058
3	1,2	2024-04-30	Manta Point	MP	South	10,15,20	-8.794145	115.526798
4	1,2	2024-04-30	Crystal Bay	CB	West	5,10,15,20,25	-8.715307	115.456154
5	1,2	2024-05-02	Batumulapan	BM	East	5,10,15,20,25	-8.684747	115.580134
6	1,2	2024-05-02	Sental	SN	North	5,10,15,20,25	-8.675579	115.532938
7	1,2	2024-05-08	Ped	PD	North	5,10,15,20,25	-8.675490	115.519206
8	1,2	2024-05-09	Mangrove	MN	West	5,10,15,20	-8.662997	115.468869
9	1,2	2024-05-09	Toyapakeh	TP	West	10,15,20,25	-8.684559	115.480805
10	1,2	2024-05-22	Manta Bay	MB	South	10,15,20	-8.738935	115.453033
11	1,2	2024-07-08	Labyrinth	LB	South	10,15,20	-8.789236	115.522868
12	1,2	2024-07-08	Rabbit Hole	RH	South	10,15,20	-8.758120	115.478953
13-17	3	2024-04-17–2024-06-19	SD Point	SD	North	2.5-7	-8.673983	115.513058

Appendix B

Figure B.1. A diver using a custom-built PVC frame (0.5 × 0.5 m) with a mounted Olympus TG6 camera to capture benthic images and assess the occurrence of the invasive coral-killing sponge *Haliclona (Chalinula) nematifera*. The structure, designed to withstand the strong currents and challenging conditions of the area, ensures that the entire quadrat area is included in each photo. Photo credit: Pedro Medeiros.

Appendix C - Occurrence frequency, linear progression rates, and host interactions

Table C.1. Mean occurrence frequency (%) of *Haliclona (Chalinula) nematifera* at each site and depth from targeted surveys (April–July 2024).

Site	Depth (m)	Mean occurrence frequency (SE)

Batumulapan	5	0.00 (0.00)
Batumulapan	10	1.56 (0.81)
Batumulapan	15	1.16 (1.16)
Batumulapan	20	0.39 (0.39)
Batumulapan	25	0.00 (0.00)
Crystal Bay	5	0.00 (0.00)
Crystal Bay	10	0.00 (0.00)
Crystal Bay	15	0.00 (0.00)
Crystal Bay	20	0.00 (0.00)
Crystal Bay	25	0.00 (0.00)
Karangsari	5	4.82 (3.28)
Karangsari	10	8.07 (3.23)
Karangsari	15	13.61 (2.95)
Karangsari	20	9.06 (2.58)
Karangsari	25	3.92 (1.75)
Labyrinth	10	0.00 (0.00)
Labyrinth	15	0.00 (0.00)
Labyrinth	20	0.00 (0.00)
Mangrove	5	0.90 (0.90)
Mangrove	10	4.39 (1.93)
Mangrove	15	5.12 (2.61)
Mangrove	20	3.82 (2.98)
Manta Bay	10	0.00 (0.00)
Manta Bay	15	0.00 (0.00)
Manta Bay	20	0.00 (0.00)
Manta Point	10	0.00 (0.00)
Manta Point	15	0.00 (0.00)
Manta Point	20	0.00 (0.00)
Ped	5	2.03 (1.30)

Ped	10	2.37 (1.73)
Ped	15	0.78 (0.52)
Ped	20	1.69 (1.35)
Ped	25	0.00 (0.00)
Rabbit Hole	10	0.00 (0.00)
Rabbit Hole	15	0.00 (0.00)
Rabbit Hole	20	0.00 (0.00)
SD Point (Sekolah Dasar Point)	5	3.38 (2.56)
SD Point	10	1.70 (1.35)
SD Point	15	2.74 (1.62)
SD Point	20	1.57 (1.21)
SD Point	25	1.02 (0.50)
Sental	5	6.65 (5.76)
Sental	10	2.32 (1.96)
Sental	15	1.72 (0.88)
Sental	20	2.03 (2.03)
Sental	25	0.70 (0.46)
Toyapakeh	5	0.00 (0.00)
Toyapakeh	10	0.00 (0.00)
Toyapakeh	15	0.00 (0.00)
Toyapakeh	20	0.00 (0.00)
Toyapakeh	25	0.00 (0.00)

Table C.2. Mean occurrence frequency (%) of *Haliclona (Chalinula) nematifera* at each site based on long-term photoquadrat surveys (January 2023–March 2024)

Date (mm/dd/yyyy)	**Site**	**Locality around the island**	**Replicates**	**Mean occurrence frequency (%)**
1/16/2023	Batumulapan	east	4	0.00

3/18/2023	Batumulapan	east	4	0.00
5/21/2023	Batumulapan	east	4	0.00
7/8/2023	Batumulapan	east	4	0.00
12/5/2023	Batumulapan	east	5	0.54
1/10/2024	Batumulapan	east	5	0.56
4/18/2023	Karangsari	east	4	7.57
6/9/2023	Karangsari	east	4	4.13
7/19/2023	Karangsari	east	4	4.73
9/12/2023	Karangsari	east	4	12.15
11/25/2023	Karangsari	east	5	1.62
1/25/2024	Karangsari	east	5	8.12
2/26/2023	Mangrove	west	3	0.00
4/14/2023	Mangrove	west	3	4.66
5/25/2023	Mangrove	west	3	0.00
7/7/2023	Mangrove	west	3	1.85
10/22/2023	Mangrove	west	4	2.94
3/16/2024	Mangrove	west	4	2.82
1/6/2023	Ped	north	4	0.89
3/16/2023	Ped	north	4	0.00
5/20/2023	Ped	north	4	0.00
7/12/2023	Ped	north	4	0.00
10/13/2023	Ped	north	5	0.00
1/6/2024	Ped	north	5	0.00
2/15/2023	SD Point (Sekolah Dasar Point)	north	4	0.68
3/10/2023	SD Point	north	4	0.00
5/19/2023	SD Point	north	4	0.70
7/4/2023	SD Point	north	4	0.68
10/12/2023	SD Point	north	5	1.10

1/6/2024	SD Point	north	5	0.00
1/15/2023	Sental	north	4	0.00
3/24/2023	Sental	north	4	0.70
5/12/2023	Sental	north	4	0.74
7/20/2023	Sental	north	4	0.00
11/21/2023	Sental	north	5	0.00
1/9/2024	Sental	north	5	0.57

Table C.3. Linear progression rates (mm day^{-1}) of *Haliclona (Chalinula) nematifera* measured on three coral genera.

Genus	**Linear progression rate (mm day^{-1})**
Pocillopora	1.41
Pocillopora	1.37
Pocillopora	1.47
Pocillopora	1.63
Pocillopora	0.30
Pocillopora	0.60
Pocillopora	0.57
Echinopora	1.83
Echinopora	0.96
Echinopora	2.81
Echinopora	1.63
Echinopora	1.02
Echinopora	1.75
Echinopora	1.88
Echinopora	1.31
Echinopora	1.46
Echinopora	1.41

Echinopora	0.84
Echinopora	0.91
Echinopora	1.78
Echinopora	0.84
Echinopora	0.80
Porites	0.22
Porites	1.18
Porites	0.23
Porites	1.25
Porites	0.47
Porites	0.28
Porites	0.78

Table C.4. Number of infected hosts at each category recorded in April–July 2024

Infected host category	**Number of infected hosts (SE)**
Hard Coral	201 (13.11)
Rock / Rubble	12 (0.91)
Dead Coral	8 (0.71)
Other Sponge	7 (0.67)
Artificial Substrate	2
Corallimorph	1
Zoanthid	1

Table C.5. Number of infected hard-coral genera recorded in April–July 2024.

Genus of infected hard coral	**Number of infected hosts (SE)**
Acropora	61 (4.50)
Merulina	5 (0.25)
Lobophyllia	4 (0.00)

Platygyra	4 (0.00)
Echinopora	33 (2.50)
Porites	33 (1.55)
Hydnophora	3 (0.00)
Galaxea	15 (1.38)
Goniopora	14 (2.19)
Pocillopora	13 (1.44)
Favites	3
Dipsastraea	2
Alveopora	1
Cyphastrea	1
Gardineroseris	1
Isopora	1
Leptoria	1
Mycedium	1
Oulophyllia	1
Pachyseris	1
Paragoniastrea	1
Pectinia	1
Turbinaria	1

Appendix D - Statistics

Table D.1. Results of ANCOVA testing differences in *Haliclona (Chalinula) nematifera* occurrence frequency between sites (January 2023–March 2024).

	Df	**Sum Sq**	**Mean Sq**	**F value**	**Pr(>F)**
site	5	750	149.99	16.50	6.36E-13

residuals	144	1301	9.04

Table D.2. Post-hoc pairwise comparisons of *Haliclona (Chalinula) nematifera* occurrence frequency between sites using Tukey HSD (January 2023–March 2024).

Comparison	Diff	Lwr	Upr	p adj
Karangsari – Batumulapan	**6.06**	**3.65**	**8.47**	**<0.001**
Mangrove – Batumulapan	1.92	-0.67	4.50	0.27
Ped – Batumulapan	-0.07	-2.48	2.34	1.00
SD Point (Sekolah Dasar Point) – Batumulapan	0.32	-2.09	2.72	1.00
Sental – Batumulapan	0.12	-2.29	2.53	1.00
Mangrove – Karangsari	**-4.14**	**-6.72**	**-1.56**	**<0.001**
Ped – Karangsari	**-6.13**	**-8.54**	**-3.72**	**<0.001**
SD Point – Karangsari	**-5.74**	**-8.15**	**-3.34**	**<0.001**
Sental – Karangsari	**-5.94**	**-8.35**	**-3.53**	**<0.001**
Ped – Mangrove	-1.99	-4.57	0.59	0.23
SD Point – Mangrove	-1.60	-4.19	0.98	0.47
Sental – Mangrove	-1.80	-4.38	0.78	0.34
SD Point – Ped	0.39	-2.02	2.80	1.00
Sental – Ped	0.19	-2.22	2.60	1.00
Sental – SD Point	-0.20	-2.60	2.21	1.00

Table D.3. Summary of ANCOVA result on *Haliclona (Chalinula) nematifera* occurrence frequency changes overtime at each site (January 2023–March 2024)

Site	Term	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Batumulapan	month_year	5	1.85	0.37	0.62	0.69
Batumulapan	Residuals	20	12.02	0.60		

Karangsari	month_year	5	297.90	59.58	1.71	0.18
Karangsari	Residuals	20	696	34.80		
Ped	month_year	5	2.70	0.54	1.13	0.38
Ped	Residuals	20	9.56	0.48		
Sental	month_year	5	2.90	0.58	0.62	0.69
Sental	Residuals	20	18.82	0.94		
SD Point (Sekolah Dasar Point)	month_year	5	4.41	0.88	0.69	0.64
SD Point	Residuals	20	25.74	1.29		
Mangrove	month_year	5	51.17	10.23	0.80	0.57
Mangrove	Residuals	14	178.21	12.73		

Table D.4. Dunn's multiple comparison results for linear progression rates of *Haliclona (Chalinula) nematifera* among three coral genera

Comparison	**Z**	**P.unadj**	**P.adj**
Echinopora – Pocillopora	1.21	0.23	0.68
Echinopora – Porites	3.04	0.00	0.01
Pocillopora – Porites	1.57	0.12	0.35