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Spatial patterns of 'pink spots' on *Porites* coral in Mo'orea, French Polynesia imply a positive association with anthropogenic impacts

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ABSTRACT

Globally, coral reefs are declining due to numerous global and local stressors, including increasing prevalence of coral diseases and other lesions. Declines in coral cover related to occurrence of lesions, which can be a symptom of disease, can have major effects on ecosystem function and services. While many coral lesions are more intense on human-impacted reefs, evidence linking some lesions, like multifocal pink spots (MPS) on *Porites* corals, to human impacts is mixed. Our study explores spatial patterns of MPS on fringing reefs off the north shore of Mo'orea, French Polynesia during 2016 and 2021. We chose sites within bays previously documented as human-impacted, as well as along the less impacted open coast. We conducted surveys quantifying prevalence, intensity, and within-colony dispersion. During both years, prevalence and intensity of MPS were highest within the bays and decreased in open coastal areas, implying MPS in Mo'orea may be positively associated with anthropogenic impacts. Further, dispersion of MPS within individual colonies in both years was Poisson-distributed, not aggregated. We hypothesize that this dispersion pattern may be related to differences in the two known causative agents' life cycles and emphasize the importance of more research on identifying causes. Our research provides the first documentation of spatial patterns of MPS for South Pacific islands and demonstrates MPS are more widespread and may have a broader relationship to human impacts than previously known.

1. Introduction

Coral reefs are biologically diverse and economically valuable ecosystems that have been declining for centuries (Jackson, 1997). This loss is driven by a combination of global and local stressors. Global threats include ocean warming and acidification associated with climate change (Hughes et al., 2007), while local impacts include overfishing (Hughes et al., 2007), nutrient enrichment (Adam et al., 2021), and sedimentation linked to coastal development (Clausing and Fong, 2016). Another major local stressor is the increasing prevalence of coral diseases (Knowlton and Jackson, 2008; Hoegh-Guldberg, 2011). Here, we consider a coral disease as any change in the healthy state of a colony (Dorland's Illustrated Medical Dictionary, 2004; Singleton and Sainsbury, 2006; Stedman's Medical Dictionary, 2006), where health is defined the ability of an organism to resist stress (Meade and Earickson, 2000). Thus, a diseased coral loses its tolerance or adaptability to environmental challenges and therefore suffers declines in functions that may reduce survival (Vega Thurber et al., 2025). As such, coral diseases can reduce reef resilience, disrupt ecosystem services, and cause declines in abundance and diversity of marine communities that depend on healthy reefs.

Coral diseases, some of which produce lesions, are important contributors to reef decline, with increases in intensity and abundance in recent years (Rodríguez-Villalobos and Reyes-Bonilla, 2019; Tracy et al., 2019; Morais and Santos, 2022). Coral lesions are areas of abnormal tissue including discoloration, loss, or changes in skeletal structure that may indicate physiological stress or infection (Ainsworth et al., 2007; Neely, 2024). Not all coral diseases produce lesions; some may cause internal effects without visible external signs (Vega Thurber et al., 2025; Ainsworth et al., 2007), highlighting the complexity of diagnosing

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disease in coral populations. Coral diseases that produce lesions can be caused by a range of pathogens including bacteria, fungi, trematodes, and protozoans (Vega Thurber et al., 2025; Rodríguez-Villalobos and Reyes-Bonilla, 2019), and can lead to tissue loss, reduced growth, and colony mortality (Ainsworth et al., 2007; Moriarty et al., 2020). Some of the most well-known coral diseases that cause lesions include white band disease, which devastated *Acropora* populations in the Caribbean (Aronson and Precht, 2001), black band disease, characterized by a dark microbial mat that kills coral tissue as it advances (Cervino et al., 2004), and yellow band disease, which affects, among others, several massive coral species and can spread rapidly across colonies (Richardson, 1998). The ecological consequences of these diseases can be severe, leading to shifts in reef composition and reduced biodiversity (Harvell et al., 2007). This global rise in coral diseases has resulted in loss of coral abundance and biodiversity (Precht et al., 2016; Estrada-Saldívar et al., 2021), can lead to phase shifts from coral to algal-dominated reefs (Aronson and Precht, 2001; Fong et al., 2011; Randazzo-Eisemann et al., 2022), and has indirect impacts on fish and other invertebrate populations (Idjadi and Edmunds, 2006; Ainsworth and Mumby, 2015). However, while these major diseases are relatively well-studied, even a basic understanding of the distribution and abundance of many other types of coral lesions has yet to be established. Thus, there are critical gaps in our understanding of coral lesions, especially in the Indo-Pacific (Rodríguez-Villalobos and Reyes-Bonilla, 2019; Willis et al., 2004a).

One morphologically distinct type of coral lesion with limited information on distribution and abundance is multifocal pink spots (MPS; in Ford (2025) these are called Small Multifocal Swollen Pink Spots (SMSPS)) that occur on massive forms of coral in the genus *Porites* (Fig. 1). *Porites* has a generalized stress response to physical damage, pathogen infections, and disruption of tissue integrity in the form of pink pigmentation (Bridges et al., 2020) that plays a role in cytotoxic defense as an immune resistance response (Bridges et al., 2020). While this general stress response can take many forms, including pink lines, patches, and spots, MPS have a distinct morphology and size that make them distinguishable from other pink lesions in field surveys (Fig. 1) (Bruckner et al., 2014; Barton et al., 2020; Kubomura et al., 2021; Ramesh et al., 2023). We define MPS as small pink-pigmented lesions within single swollen polyps of massive colonies of *Porites*. These lesions are of unclear etiology; however, prior studies have identified lesions with this morphology as caused by trematodes (Aeby, 2003, 2007; Aeby et al., 2014) or barnacles (Benzoni et al., 2010). MPS on *Porites* have been described in relatively few locations compared to the wide distribution of *Porites* across the Indo-Pacific (Veron, 2000). At present, to the best of our knowledge, the only places where MPS on *Porites* spp. have been documented are Hawai'i (Aeby, 2003, 2007), New Caledonia (Work et al., 2014; Aeby et al., 2016), the Great Barrier Reef (Willis et al., 2004b), Guam and Papua New Guinea (Aeby, 2007), the Persian Gulf (Riegl et al., 2012), the Philippines (Raymundo et al., 2005), and Yemen (Benzoni et al., 2010). Thus, expanding our knowledge of the geographic distribution and abundance of MPS on *Porites* is important.

There is mixed evidence that environmental stressors promote prevalence and intensity of MPS on *Porites*. As an example, higher sea surface temperatures were linked to increased MPS prevalence in Okinawa (Kubomura et al., 2021), whereas in the Great Barrier Reef, MPS prevalence was higher in austral winter than summer (Willis et al., 2004b). Thus, these studies suggest the relationship between temperature and prevalence is not universal. Similarly, in the Gulf of Thailand, the Andaman Sea (Samsuvan et al., 2019), and in New Caledonia (Heintz

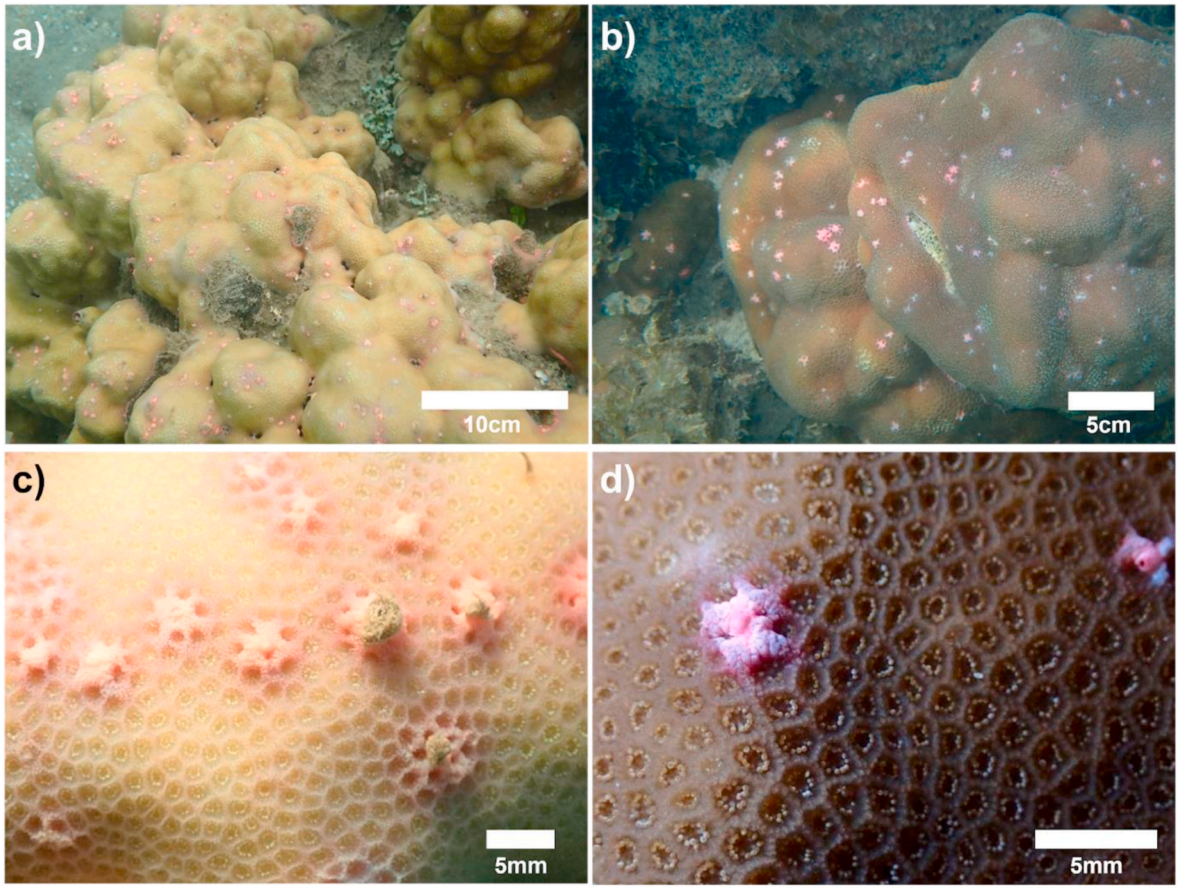

Fig. 1. Photographs of *Porites* colonies affected by Multifocal Pink Spots (MPS) of unknown etiology. (a) Larger and (b) smaller colonies with multiple MPS visible as small inflamed pink polyps across the colony surface. (c) and (d) Close up photographs of single inflamed pink polyps. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

et al., 2015) sites impacted by tourism, freshwater runoff, and/or sedimentation also had higher MPS prevalence, suggesting a positive relationship between stress and prevalence; however, none of these four studies identified the cause of MPS lesions. In contrast, in Hawai'i MPS prevalence was highest on reefs with abundant coral and fewer human impacts (Aeby, 1998, 2007; Aeby et al., 2011, 2016); in three of four of these studies trematodes were identified as the causative agent. MPS on *Porites* were also more prevalent at a remote site in Malaysia with few human impacts (Miller et al., 2015), though the cause of these lesions was not identified. One possible explanation is that these lesions have at least two known causative agents: a digenetic trematode was identified in Hawai'i (Aeby, 2003, 2007; Aeby et al., 2014) and a coral-inhabiting barnacle in Yemen (Benzoni et al., 2010). While lesion prevalence due to the trematode has been negatively linked to human impacts, this pattern has not been explored for barnacle-associated lesions. These findings demonstrate the need for more information on patterns of prevalence and intensity of MPS on *Porites* in areas with known differences in environmental stressors.

Dispersion, broadly defined as the distribution pattern of pathogens across a host population (Crofton, 1971; Anderson and Gordon, 1982; Shaw et al., 1998), is commonly measured in disease ecology to describe the spatial structure of a disease across host organisms. For example, diseases can exhibit aggregated, random, or uniform distributions across hosts or host's tissue, though these patterns alone cannot confirm the causes of disease. An aggregated distribution, defined as a pattern in which the sample variance is significantly greater than the mean (Taylor, 1961), is commonly observed within host-pathogen systems. Examples include aspergillosis in sea fans (Jolles et al., 2002), *Aplysina* red band syndrome on Caribbean reef sponges (presumed to be caused by a microbial agent) (Easson et al., 2013), and digenetic trematodes in butterfly fish (Aeby, 1998). In contrast, a random or Poisson distribution is defined as when the variance approximates the mean (Consul and Shoukri, 1985; Shaw and Dobson, 1995) and can emerge when occurrences of a disease arise independently, particularly during early stages of spread (Shaw and Dobson, 1995; Poulin, 2007). This pattern has been documented in some parasite–host systems in reef fishes (Rohde et al., 1995; Lester, 2012), for white-band disease when measured at the scale of the individual on the coral *Acropora palmata* (Lentz et al., 2011), and for aspergillosis on sea fans at low density (Jolles et al., 2002), Finally, uniform distributions are when the variance is lower than the mean (Poulin, 1993; McVinish and Lester, 2020), which indicates the disease is more evenly spaced than by random chance. This pattern can reflect inhibitory processes such as competition for space or host defensive responses (Poulin, 1993; Bush et al., 1997). Such patterns have been documented for parasitic and predatory isopods on reef fishes (Jones and Grutter, 2007) and yellow band syndrome when compared to the distribution of the host coral, *Montastrea* (Foley et al., 2005). Taken together, these studies identify a need for more studies on dispersion of lesions to set them in context with other diseases of known or unknown etiology. Field surveys are useful tools to explore potential links between variation in coral lesions and sites with different human impacts (Sato et al., 2009; Chaves-Fonnegra et al., 2021). Common measures in surveys of spatial patterns are prevalence, intensity, and dispersion. Thus, our overall objective was to quantify spatial patterns in these three metrics of MPS and determine if they vary among sites known to differ in a broad suite of human impacts.

2. Materials and methods

2.1. Overview

We conducted visual surveys of colonies of stony corals (Scleractinia) in the genus *Porites* quantifying prevalence (the percent of colonies that are affected in an area), intensity (defined as the density of lesions on a colony), and dispersion (here, defined as the spatial distribution of individual MPS within a single colony) of MPS in two years in Mo'orea, French Polynesia (Fig. 2). These years were selected because we observed numerous lesions on coral colonies across a large area of the north shore of the island during our annual research trip. We used a broad set of 205 sites for the first year (2016) and chose a subset of 10 sites to confirm patterns during the second year (2021). Specifically, we established spatial patterns of MPS prevalence across sites that previous research demonstrated varied in a wide suite of human influences (Becker and Silbiger, 2020; Loiseau et al., 2021; Holbrook et al., 2022), measured intensity on individual hosts within sites, visualized how intensity varies with prevalence, and quantified dispersion of MPS within individual coral colonies. Due to the large difference in sampling effort between 2016 (205 sites) and 2021 (10 sites), analyses were conducted within each year without direct comparisons between years.

2.2. Study system, sites, and colony criteria

Mo'orea, French Polynesia (17°32′S 149°50′W) is one of the Society Islands in the South Pacific (Fig. 2a and b). Since the 1970's, the coral reefs of Mo'orea have experienced seven coral bleaching events, two cyclones, and two major outbreaks of the corallivore *Acanthaster planci,* resulting in episodic reduction in coral cover of up to 50% (Trapon et al., 2011; Adjeroud et al., 2018). Species of *Porites* characterized by a massive growth form are common on the reefs of Mo'orea (Edmunds et al., 2016; Holbrook et al., 2018) and exhibit more resistance to these environmental disturbances compared to branching corals such as *Acropora* spp. and *Pocillopora* spp. (Penin and Adjeroud, 2013; Rouzé et al., 2017).

Like many South Pacific Islands, Mo'orea's reef system consists of a forereef that encloses a lagoon (Leichter et al., 2013). Within the lagoon there is a back reef zone comprising patches of coral interspersed within hard bottom substrates and sand flats as well as fringing reefs in close proximity to the island. Our study included fringing reefs along the north shore and the margins of two large bays as well as back reefs on the north shore of Moorea (Fig. 2c). The two bays, Opunohu Bay and PaoPao Bay (also known as Cook's Bay), have undergone rapid watershed development over the last few decades that likely accelerated human impacts on the marine environment (Walker et al., 2014). During rainfall events, these bays are subject to episodic terrestrial runoff (Fong et al., 2020) as well as sewage influx from septic systems (Fajemila et al., 2015). Other land-based sources of degradation in the lagoon include increased influx of sediment (Gabrie et al., 1988) and agricultural chemicals (Aubanel et al., 1999) from runoff, as well as coastal construction (Aubanel et al., 1999; Lafforgue and Robin, 1986). Compounding these stressors, hydrodynamic conditions in the bays differ notably from those along the open north shore. Specifically, water residence times are longer, and circulation is slower in both PaoPao and Opunohu Bays, particularly during the dry season, compared to more exposed reef areas (Letourneur et al., 2013; Knee et al., 2016; Poulin, 2013).

To capture variation in reef types and include areas documented to be subject to a myriad of human influences in our surveys, we chose 205 survey sites in 2016 (Fig. 3). Due to logistical and time constraints in 2021, we re-surveyed a subset of ten sites within the bays that varied in prevalence in 2016. In both years, site selection was constrained by depth (<2 m), habitat (at least partially hard bottom), location (north shore of Mo'orea), and proximity (at least 20 m apart). To standardize our searches for *Porites* colonies during surveys, we only categorized coral colonies that were attached to the substrate and had the largest diameter that was >15 cm; smaller colonies were excluded. Many corals experience partial mortality and remain as patches of the original colony; however, the dead skeleton can also be a recruitment substrate for new colonies. As these processes cannot be distinguished in the field, we decided to count living coral patches on a single coral skeleton as individual colonies if they were greater than 0.5 m apart. Consistent with the definition provided above, we recorded corals as affected when any polyp of the colony showed the distinct morphological characteristics of

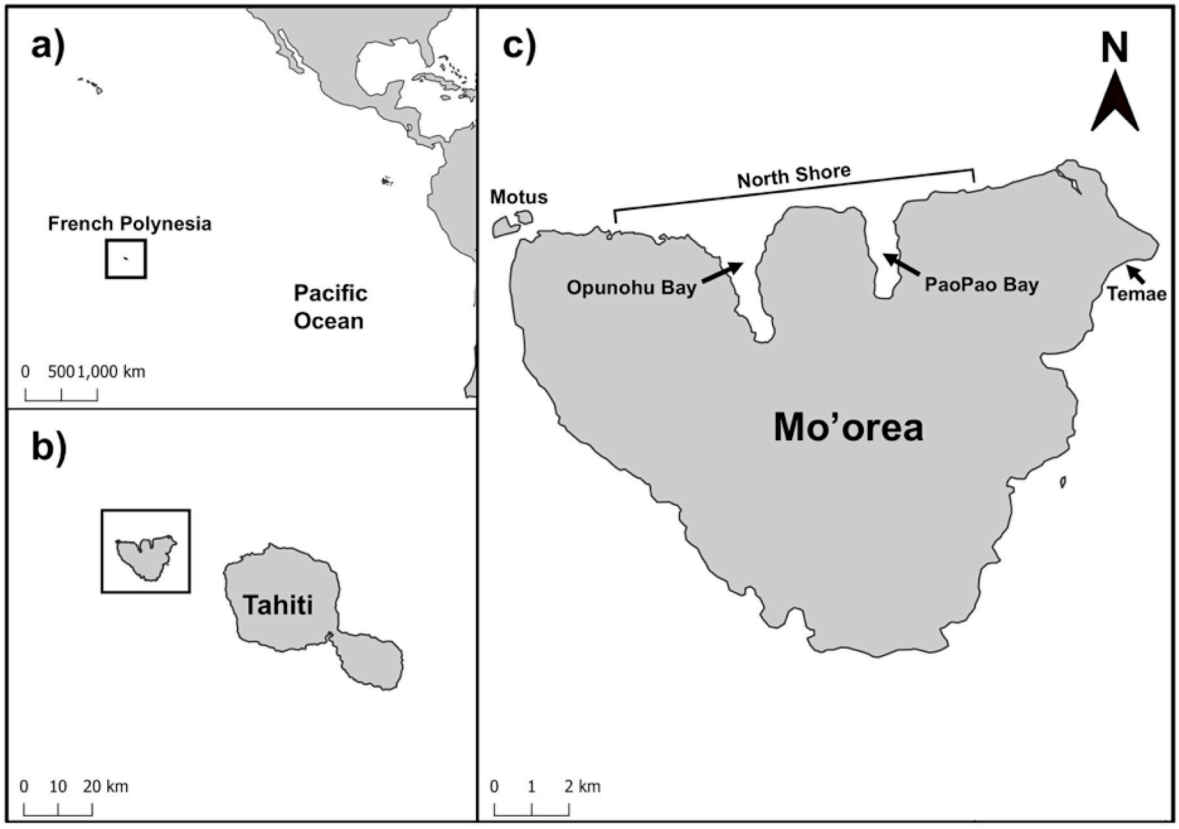

Fig. 2. (a) Map of French Polynesia (indicated by a square) in the Pacific Ocean. (b) The location of Mo'orea west of Tahiti in the South Pacific. (c) The island of Mo'orea with the locations of our study areas: along the north shore, within the two bays, around the Motus (smaller lagoonal islands), and at Temae in the northeast.

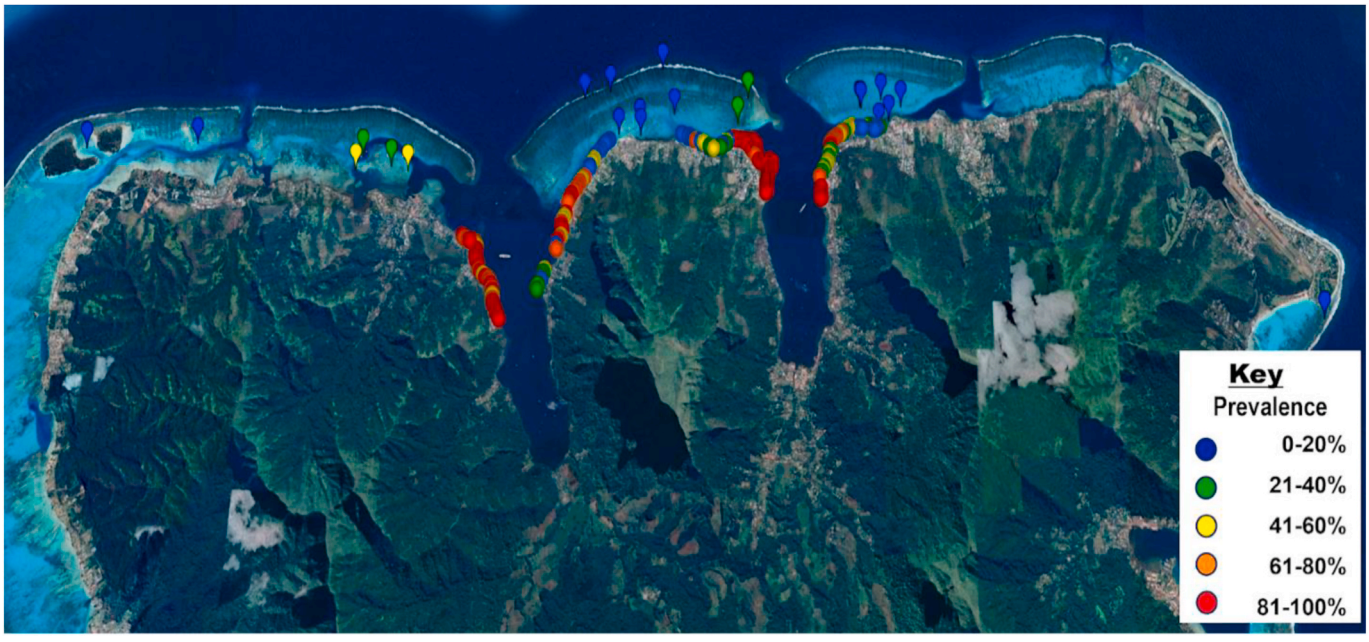

Fig. 3. Prevalence of MPS at study sites along the north shore of Mo'orea, French Polynesia in 2016. Circles indicate sites surveyed along 2 × 20 m belt transects; balloons indicate sites where 300 *Porites* colonies were surveyed. Symbols are color-coded by prevalence. A total of 205 sites were surveyed. Satellite map generated using Google Earth. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

MPS (swollen and bright pink single polyps), and as unaffected when no polyps had any characteristics of MPS. This approach allowed us to consistently quantify prevalence, intensity, and dispersion across affected colonies; however, it is important to note that we did not know the etiology of these lesions and that they may arise from multiple underlying causes.

2.3. Patterns of prevalence across sites

2.3.1. 2016

To quantify spatial patterns of MPS across sites, we calculated prevalence, defined as the percentage of colonies with MPS. At each site we first made an initial visual assessment of coral prevalence. Where prevalence appeared to be >20%, we conducted surveys along 2 × 20 m belt transects (40 m^2) with GPS coordinates recorded at the beginning (n = 183 sites). Each colony in the belt transect was categorized as affected (MPS present) or unaffected (no MPS observed anywhere on the colony). At sites where prevalence appeared to be <20%, we started at a random point and swam in haphazardly-determined directions categorizing each colony of *Porites* we encountered until we reach a total of 300 colonies per site (n = 22 sites). We chose 300 colonies to include in these swimming survey as this exceeded the numbers of coral surveyed in transects (range 1-30), ensuring we included a sufficient number of affected colonies to calculate prevalence. We took a GPS reading at the point we began each survey. Between our two sampling methods, we quantified prevalence at a total of 205 sites in 2016.

We calculated prevalence (%) by dividing the number of affected colonies by the total number of colonies surveyed and multiplying by 100. To visualize spatial patterns in MPS prevalence, we sorted sites into five prevalence categories in bin widths of 20% and visualized prevalence on a map using Google Earth. Sites were located on each map with prevalence categories color coded.

2.3.2. 2021

In 2021, we reassessed MPS prevalence at a subset of ten sites that represented the range of prevalences documented in 2016 to confirm whether similar spatial patterns of prevalence occurred in the two years. We used the swimming survey approach (as described for 2016) in all ten sites but categorized the first 100 coral colonies encountered at each site instead of 300, as our objective was to conduct rapid surveys to confirm previous patterns. Again, we calculated prevalence as the percent of affected colonies in each site and results were visualized in the same manner as in 2016.

2.4. Relationship between prevalence and intensity

2.4.1. 2016

We assessed the relationship between prevalence and intensity (number of MPS per m^2 of affected corals) by quantifying intensity for haphazardly chosen colonies within a 20 m^2 belt transect at sampling locations that included sites with different prevalences of MPS. For this component of the study, we returned to locations of the fringing reef where the average prevalences across several sites that were in close proximity were low (average of 19% affected; n = 3 sites), medium (average of 55% affected; n = 4 sites), and high (average of 94% affected; n = 9 sites). We chose sampling locations within these sites that were accessible and visually representative of the average prevalence. At the low (n = 101 colonies) and the medium (n = 107 colonies) prevalence sampling locations, we quantified intensity on coral colonies in the field. On each colony, we randomly selected ten points where we placed a 27 cm^2 quadrat made from hardware cloth with 1.3 cm^2 openings. To randomize quadrat placement, we used a random number generator to select numbers along a transect laid on each colony where we placed each quadrat. These openings created a grid to facilitate counts of the number of affected polyps per quadrat. The ten replicate counts of intensity were averaged per colony, then normalized to m^2. At the high prevalence sampling locations (n = 51 colonies), intensities were too high to count in the field. Therefore, we randomly selected points to place our quadrat (as before) then took a photograph of each quadrat. Because preliminary data demonstrated that colonies with high intensities had lower within-colony variance in intensity (≤20 %), we photographed and counted lesions in only one quadrat for each colony. We also normalized these counts of MPS to number per m^2. We constructed percent frequency distribution graphs for all sites.

2.4.2. 2021

To assess patterns in intensity in 2021, we quantified intensity on 8 to 13 affected coral colonies along 2 × 20 m transects at high (n = 3 sites) and medium (n = 2 sites) prevalence sites. This year, we measured intensity at the same sites where prevalence data were collected as our sites were far from each other compared to 2016 (compare Figs. 3 and 4). We then averaged prevalence across sites within the same prevalence category.

On each colony, we haphazardly selected and photographed one to six quadrats depending on colony size. In 2021, we used a larger quadrat (40 cm^2) than in 2016 because our previous data showed that, with good water quality, photo resolution was generally sufficient to count larger areas. Using a larger quadrat, we incorporated more spatial variability in each quadrat and therefore could use fewer replicate photos per colony. However, the number of photo quadrats that we were able to count for each coral colony varied due to some instances of poor water quality limiting photo quality and some photos capturing overlapping areas of coral. For small colonies (<50 cm^2 coral colony total area), the range of photos used was between one to three, while larger colonies (≥50 cm^2 coral colony total area) ranged between four to six. From each photo, we counted the number of MPS per area (intensity), calculated average MPS per quadrat, and then normalized estimates of intensity per colony as MPS per m^2. For each site type (medium and high intensities), we constructed a percentage frequency distribution of MPS intensities using average intensities for individual colonies.

2.5. Patterns of dispersion across densities of MPS on coral colonies

2.5.1. 2016

We quantified patterns of within colony dispersion on coral colonies across different lesion intensities by surveying 50 haphazardly chosen corals at the sampling location with the highest average prevalence across sites (94% affected; n = 9 sites). We chose this sampling location because it had the widest range of MPS intensities. For each coral colony, we randomly placed and photographed a quadrat composed of a grid of 16 1.3 × 1.3 cm cells (total area of 27 cm^2). For each photograph, intensity was measured as the number of lesions per cell (n = 16) and normalized to the number of MPS per m^2.

To quantify patterns of dispersion within coral colonies across sampling locations, we used the slope of the variance to mean regression, "*b*", which is based on Taylor's law (Taylor, 1961). Numerous empirical studies have used this method to illustrate the dispersion of populations (e.g. (Baumgartner and Peláez, 2024; Zvuloni et al., 2009; Burns et al., 2016; Work et al., 2008; Hamman, 2019; Lester and Blomberg, 2021),). We used this index to compare the level of aggregation of MPS within coral colonies by calculating the mean and variance of lesions per cell for each colony. To calculate the slope of the mean to variance ratio (b = MVR), we regressed log variance of lesion abundance (y) against log mean of lesion abundance (x) for each coral colony (1 quadrat/individual) across all colonies (n = 50). $b > 1$ indicates an aggregated distribution, $b = 1$ indicates a Poisson distribution, and $b < 1$ indicates a uniform distribution (Taylor, 1961; Poulin, 2013; Baumgartner and Peláez, 2024).

2.5.2. 2021

To investigate dispersion in 2021, we utilized the same 8 to 13 affected coral colonies along the 2 × 20 m transect at each of the five sites that we used to analyze intensity. For each colony, we randomly placed and photographed a quadrat, as above, but in 2021 the grid was composed of 64 1.3 × 1.3 cm cells (total area of 108 cm^2), not 16. We calculated the mean variance ratio as in the 2016 surveys.

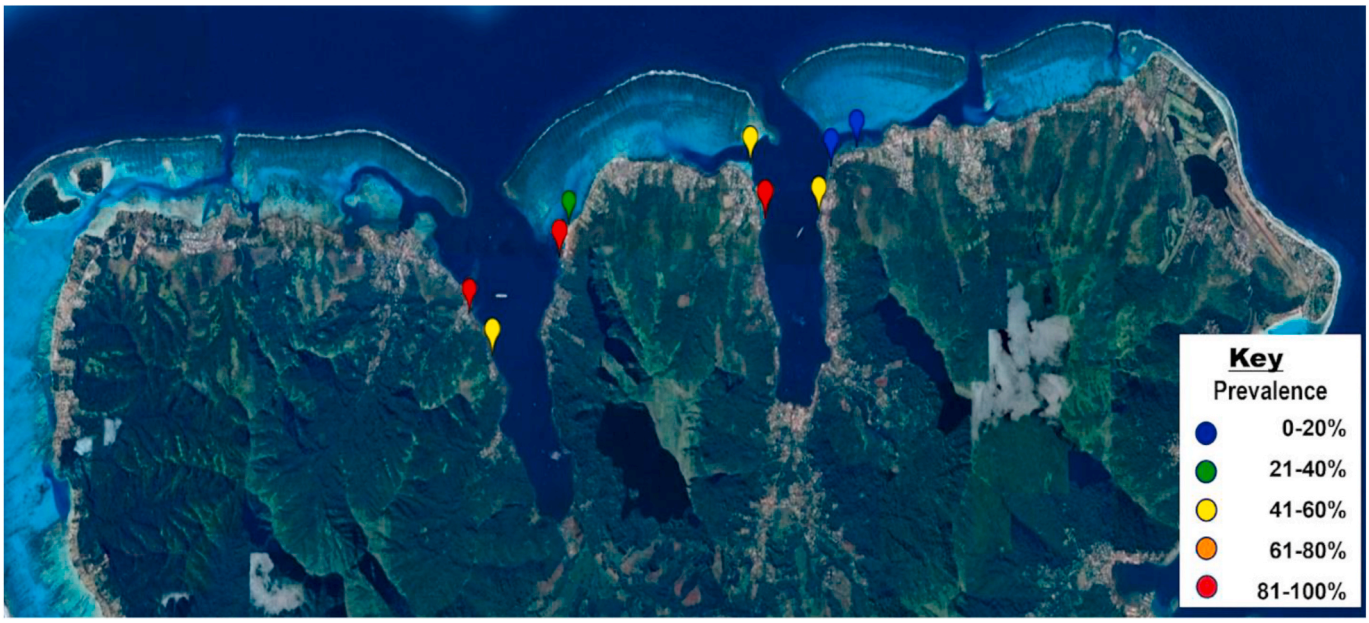

Fig. 4. Map of the prevalence of MPS in our study sites along the north shore of Mo'orea, French Polynesia in 2021. Symbols are color-coded by prevalence. A total of ten sites were surveyed. (Satellite maps in this figure were generated using Google Earth). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3. Results

3.1. Spatial patterns of prevalence across sites

In 2016, the overall prevalence of MPS was highest within the interior of both bays and decreased with increasing distance from the mouth of each bay (Fig. 3). For example, 79% of the sites within the bays had prevalence between 61 and 100% (red and orange symbols), whereas prevalence was lowest at fringing reef sites (≤20 % prevalence, blue symbols), closer to the reef crest, and more distant from the mouth of the bays. There were two exceptions to this pattern. First, there were a few cases of 21-40 % prevalence within both bays (green symbols), always along their eastern shores. Second, there was also a broad range of prevalences (between 21 and 60 %, green and yellow symbols) along the shore outside of the bays, but only to the west of each bay. Overall, the majority of back reef sites were in the lowest prevalence category (≤20 % prevalence, blue symbols), with four sites between 21 and 40% (green), and only two sites between 41 and 60% prevalence (yellow) to the west of Opunohu Bay.

In 2021, MPS prevalence also varied spatially across Mo'orea (Fig. 4). The sites in the highest prevalence categories were inside the bays (61-100 %, red and orange symbols), while the two lowest prevalence sites (≤20 % prevalence, blue symbols) were on the north shore outside of the bays. Two sites had intermediate prevalence (41-60%, yellow symbol), with one in the north shore west of PaoPao Bay and one along the eastern shore of Opunohu Bay that was 21-40% (green symbol).

3.2. Relationship between prevalence and intensity

In 2016, we established sampling locations for intensity across sites where the average prevalence was low (19%, n = 3), medium (55%, n = 4), and high (94%, n = 9) (Fig. 5a). As prevalence of MPS increased, a greater proportion of affected colonies had higher MPS intensities (Fig. 5b–d). The average intensity per affected colony was 69 ± 93 (SE) per m^2 in the low, 515 ± 23 (SE) per m^2 in the medium, and 2045 ± 157 (SE) per m^2 in the high prevalence sampling locations. As both the low and medium intensity sampling locations had strong right-skewed distributions, the median intensity was zero per m^2 for both. In contrast, the median of 1960 per m^2 in the high prevalence sampling locations was relatively closer to the mean.

In 2021, the average intensity across the medium prevalence sampling locations was 180 ± 61 (SE) per m^2 with a median of 56 per m^2, reflecting the slightly less skewed distribution in medium prevalence sites (Fig. 6a). For the high prevalence sampling locations, the mean intensity was 522 ± 81 (SE) per m^2 with a median intensity of 438 per m^2, indicating a more strongly skewed distribution.

3.3. Dispersion of MPS on coral colonies

In 2016, there was a significant positive linear relationship between the log mean and the log variance of MPS density across all colonies (slope = 1.18, 95% confidence interval = 0.957 - 1.393) (Fig. 7a). The confidence interval of the slope encompassed the 1:1 ratio, demonstrating that the dispersion of MPS within host colonies was consistent with a Poisson distribution.

In 2021, we also observed a significant positive linear relationship between the log mean and log variance of MPS density (slope = 1.10, 95% confidence interval = 1.062 - 1.134) (Fig. 7b). Similar to 2016, the confidence interval of the slope encompassed the 1:1 ratio and therefore is well modeled by a Poisson distribution.

4. Discussion

Increasingly, researchers are documenting the negative impacts of coral diseases on reef health, highlighting their role in driving coral decline and altering ecosystem dynamics (Ruiz-Moreno et al., 2012; Forster et al., 2017; Vega Thurber et al., 2014). Much of this work has focused on bacterial, fungal, and viral pathogens, but other lesions such as MPS remain comparatively underexplored despite their potential to compromise coral health (Moriarty et al., 2020; Vega Thurber et al., 2014). In this study, we document MPS on *Porites* colonies on reefs of the South Pacific Island of Mo'orea. To our knowledge, this is the first report of MPS in this region, expanding the known distribution of these lesions into the Indo-Pacific. Thus, our research adds to a growing body of knowledge of the distribution of MPS on *Porites* spp. While the range of massive *Porites* spp. in the Indo-Pacific is extremely large, the reported geographical distribution of MPS is very patchy. One possible explanation for this patchy distribution of reports may be a lack of widespread

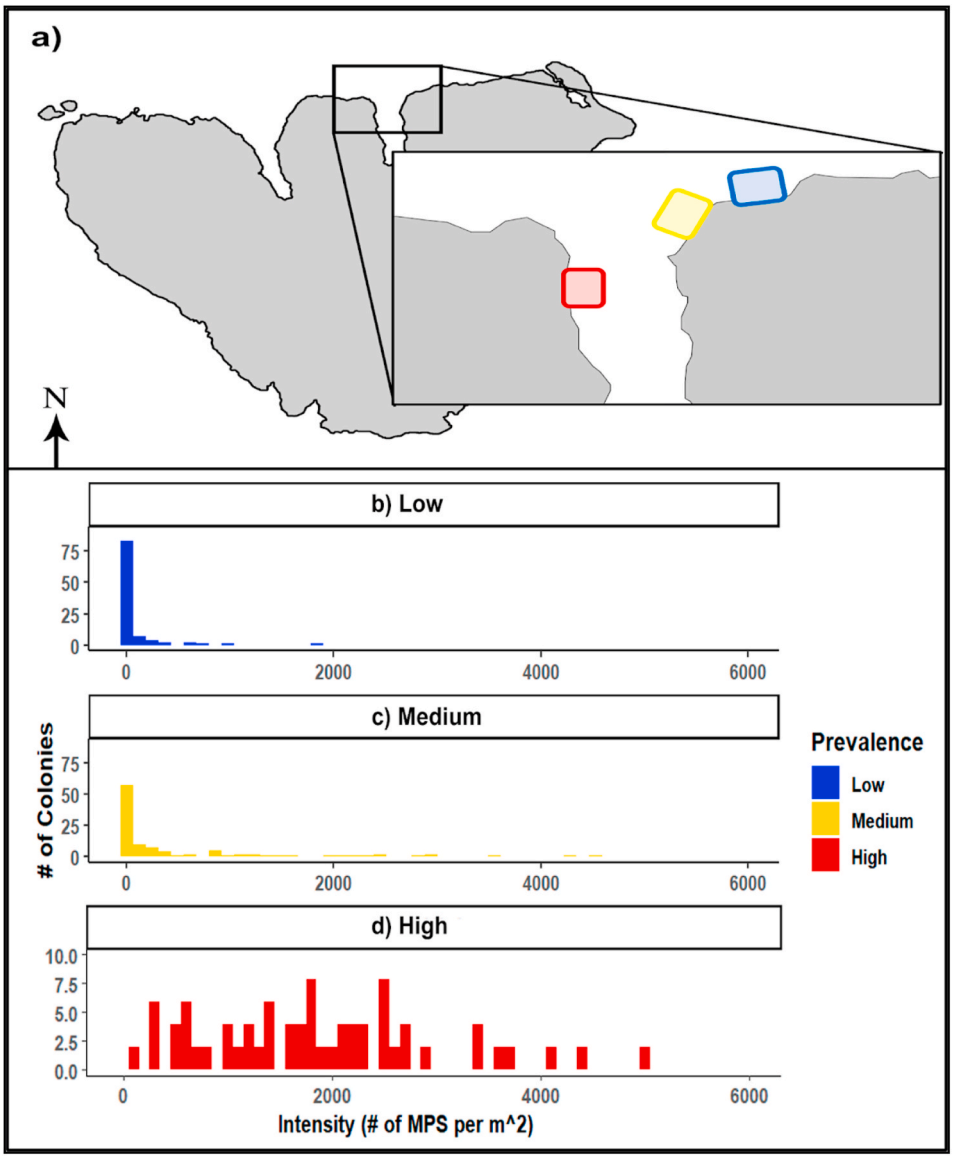

Fig. 5. (a) Map with boxes enclosing sites where we averaged prevalence to characterize the three sampling locations where we measured intensity. Sampling locations were centered within each box in PaoPao Bay (high prevalence in red, medium prevalence in yellow) and along the north shore (low prevalence in blue). The sampling location within the red box is also where we measured dispersion. Percent frequency distributions of MPS intensity (number of affected polyps (lesion spots) per m^2) of affected colonies in three sampling locations with average site prevalence of (b) 19% (low), (c) 55% (medium), and (d) 94% (high). Note y-axis scale change in (c). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

search efforts due to limited accessibility or history of research across the region. Further, some reports are not descriptive enough to determine if they include MPS; for example, the only report of pigmentation on corals in French Polynesia (Clampitt, 2023) did not confirm pigment color. Thus, we discovered these types of coral lesions occur in a wider geographical distribution than previously known, adding new information to a growing understanding of their distribution.

Patterns of prevalence of MPS on *Porites* in our study reflect the wide range of prevalences found in previous studies. For example, in New Caledonia average prevalence of discoloration that included MPS on *Porites* was 30% across sites (Tribollet et al., 2011), while in Clipperton Island average prevalence was 26% (Pogoreutz et al., 2022); however, neither of these studies distinguished MPS from other type of discoloration. Further, in both of these studies prevalences were much lower than our overall average of ~60% across both survey years, but comparable to the lower prevalence found in some sites in our study. In Hawai'i, two studies showed large differences in average prevalence of MPS that were similar to our findings in Mo'orea (we found 0% to 100% in 2016 and 4% to 94% in 2021), as one reported 73.97% (Williams et al., 2010) and the other 5.3% affected colonies (Aeby et al., 2011). Possible explanations for wide ranges of prevalence across studies may be differences in susceptibility across host species of *Porites* or variance in the relative abundance of causative agents of MPS. Histological, or possibly DNA, approaches are a critical next step in determining causes of MPS in Mo'orea. Another possible explanation is that MPS have historically gone undetected due to previous low densities or lack of monitoring, underscoring the need for more focused and longer-term monitoring as well as histopathological analyses to better characterize these lesions. Further investigation is essential to elucidate the underlying factors contributing to these wide ranges in prevalence.

Our results demonstrate that prevalence and intensity of MPS were highest in the two northern bays in 2016 and were again higher in the subset of sites in the bays in 2021, though sample size in this year was modest. One possible explanation for this pattern is that one or more of the myriad of human impacts documented as higher in the bays (Moriarty et al., 2020; Trapon et al., 2011; Leichter et al., 2013; Walker

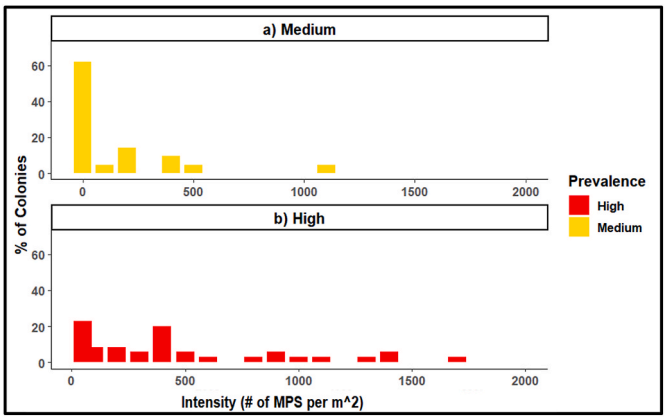

Fig. 6. Percent frequency distributions of MPS intensity (number of MPS polyps per m^2) on affected colonies across sites that have (a) 69% (medium, n = 2) and (b) 88% (high, n = 3) prevalence.

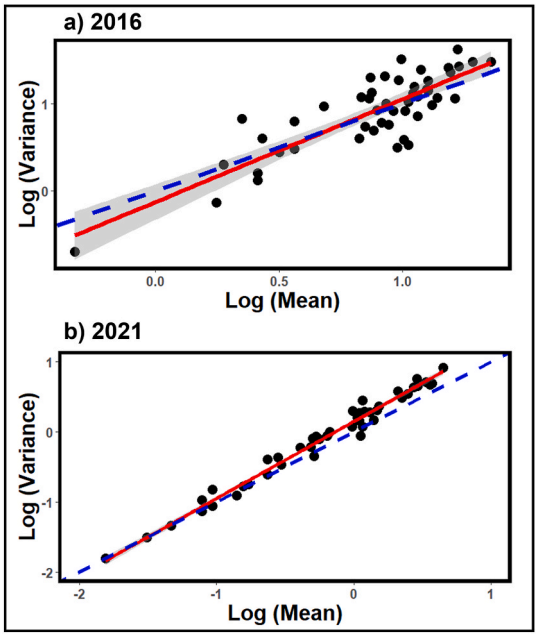

Fig. 7. The relationship between the log of the mean and the log of the variance of lesions within individual coral colonies in a) 2016 and b) 2021. Each point is the mean and variance for 1 quadrat (n = 16) on a single colony in a single sampling location per year. The solid red line represents the regression line for a) 2016 ($r^2 = 0.71$, RSE = 0.25, $p < 0.001$) and b) 2021 ($r^2 = 0.99$, RSE = 0.09, $p < 0.001$) while the dotted blue lines represent the 1:1 relationship between log variance and log mean. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

et al., 2014; Fong et al., 2020) caused corals to be more susceptible to these lesions. For example, previous studies have shown runoff from watersheds developed by agriculture as well as sewage from human populations is entering PaoPao and Opunohu Bays (Adam et al., 2021; Neumann, 2023; Adjeroud, 2000) and has been associated with reduced coral diversity (Adjeroud, 1997, 2000) and abundance (Adam et al., 2021) within the bays. Coral stress and damage from anthropogenic impacts may lead to an increase in susceptibility to lesions. For example, if MPS are caused by infectious agents, then weakening the immunity of the coral may provide more opportunities for causative agents to enter these more vulnerable hosts (Moriarty et al., 2020; Burns et al., 2016; Pogoreutz et al., 2022). In addition, disease dynamics may depend on the method of pathogen transmission or whether infection rates are influenced by host density. Further, human related stressors such as increased sedimentation or nutrient enrichment can further compromise coral health (Vega Thurber et al., 2014; Koop et al., 2001), possibly increasing the likelihood of lesion development. We hypothesize that terrestrial runoff can stress corals and contribute to our observed spatial patterns in MPS prevalence and intensity (Koop et al., 2001; Adjeroud, 1997; Bruno et al., 2003; Ford, 2025). We hope our findings motivate future research into this potential link between human impacts and MPS.

The pattern of within-colony dispersion of MPS across both survey years was consistent with a Poisson distribution rather than the aggregated dispersion commonly reported for infectious diseases (Anderson and Gordon, 1982; Crofton, 1971; Shaw et al., 1998; Taylor, 1961). One potential explanation of the pattern of dispersion we observed may be that lesions classified as MPS in the field may include multiple underlying causes, including trematodes, barnacle colonization, or other agents, which could influence their spatial distribution. Species with direct life cycles are generally more likely to produce Poisson distributions, whereas those with complex or multi-host life cycles, such as many parasites, often exhibit aggregated distributions (Lester, 2012). Of the two known causative agents, a trematode and a barnacle, the latter has a direct life cycle. While only histology or DNA techniques can provide evidence of the cause of MPS in our system, this distributional evidence would suggest a higher incidence of inflammation caused by non-infectious agents, such as barnacles or other organisms with direct life cycles. Thus, we hope our study motivates future research on the etiology of MPS across the Tropical South Pacific.

In conclusion, coral diseases are playing an increasingly critical role in reef degradation, driving declines in coral populations (Moriarty et al., 2020; Vega Thurber et al., 2014). These effects are further exacerbated by climate-related stressors such as marine heatwaves and mass bleaching events, which are rising in frequency and intensity (Lafferty and Holt, 2003; Sokolow, 2009; Maynard et al., 2015; Burke et al., 2023). While much attention has focused on bacterial, fungal, and viral pathogens, our findings add to a growing body of evidence suggesting that lesions like MPS on *Porites* are both more widespread and more ecologically significant than previously recognized. By examining spatial patterns of MPS, we hope our study motivates future research into how these coral lesions are linked to human impacts. This is particularly important given the broad spatial extent and high intensity of occurrence of MPS observed across Mo'orea's north shore. These results highlight the urgent need for future mechanistic studies to better understand the environmental and biological drivers of MPS distribution especially as anthropogenic pressures on reef systems continue to grow.

CRediT authorship contribution statement

Ashlyn Ford: Writing – original draft, Visualization, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Richard Laplace:** Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **J. David Muñoz-Maravilla:** Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Sennai Habtes:** Visualization, Supervision, Investigation. **Paul Barber:** Writing – review & editing, Supervision, Project administration, Funding acquisition, Conceptualization. **Caitlin Fong:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Peggy Fong:** Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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