Coral Reefs
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RESEARCH

Larval dispersal models predict reefs that experience crown-of-thorns starfish outbreaks receive more larvae

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Abstract Crown-of-thorns starfish (COTS) are a leading cause of coral decline on the Great Barrier Reef (GBR), with the majority of their impact occurring during outbreaks. These outbreaks involve rapid increases in populations followed by abrupt declines, and spread between reefs via larval dispersal—a key process in COTS reproduction. Given the difficulty in quantifying dispersal empirically, predictions are instead formed using coupled models of ocean currents and larval biology. Previous efforts have linked dispersal models to COTS population dynamics, however do so indirectly, or at spatiotemporally limited scales. Using an improved set of dispersal estimates and expanded COTS monitoring data, we assess the role of dispersal in determining a reef's susceptibility to outbreaks. Our results indicate that while there is minimal evidence that dispersal patterns alone drive outbreaks, once combined with COTS population data it becomes clear that dispersal still plays a major role. By predicting COTS populations on undersampled reefs, we estimate that, on average, reefs that have experienced an outbreak receive 50–100% more larvae than those that have not. This is irrespective of whether we assume reefs hold their long-term predicted average COTS abundance, or their predicted maximum abundance. Given the difficulty in directly validating dispersal models, these results provide evidence that highlights their utility in understanding marine population dynamics. Furthermore, our results emphasise the critical role of resolving dispersal networks in guiding COTS control efforts. Specifically, they indicate that suppressing larval production through culling may reduce the risk of outbreaks on downstream reefs connected via larval dispersal.

Keywords Biophysical modelling · Larval dispersal · Crown-of-thorns starfish · Network theory · Pests

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Introduction

Irruptive species can exhibit rapid and extreme increases in abundance, interspersed with periods of low but nonzero abundance (Ostfeld and Keesing 2000). On coral reefs, including the Great Barrier Reef (GBR), crown-of-thorns starfish (COTS; *Acanthaster Spp.*) are a particularly damaging irruptive species. Given that their primary food source is coral, COTS are a major threat to coral cover on the GBR, and are estimated to be responsible for 42% of its decline between 1985 and 2012 (De'ath et al. 2012). The majority of this damage at individual reefs occurs during irruptions—referred to as "outbreaks"—that involve swift population increases followed by crashes over a 2–5-year period (Matthews et al. 2024). As such, understanding and predicting COTS population dynamics has been a key research focus for scientists and managers since the first outbreaks were detected in the 1960s (Endean 1982; Birkeland and Lucas 1990; Moran et al. 1992; Pratchett 2005; Deaker and Byrne 2022).

COTS outbreaks exhibit significant spatiotemporal variability (Vanhatalo et al. 2016; Pratchett et al. 2024), partly driven by outbreak "waves". These waves consist of a front of multiple outbreaking reefs across a latitudinal band that appear to originate in the Cairns–Cooktown region before travelling southward through the central GBR (Moran et al. 1992). This is contrasted by the southern Swains group of reefs that appear to experience almost endemic levels of high COTS abundances (Pratchett et al. 2024). However, while some reefs seem prone to outbreaks, others nearby appear resistant despite repeated sampling (Matthews et al. 2020). Understanding these patterns is crucial for guiding critical COTS culling operations, which have a demonstrated ability to protect the GBR's precious yet imperilled coral (Matthews et al. 2024). Several hypothesises attempt to explain these dynamics, including the availability of nutrients (Brodie et al. 2005; Wolfe et al. 2015; Brodie et al. 2017), overfishing of predators (Kroon et al. 2021), changes in environmental conditions (Kamya et al. 2014; Caballes et al. 2017), or a combination of multiple interacting factors (Wooldridge and Brodie 2015).

A key process underpinning multiple hypotheses is larval dispersal (Wooldridge and Brodie 2015), the mechanism by which COTS reproduce and spread their offspring between reefs. Larval dispersal involves the release of larvae into the water column, where they are transported by ocean currents. Larvae that survive and reach maturity can descend and settle when in the proximity of a reef. Here, they enter the benthic stage of their life cycle, with settlers that survive being recruited into the adult population of the reef.

It is hypothesised that as outbreak waves propagate through the GBR, outbreaking reefs produce immense quantities of larvae that subsequently settle at reefs not yet in an outbreak state. In the years following, these downstream reefs will experience a near-simultaneous maturation of an immense number of COTS, causing outbreaks that continue to spread like a chain of dominoes. This basic hypothesis has the advantage of being conceptually simple, and is supported by evidence of along-shore transport directions (Dight et al. 1990; Wooldridge and Brodie 2015) and exceptionally high larval production by adults (Conand 1985; Babcock et al. 2016).

To evaluate the role of larval dispersal in COTS outbreak dynamics, it would be valuable to measure patterns of larval dispersal directly, to determine whether outbreaking reefs do in fact receive higher numbers of settlers. However, such measurements are not feasible, as it is effectively impossible to track millions of microscopic larvae across the open ocean over hundreds of kilometres and several weeks. Given this limitation, COTS dispersal patterns are instead predicted by simulating the behaviour of larvae and their transport through ocean currents produced by hydrodynamic models (James et al. 1990; Hock et al. 2014, 2017). Some of the earliest applications of these "biophysical models" were developed for COTS to explain observed outbreak waves (Dight et al. 1990; James et al. 1990), and the approach has since been extended to other marine systems and taxa (Black et al. 1991; James et al. 2002; Murray and Gillibrand 2006). In other systems, these models have been independently validated using genetic parentage studies (Bode et al. 2019) and otolith microchemistry (Paoletti et al. 2021), providing confidence in their ability to reproduce key features of real-world dispersal patterns when appropriately parameterised.

In lieu of direct validation techniques for biophysical models of COTS, multiple studies have demonstrated relationships between biophysical model predictions and COTS populations. Some studies have used dispersal patterns to aid in predicting which reefs are likely to experience outbreaks, through logistic regression (Hock et al. 2014) and machine learning (Matthews et al. 2020). Other studies instead examined whether local characteristics of dispersal can explain which reefs experience outbreaks (Hock et al. 2014, 2017), without considering the size of the larvae-producing COTS populations at each reef. Furthermore, Hock et al. (2014) identify both the Cairns–Cooktown and Swains regions as areas with connectivity dynamics uniquely favourable for the initiation and spread of outbreaks. These predictions of COTS dispersal (Hock et al. 2014, 2017) are also used to drive COTS metapopulation models (Bozec et al. 2022) capable of recreating observed COTS outbreak dynamics (Skinner et al. 2024).

However, several dimensions of these analyses warrant further investigation. First, they often relied on temporally (Hock et al. 2014) and/or spatially limited (Hock et al. 2017) datasets. It is therefore unclear whether reefs without detected outbreaks are truly outbreak-free, or simply did not experience one during the survey period. Second, due to the scarcity of empirical data on COTS larval biology at the time, dispersal modellers incorporated large and sometimes uncertain assumptions about key traits such as maturation and mortality rates. Finally, due to contemporaneous limitations in computational power, the underlying hydrodynamic models (Hock et al. 2014, 2017) operated at spatial resolutions that constrain their ability to resolve fine-scale dispersal pathways around complex reef structures. For similar reasons, a single hydrodynamic model was used; however, subsequent work has identified that models with differing yet defensible modelling approaches can produce divergent estimates of COTS dispersal (Choukroun et al. 2025). Together, these limitations suggest that while larval dispersal information is clearly important for understanding and predicting outbreak dynamics, updated and expanded analyses are needed to strengthen these links.

Additionally, it is not clear whether elevated levels of larval production are the sole driver of dispersal-mediated outbreaks, or whether the influence of oceanographic conditions on dispersal pathways plays a role. For example, barriers formed by prevailing currents may isolate particular reefs from settlement, irrespective of larval production at upstream reefs (Teske et al. 2008; Thomas et al. 2014; Treml et al. 2015; Thompson et al. 2018). A common method for assessing the sole influence of dispersal patterns on population dynamics involves the use of metrics drawn from network theory (Rayfield et al. 2011; Keeley et al. 2021), a mathematical field focused on networks connecting a set of distinct nodes. Examples of simple network metrics applied to marine systems include the number of incoming and outgoing dispersal connections to a reef, which for COTS may influence the build-up of populations and their risk of spread, respectively. Similar metrics have been applied to larval dispersal networks to guide conservation actions (Treml et al. 2008; Hock et al. 2017), inform marine protected area designation (Andrello et al. 2015; Schill et al. 2015; Engelhard et al. 2017; Muenzel et al. 2023), and explain population dynamics (Hock et al. 2014; Cecino et al. 2021).

The recent development of COTS dispersal models that include empirically informed larval biology, multiple hydrodynamic models, and a higher spatial resolution (Choukroun et al. 2025) have improved our ability to form and analyse COTS dispersal networks. Furthermore, 41 years of extensive COTS monitoring data across the GBR (AIMS 2025; GBRMPA 2025) allow us to better understand long-term COTS population trends, and identify reefs that are prone to or devoid of outbreaks. In this paper, we assess whether predictions from larval dispersal models can explain differences between reefs with and without a history of COTS outbreaks. Specifically, we first determine whether differences are detectable solely based on predicted dispersal patterns without considering source populations, by examining metrics drawn from network theory. We then expand this approach by estimating larval production using COTS monitoring data, to examine whether reefs that experience outbreaks are predicted to receive more larval settlers than those that do not.

Methods

Our primary goal is to evaluate the importance of larval dispersal in individual COTS outbreaks, by comparing dispersal-mediated properties of reefs that do and do not experience outbreaks. This requires a consideration of both the networks formed by larval dispersal and the populations proliferating through them. In the sections that follow, we first describe the COTS monitoring data used in our investigation and define what differentiates an outbreak reef from a non-outbreak reef. Next, we detail our models of COTS larval dispersal and apply network-theoretic metrics to their outputs in an attempt to explain differences in each reef's susceptibility to outbreaks. Finally, we estimate long-term COTS abundances at all reefs on the GBR, before combining estimates with dispersal modelling to predict and contrast each reef's levels of larval settlement.

COTS monitoring data

Our observational data on COTS populations consist of COTS density estimates from both the Australian Institute of Marine Science's (AIMS) Long-Term Monitoring Program (LTMP, AIMS 2025) and the COTS Control Program (GBRMPA 2025). Both datasets consist of surveys conducted via manta tow, a standardised procedure which measures COTS abundance among other quantities. These surveys can be aggregated at the reef and year level to estimate COTS population density, in units COTS per tow. The AIMS LTMP dataset consists of 3206 aggregated COTS per tow observations from 1983 to 2024, and the COTS Control Program data adds 1979 observations from 2012 to 2025. To classify whether or not an outbreak has occurred on a reef in a given year, we use the standard outbreak definition: densities exceeding 0.22 COTS per tow indicate an outbreak (Moran and De'Ath 1992). We then classify reefs as an "outbreak reef" if at least one outbreak has been observed in any year and as a "non-outbreak reef" if an outbreak has never been observed for reefs with a minimum of 8 total yearly observations. This results in 283 reefs classified as outbreak reefs and 90 reefs classified as non-outbreak reefs, with their spatial distribution shown in Fig. 1.

Larval dispersal ensemble modelling

Ensemble modelling involves aggregating predictions from multiple competing models, often differentiated by factors such as their initial conditions or parameterisations. This process can result in improved accuracy compared to the individual component models, capture a wider range of outcomes, and address modelling uncertainty. In Choukroun et al. (2025), we estimated COTS dispersal patterns using an ensemble-based approach, which addressed uncertainty in the generation of the ocean currents used to advect simulated larvae. Specifically, we did so by estimating currents using three different hydrodynamic models, which despite utilising different model architectures and forcings, perform comparably when validated. Here, we extend this work by forming an expanded model ensemble that also considers uncertainty in COTS larval biology. In lieu of techniques capable of weighting individual ensemble members, we simply average our model predictions equally across different hydrodynamic models and larval biology characteristics. Once formed, these ensemble models estimate the probability that a larva produced at a reef will settle at a specific reef for a given spawning event, for all pairs of reefs on the

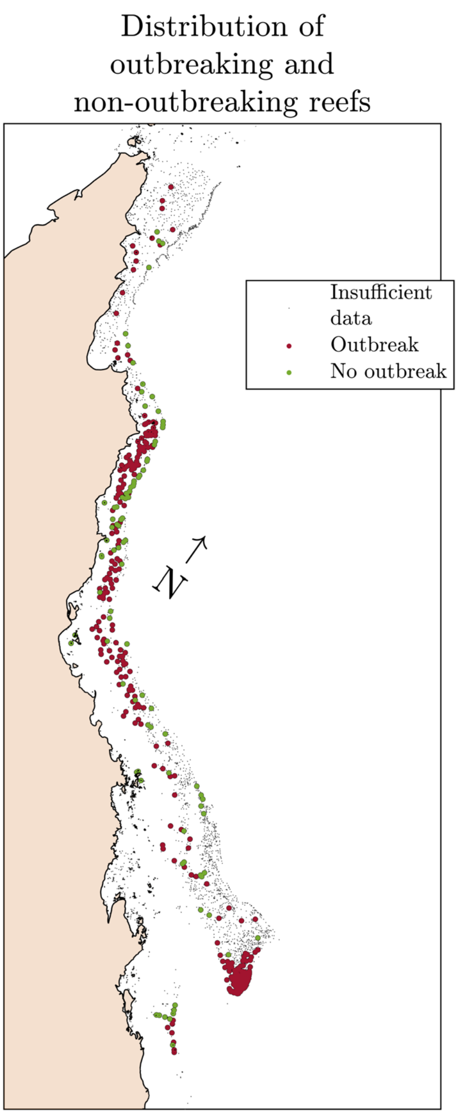

Fig. 1 Spatial distribution of outbreak and non-outbreak reefs across the Great Barrier Reef

GBR. We denote these probabilities "dispersal strengths", represented by $C_{i,j}$—the probability that a larva produced at reef i will settle at reef j. Below, we include a summary of the larval dispersal modelling procedure, with additional details included in Sect. S1 of Supplementary Materials.

Hydrodynamic modelling

The three hydrodynamic models used to compute ocean currents include SLIM (Lambrechts et al. 2008), GBR1 (Herzfeld 2006; Steven et al. 2019), and GBRL (James et al. 2002; Luick et al. 2007), each of which use alternative yet defensible physical assumptions and numerical techniques that lead to different predictions of dispersal (Choukroun et al. 2025). A summary of the hydrodynamic models is contained in Table 1, with a more comprehensive description and validation included in Choukroun et al. (2025) and the associated supplementary materials.

Larval releases and dispersal pathways

Simulated larvae were released from inside reef polygons to simulate spawning events, before being subjected to the ocean currents generated by the hydrodynamic models listed above. Releases were performed between December and January following observed COTS spawning patterns (Caballes et al. 2021) for spawning seasons from 2018–2019 to 2021–2022 for GBR1, and to 2022–2023 for the remaining models. For GBRL and SLIM, larvae were released on 10 distinct days per spawning season, whereas GBR1 involved continuous releases across 40 days per season. For GBR1, larvae remained at a depth of 0.5m below the surface, whereas in GBRL larvae were positively buoyant for the first 24 hr before generating two separate trajectories. In the first, larvae were centred at one-third of the height of the water column, with larvae centred at two-thirds of the height for the second.

Settlement radius

To account for the inability of hydrodynamic models to resolve sub-grid-scale processes, as well as uncertainty surrounding COTS larval settlement behaviour, we allow larvae to settle when in the proximity of a reef. To do so,

Table 1 Summary of physical and biological aspects of the hydrodynamic models used, reproduced from Choukroun et al. (2025)

Model	Horizontal resolution	Vertical resolution	Temporal resolution (LPT)	Baroclinic/ barotropic	Numerical scheme	Depth of egg releaes	Period modelled
GBR1	1 km	48 z-layers	60 min	Baroclinic	Finite difference	5 m	2018–2019 to 2021–2022
SLIM	250 m–4 km	2D depth-averaged	60 min	No depth	Finite element	NA	2018–2019 to 2022–2023
GBRL	1.85 km	6 σ-layers, barotropic	60 min	Barotropic	Finite difference	5 m	2018–2019 to 2022–2023

we specify a radius extending from the borders of each reef polygon, referred to as the settlement radius, and stipulate that it is only when a larva is within this radius that it can settle. We apply three different settlement radii: 0.5 km, 1 km, and 1.5 km, informed by the 1 km radius applied by Hock et al. (2014, 2017), and observations of COTS settlement at depths of up to 18 m (Wilmes et al. 2020). This is with the exception of the SLIM model, where positions were only recorded when larvae were within 1 km of a reef, precluding the application of a 1.5 km settlement radius.

Larval biology

Two key aspects of COTS larval biology are the rates at which larvae develop the ability to settle (competency) and experience mortality. These processes were represented by fitting piecewise curves described in Moneghetti et al. (2019) to experimental data on COTS competency and mortality from Pratchett et al. (2017b). Given that the data on COTS competency begin at 17 days post-fertilisation (DPF), yet Lucas (1973) estimated COTS may settle as early as 9 DPF, we fit three competency curves for a minimum time to competency of 9, 12, and 15 DPF. Similarly, mortality rates were only measured from 3 DPF, and so, mortality before 3 DPF was modelled using with an exponential decay with rate parameter 0.954 as estimated by Wilmes et al. (2018). Models are fit using a maximum likelihood method and are visualised in Fig. 2.

Forming the connectivity matrices and dispersal ensemble model

To estimate the probability a larva produced at one reef will settle at another, we must combine the tracked positions of each simulated larva with the settlement radii and larval biology detailed above. For each simulated larva, we approximate the competency and mortality curves (Fig. 2) by drawing a random sample from each, representing periods in which the simulated larva is competent and alive. This process is repeated separately for each of the competency curves fit, which vary in their minimum time of competency (t_c). The larva is then settled at the first reef whose settlement radius it enters while in a competent state, provided this occurs before mortality. For each simulated larva, we repeat this process 10000 times to produce many possible settlement events for a single larva's trajectory. By counting the frequency of these settlement events across each of the simulated larvae released from a reef, we compute $C_{i,j}$ values that correspond to the probability a larva produced at reef i will survive, mature, and settle at reef j. When collected across all i and j pairs, these values form a connectivity matrix that describes the entire COTS larval dispersal network across the GBR.

To form our ensemble, we create connectivity matrices separately for all possible combinations of the previously discussed factors. These include the four larval tracking models (as GBRL was split into two buoyancy levels), the three settlement radii (0.5 km, 1 km, and 1.5 km), and the three survivorship and competency distributions

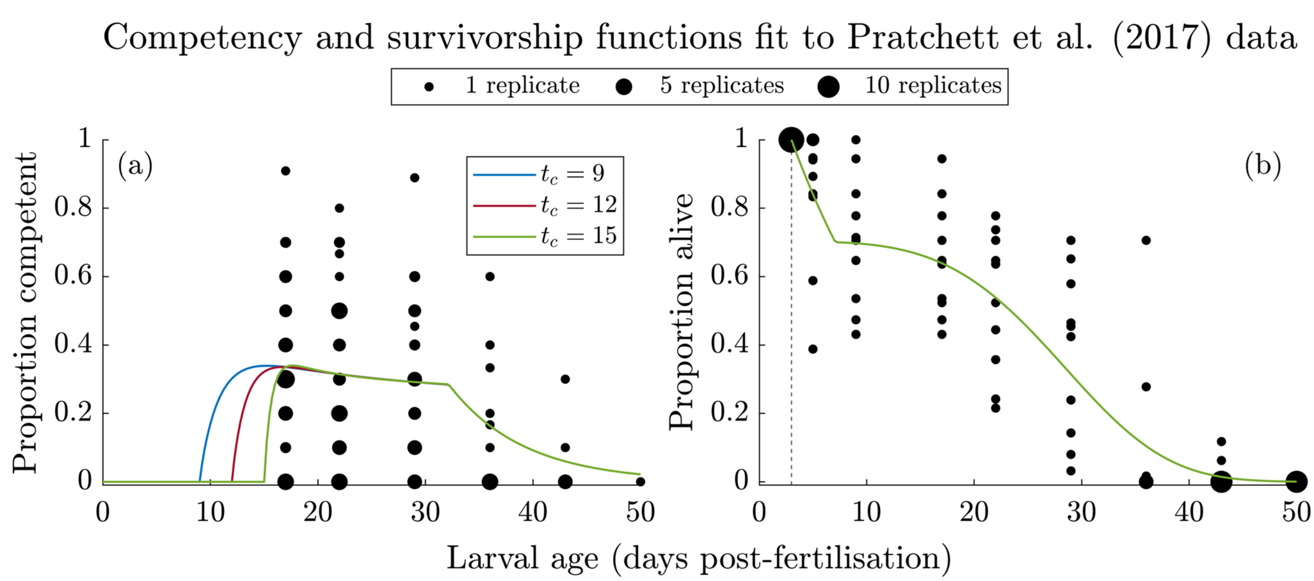

Fig. 2 Piecewise **a** competency and **b** survivorship curves described by Moneghetti et al. (2019) fit to experimental data on crown-of-thorns starfish larval development and mortality from Pratchett et al. (2017b). Experimental data consist of multiple replicates, with overlaps between replicates indicated by the size of data points. For competency, three curves are fit with a different minimum time of competency gain denoted t_c in days post-fertilisation

($t_c \in \{9, 12, 15\}$). As such, we form a total of 33 dispersal models, given a settlement radius of 1.5 km for SLIM is not possible. For use in this paper, we average across all 33 ensemble members to produce a single "global" model. First, we average connectivity matrices across settlement radii and competency distributions separately for each larval tracking model, before averaging across larval tracking models for each spawning season. Finally, we can average across the global model's predictions for each of the 5 spawning seasons, or examine them separately.

Network-theoretic analysis

Our first aim is to assess whether COTS outbreak patterns can be explained purely by dispersal patterns, by comparing network-theoretic metrics calculated using connectivity matrices for outbreak and non-outbreak reefs. While there are a plethora of network-theoretic metrics available (Minor and Urban 2008; Rayfield et al. 2011; Keeley et al. 2021), we consider a subset with a direct mechanistic interpretation of their potential role in outbreak formation. Importantly, we are interested in both long-term larval dispersal patterns and spikes in settlement that may trigger outbreaks. We therefore conduct our analyses twice, first using a single connectivity matrix that has been averaged across the 5 spawning seasons to represent long-term dispersal patterns. However, Choukroun et al. (2025) demonstrated that modelled COTS dispersal strengths ($C_{i,j}$ values) on the GBR can vary significantly between spawning season. Further analyses by Stewart and Bode (2025) found that the median coefficient of variation for COTS dispersal strengths between spawning seasons was approximately 3, with individual values ranging from 0 to 5.5. As such, we contrast our long-term analysis by also computing metric values for each of the 5 connectivity matrices representing the 5 spawning seasons modelled, and record each reef's maximum values.

First, we calculate the constant density settlement—that is, the larval settlement we would expect if all reefs released the same number of COTS larvae per unit area. As the levels of potential settlement increase, we would expect the probability of an outbreak occurring to follow suit. This is equivalent to calculating the in-strength of a node, i.e. the sum of weights of incoming connections, however, scaled by the area of the source reef to account for the disparity in reef sizes. We denote the constant density settlement for reef j as $s_j^{(\mathrm{CD})}$, which is calculated as follows:

$$s_j^{(\mathrm{CD})} = \sum_i C_{i,j} a_i, \tag{1}$$

where a_i is the area of reef i. Another factor to consider is the number of reefs that could supply larvae to a given reef, as we might expect that reefs with more potential sources may be more likely to experience an outbreak. We therefore compute the in-degree for each reef, denoted $s_j^{(\mathrm{ID})}$, which counts the number of potential source reefs for reef j:

$$s_j^{(ID)} = \sum_i I(C_{i,j} > 0), \tag{2}$$

where $I(\cdot)$ is the indicator function, which takes a value of 1 if its condition is true (in this case, whether a connection exists from reef i to j). However, given the ensemble modelling approach employed across multiple spawning events, many connections between reefs with negligible strengths are formed. To avoid their influence, we also compute the "substantial" in-degree, which only counts connections for which at least 1% of the average reef's settling larvae would traverse:

$$s_j^{(\mathrm{SID})} = \sum_i I(C_{i,j} > 0.0015), \tag{3}$$

where 0.0015 represents 1% of the settling larvae from the average reef, given that 15% of the average reef's larvae are predicted to survive and settle. In a similar manner, we also compute a reef's substantial in-component, given that Hock et al. (2014) identified in-component as a statistically significant predictor of COTS outbreaks. The in-component simply refers to the number of reefs that can reach a given reef across an unlimited number of steps through a dispersal network. As such, we would expect that reefs with a higher in-component to have an increased risk of outbreaks, given their elevated levels of connectedness. Our substantial version using only connections with strengths greater than 0.0015 and only considers 5 steps through the network—without either constraint, all reefs can connect to almost all others in the network, rendering comparisons redundant.

Another mechanism that may contribute to outbreak formation is the return of larvae to their source reef, creating a positive feedback loop. We therefore consider the local retention of a reef, which corresponds to $C_{j,j}$—the probability that a larva produced at reef j will settle at reef j. Similarly, Wooldridge and Brodie (2015) hypothesised that highly connected regions could form feedback loops between groups of reefs, leading to higher probabilities of outbreaks occurring. We therefore calculate a measure of clustering, corresponding to the probability that a reef's source reef is also supplying larvae to other source reefs, multiplied by the number of source reefs. Similar to previous metrics, we do so only using substantial connections and therefore calculate this metric as follows:

$$s_j^{(\mathrm{CL})} = \sum_i \left(I(C_{i,j} > 0.0015) \frac{\sum_{k \in K} I(C_{i,k} > 0.0015)}{|K|} \right), \tag{4}$$

$$\text{where } C_{k,j} > 0.0015,\ \forall k \in K,$$

where $s_j^{(CL)}$ is our metric of clustering for reef j and K is the set of all substantial sources for reef j.

Finally, we include two additional metrics that act as an extension to the in-degree, namely by considering not just the number of incoming connections to a node, but also the "importance" of each connection's source node. Here, the importance of a node is dependent on both the importance of its source nodes and the strength of their connections, and is thus calculated in a recursive manner. As such, we would expect reefs with a higher "importance" value to be more susceptible to outbreaks. Both metrics are computed using MATLAB's "centrality()" function with default settings (The MathWorks Inc. 2023).

The first is PageRank (Page et al. 1999), the original algorithm used in the Google Search engine to rank websites. Effectively, it represents a probability distribution of a random walker's position as they traverse a directed network. The walker travels stochastically between the nodes through the links defined by the network, while periodically jumping at random to a new node before continuing to traverse the network. In our application, the links between nodes consist of our $C_{i,j}$ values—therefore, the random walker is more likely to travel between reefs with a high probability of dispersal.

The second is the authority score (Kleinberg 1999), another iterative algorithm aimed at scoring the importance of websites. The authority score aims to identify "authoritative" websites, while simultaneously identifying "hubs". Both are defined in a mutually reinforcing relationship, where hubs are pages that link to many good authoritative pages, and authoritative pages have many incoming links from good hubs. The authority score of a page is therefore equal to the sum of the hub scores of pages with incoming links, and the hub score is equal to the sum of the authority scores of the pages it links to. In our application, these sums are weighted by the dispersal strengths between reefs, $C_{i,j}$. As such, we would expect reefs with a high hub score to play a role in spreading outbreaks, while reefs with a high authority score to receive more larvae, and thus have an elevated risk of experiencing an outbreak.

Larval settlement estimation

After analysing the isolated effect of dispersal patterns using network theory, we extend our focus to consider the size of COTS populations and their associated production of larvae. Specifically, we estimate larval settlement at outbreak and non-outbreak reefs, which requires us to supplement observational data with predictions of COTS populations for undersampled or unsampled reefs. Failure to do so would lead to estimates of larval settlement with high variability and questionable accuracy that would be sensitive to the spatial distribution of COTS density observations. Similar to our network-theoretic analysis, we consider both average levels of larval settlement and elevated pulses that may precede outbreaks. This is achieved by estimating both average and maximum COTS population sizes, the latter aimed at being representative of increased larval production during outbreak waves.

First, we summarise observed COTS density datasets to estimate long-term COTS densities, computing the mean, median, and maximum COTS densities for reefs with 4 or more observations. This results in 404 reefs out of 3861 with long-term density estimates, with the remaining 3457 reefs requiring predictive estimates (see Fig. S13). For this estimation process, we trialled three different methods: spatial averaging, a spatially constrained K-nearest neighbours approach, and boosted regression trees.

Spatial averaging involved predicting the density statistic by taking the average value of the statistic from reefs in a 110 km radius, given this is the distance at which 90% of COTS larvae will settle (Fig. 3). For the spatially constrained K-nearest neighbours (KNN) approach, the missing density values were assigned to the average value of the density observed at up to N closest neighbours by Euclidean distance within a radius of r km from the reef being estimated. Finally, boosted regression trees (BRTs) were applied using the covariates summarised in Tables 6 and 7 in Appendices A and B, using the R package "xgboost" (Chen et al. 2024). These covariates included variables capturing environmental conditions, disturbance history, spatially constrained KNN estimates of COTS populations, and predictors from a previous model of COTS outbreaks (Matthews et al. 2020).

Observations of long-term COTS densities were split into a held-out testing set consisting of 10% of the data, with the remaining 90% used for training models. Using this training set, models were tuned and evaluated using Monte Carlo cross-validation with a 90–10 train–validation split over 20 repetitions. Cross-validation indicated that BRTs minimised the root mean square error (RMSE) for the mean and median COTS densities, with spatially constrained KNNs minimising the RMSE for the maximum COTS density. The performance of these methods during both cross-validation and the held-out testing set is detailed in Table 2, with further detail on included in the Supplementary Material. When predicting larval settlement, reefs with observed long-term COTS density estimates were set to their observed values, with the remainder predicted using the optimal models detailed above (spatially constrained KNN for maximum densities, and BRT for median and mean).

We can then estimate average larval settlement at each reef as follows:

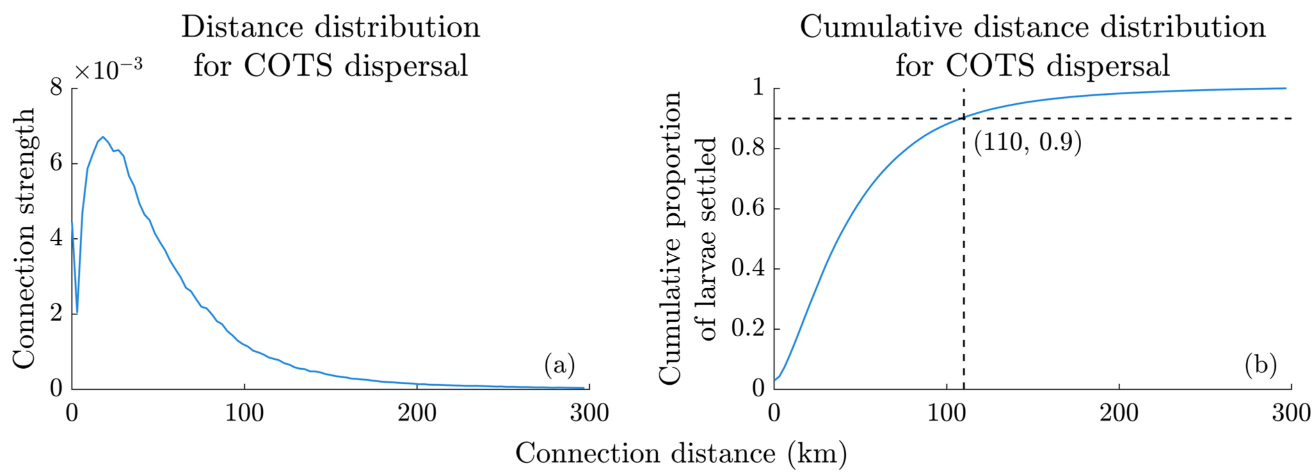

Fig. 3 Relationships between distance and COTS settlement probabilities. This includes **a** the relationship between distance and dispersal strength averaged ($C_{i,j}$) across the GBR, and **b** the cumulative proportion of settled larvae with respect to the distance from the source reef

Table 2 Cross-validation and testing set accuracy metrics for estimating the long-term mean, median, and maximum COTS densities at unsampled reefs

Density statistic	Estimation method	Cross-validation		Test set	
		RMSE	R^2	RMSE	R^2
Mean	BRT	1.16	0.229	1.1	0.545
Median	BRT	0.21	0.099	0.23	0.08
Maximum	KNN	1.28	0.254	5.63	0.307

RMSE represents the root mean square error between observations and predictions, and R^2 represents the coefficient of determination between observations and predictions. BRT indicates boosted regression trees were used for density estimation, whereas KNN refers to spatially constrained K-nearest neighbours

$$s_j = \sum_{i=1}^{R} C_{i,j} a_i d_i, \tag{5}$$

where s_j is the estimated larval settlement at reef j, R is the total number of reefs (here 3861), and d_i is our estimate for COTS density, which could be the mean, median, or maximum. To ensure any differences in larval settlement are not driven purely by larvae settling at their natal reef, we also examine levels of self-recruitment predicted purely by biophysical modelling. Here, we define self-recruitment as the proportion of larvae settling at a reef that were produced at the same reef, without considering the size of source populations. Self-recruitment is therefore calculated as $C_{i,i} / \sum_j C_{j,i}$. Additionally, we repeat our analyses of larval settlement twice: first with the effects of self-recruitment disabled, and the second under the worst-case connectivity conditions. The first case involves manually setting $C_{i,i} = 0$, and the second requires the estimation of larval settlement using connectivity matrices from each of the 5 spawning seasons separately, before taking the maximum value for each reef.

Statistical testing

We test for differences in the distributions of network-theoretic metrics and larval settlement for outbreak and non-outbreak reefs using a two-sample Kolmogorov–Smirnov (KS) test. The two-sample KS test is a nonparametric test used to determine whether two samples were drawn from the same (albeit unknown) probability distribution. Next, we test for differences between the median values of network-theoretic metrics and larval settlement at outbreak and non-outbreak reefs, using Mood's median test. Mood's median test is another nonparametric test, used to determine whether the median values of the populations from which two or more samples are drawn are equivalent. We visualise the distribution of values using both boxplots and kernel density estimates produced using MATLAB's default settings.

Results

Network-theoretic metrics

For most of the network-theoretic metrics examined, statistically significant differences between outbreak and non-outbreak reefs were not detected when using both temporally averaged connectivity and yearly maximums (Tables 3 and 4). When differences were detected, they were either in direct contrast to their expected role in driving outbreaks, or quantitatively minor. For example, both local retention and authority score exhibited statistically significant differences in distribution and median value for both their averaged and maximum yearly values. However, mean values of local retention were 14% and 18% higher at non-outbreak reefs for averaged and maximum connectivity, respectively. Similarly, mean values of authority were 128% higher at non-outbreak reefs when using averaged connectivity, and 100% higher when using maximised connectivity. This is in spite of the fact that we would expect the opposite relationships to emerge, as higher values in either metric could be hypothesised to increase a reef's susceptibility to outbreaks.

The only other metric to exhibit statistically significant differences in median values was PageRank when using the averaged connectivity matrix, with mean values 10% higher on outbreak reefs. While this represents the expected relationship, the difference is minor, not statistically significant when using maximised connectivity, and the distributions of values remain markedly similar between outbreak and non-outbreak reefs (Figs. 4 and 5). The only remaining statistically significant differences detected were the distributions the substantial in-component. While median values do not

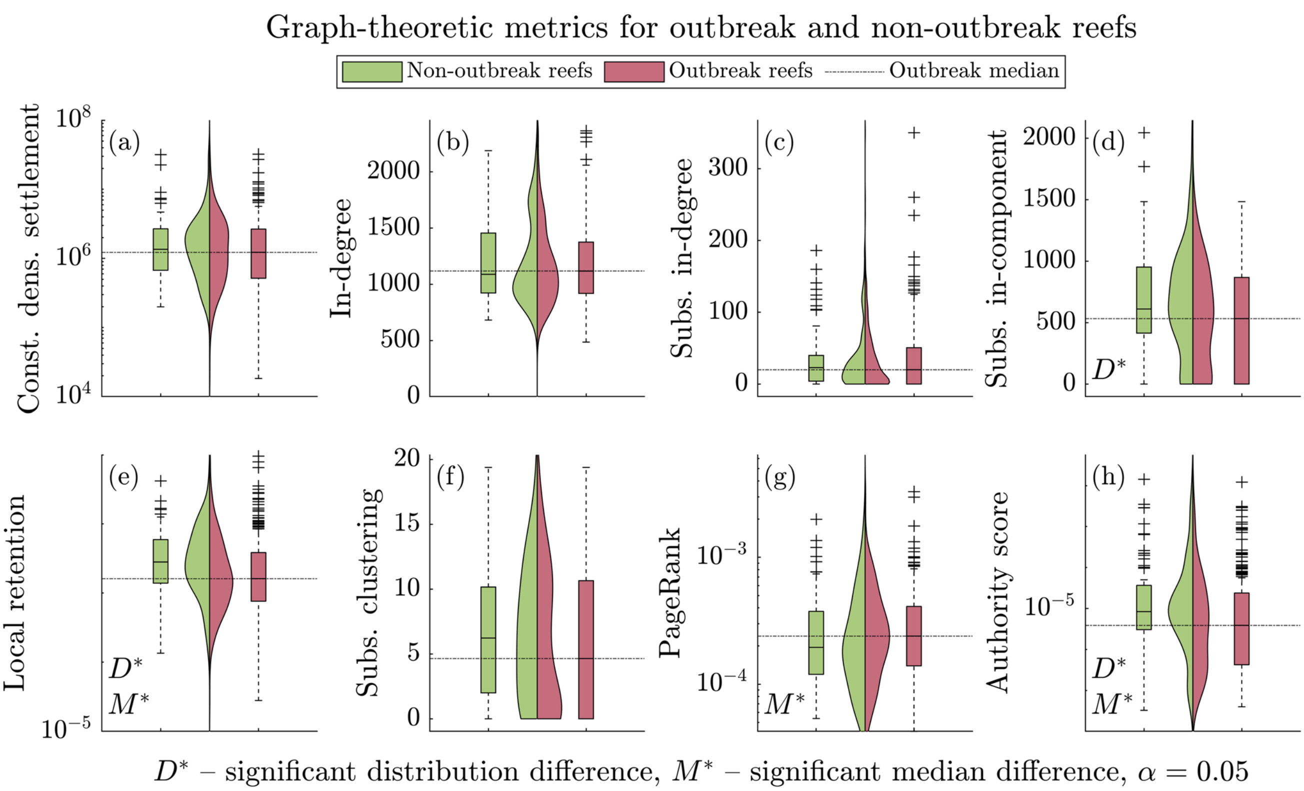

Fig. 4 Network-theoretic metrics at both outbreak and non-outbreak reefs, including **a** constant density settlement, **b** in-degree, **c** substantial in-degree, **d** substantial in-component, **e** local retention, **f** substantial clustering, **g** PageRank, and **h** authority score. Here, the substantial prefix indicates that metrics are computed only using connections for which greater than 1% of an average reef's settling larvae would traverse

Table 3 Summary of methods and statistical test results comparing network-theoretic metrics at outbreak and non-outbreak reefs

Metric	Mean metric value		K–S test p-value	Median test p-value
	Non-outbreak	Outbreak		
Constant density settlement	2.4×10^6	2.2×10^6	0.25	0.31
In-degree	1.2×10^3	1.2×10^3	0.53	0.49
Substantial in-degree	34	34.9	0.079	0.65
Substantial in-component	653	508	0.023	0.12
Local retention	0.0048	0.0042	0.0026	6.3×10^{-4}
Clustering	6.42	5.79	0.1	0.085
PageRank	3×10^{-4}	3.3×10^{-4}	0.16	0.032
Authority score	3.2×10^{-4}	1.4×10^{-4}	2.6×10^{-4}	6.3×10^{-4}

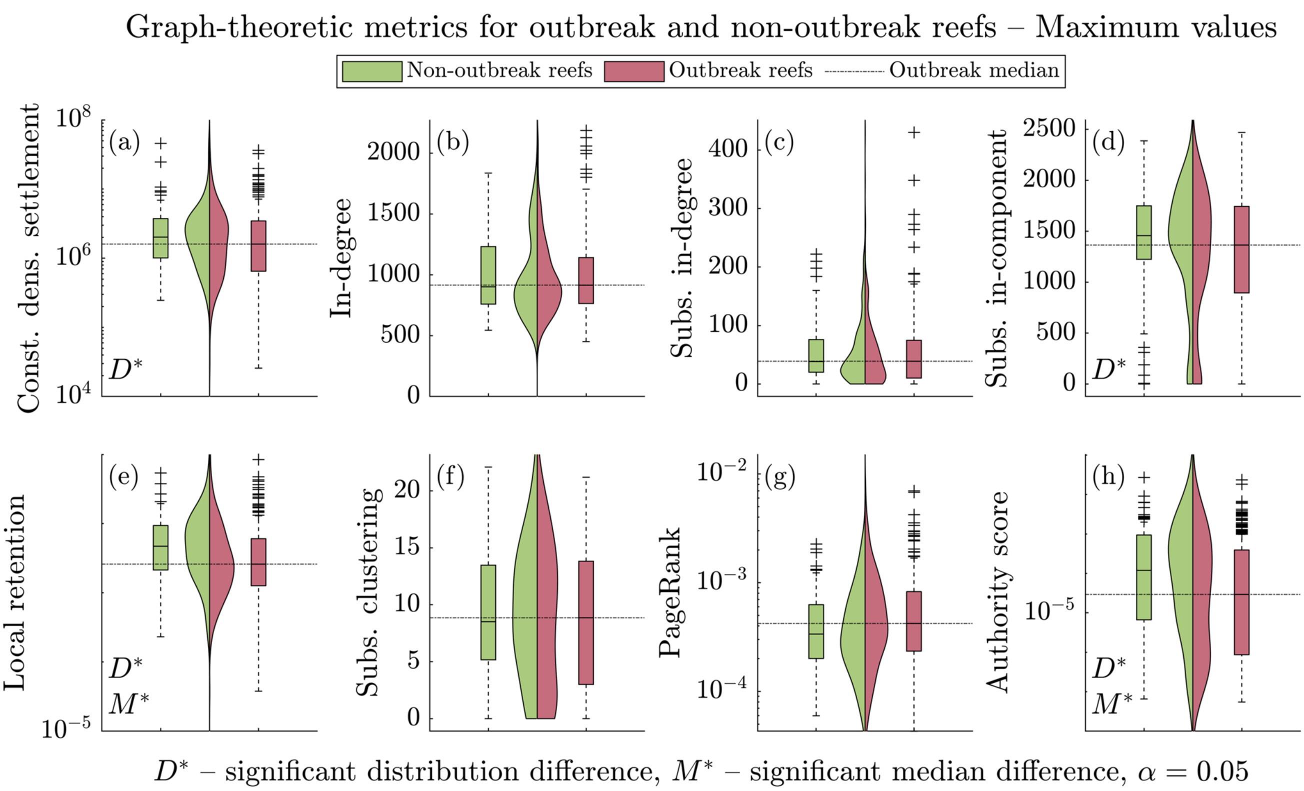

Fig. 5 Maximum value of network-theoretic metrics over the 5 spawning seasons modelled (2018–2019 to 2022–2023) at both outbreak and non-outbreak reefs. These metrics are the **a** constant density settlement, **b** in-degree, **c** substantial in-degree, **d** substantial in-component, **e** local retention, **f** substantial clustering, **g** PageRank, and **h** authority score. Here, the substantial prefix indicates that metrics are computed only using connections for which greater than 1% of an average reef's settling larvae would traverse

Table 4 Summary of methods and statistical test results comparing the maximum yearly values of network-theoretic metrics at outbreak and non-outbreak reefs over the 5 spawning seasons modelled (2018–2019 to 2022–2023)

Metric	Mean metric value		K–S test p-value	Median test p-value
	Non-outbreak	Outbreak		
Constant density settlement	3.3×10^6	2.8×10^6	0.042	0.14
In-degree	993	989	0.63	0.78
Substantial in-degree	54.2	54.1	0.3	0.78
Substantial in-component	1.4×10^3	1.2×10^3	0.018	0.32
Local retention	0.0072	0.0061	0.0019	0.0071
Clustering	9.37	8.61	0.1	0.83
PageRank	5×10^{-4}	6.9×10^{-4}	0.14	0.096
Authority score	0.0012	6.2×10^{-4}	0.0017	0.027

differ to a statistically significant degree, the distribution of substantial in-component values appears more negatively skewed at outbreak reefs when using both averaged connectivity and maximum values (Figs. 4 and 5). As such, mean values are 29% and 17% higher at non-outbreak reefs, which once again opposes the expected relationship between the substantial in-component and outbreaks.

Predicted larval settlement

Results indicate that the distributions of estimated larval settlement at outbreak and non-outbreak reefs differ to a statistically significant degree (Table 5). Furthermore, statistically significant differences in median estimated settlement were also detected, with outbreak reefs experiencing higher median settlement (Fig. 6). Similarly, mean larval settlement was approximately 86%, 48%, and 104%

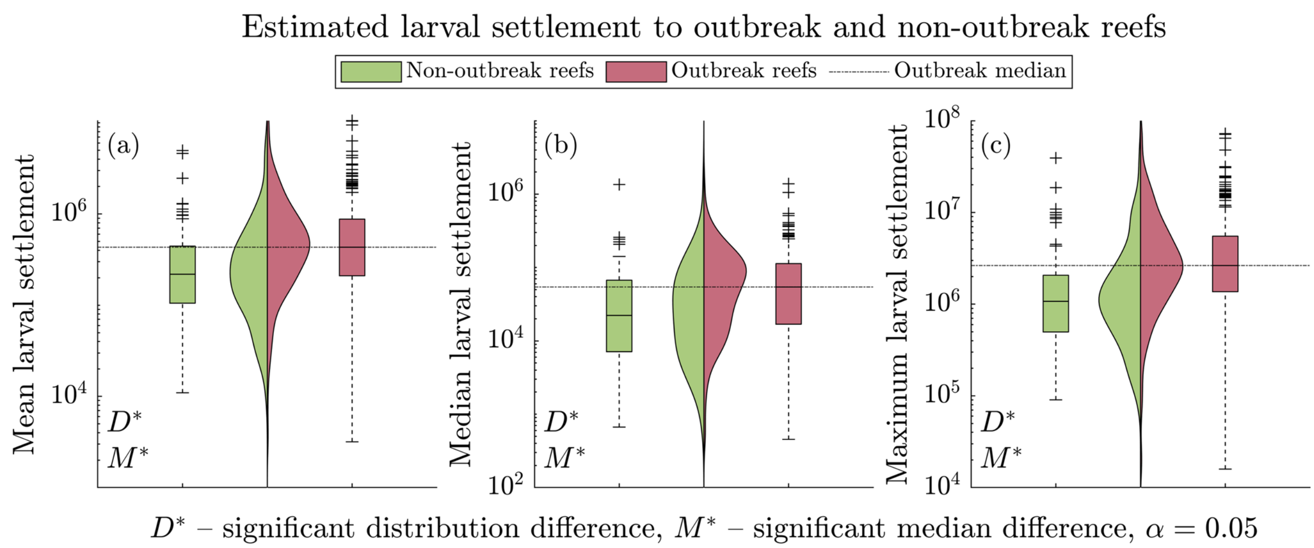

Fig. 6 Estimated larval settlement at to outbreak and non-outbreak reefs when it is assumed that all reefs on the GBR have their **a** mean COTS density, **b** median COTS density, and **c** maximum COTS density

Table 5 Summary of methods and statistical test results comparing estimates of larval settlement at outbreak and non-outbreak reefs

COTS density assumed	COTS density estimation method	Mean predicted larval settlement		K–S test *p*-value	Median test *p*-value
		Non-outbreak	Outbreak		
Mean	BRT	4.3×10^5	8×10^5	2×10^{-5}	4.9×10^{-6}
Median	BRT	6×10^4	8.9×10^4	0.0011	7.8×10^{-4}
Maximum	KNN	2.7×10^6	5.5×10^6	1.1×10^{-8}	3.1×10^{-8}

BRT indicates that long-term COTS density statistics were computed with boosted regression trees, while KNN indicates a K-nearest neighbours approach was utilised

higher at outbreak reefs when assuming reefs hold their mean, median, and maximum COTS densities, respectively. Additionally, median larval settlement at outbreak reefs is higher than approximately 75% of non-outbreak reefs, irrespective of the COTS density assumed (Fig. 6). These outcomes were retained when repeating the analysis using the worst-case connectivity conditions, producing extremely similar results (see Table S8 and Fig. S8 in Supplementary Materials).

Removing local retention and repeating our analyses did not significantly alter our results (see Table S7 and Fig. S7 in Supplementary Materials). This suggests that our results are not due to elevated levels of larvae being produced at outbreaking reefs, which then return to the same reef. The distribution of self-recruitment values—calculated without considering source population sizes—indicates that the majority of reefs receive less than 10% of their larvae from themselves, with half of reefs receiving less than 1% (Fig. 7). Furthermore, results were consistent irrespective of the technique used to estimate COTS densities at unsampled reefs, including an approach for which only observed densities were used (see Figs. S9–S12 in Supplementary Materials).

Discussion

This study represents an expanded and substantially refined investigation into the relationship between COTS outbreaks and larval dispersal, and reaffirms the previously established links between the two. While dispersal patterns exhibit only minor differences across outbreak and non-outbreak reefs, when combined with COTS population data substantial and statistically significant differences emerge. Specifically, we find that outbreak reefs receive more larvae on average than non-outbreak reefs. These findings are robust to the method used to estimate COTS populations at under or unsampled reefs, as well as the inclusion of local retention.

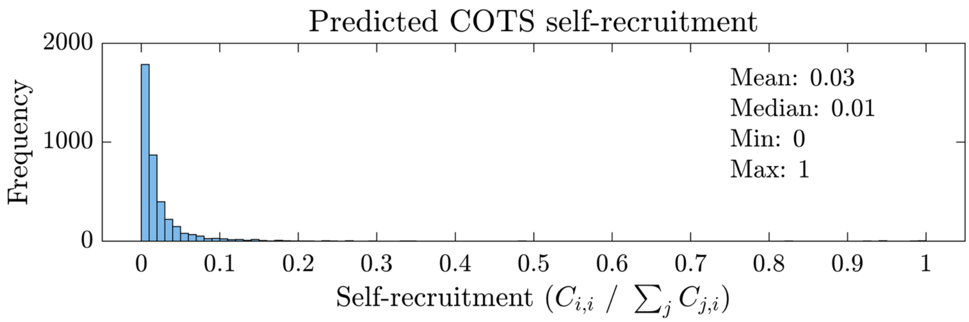

Fig. 7 Estimated self-recruitment across all reefs on the Great Barrier Reef. Self-recruitment is an estimate of the proportion of larvae settling at a reef that were produced on the same reef, here based only on modelled dispersal without consideration of population density. $C_{i,j}$ represents the probability that a COTS larva produced at reef i will survive and settle at reef j, based on larval dispersal modelling

Our results mirror previous findings by Hock et al. (2014, 2017) and Matthews et al. (2020), while extending upon their approaches. Hock et al. (2014) demonstrated that predicted dispersal strength to reefs experiencing outbreaks was a statistically significant predictor of COTS detection at reefs without any recently observed COTS. Additionally, they used a reef's in-component, a weighted composite of in-degree and in-strength, and the weighted composite score of a reef's neighbours in a logistic regression of COTS outbreak status. However, only the in-component proved to be a statistically significant predictor. Both analyses, however, were constrained to smaller temporal scales than our study, focusing on outbreak transmission among 17 source–destination pairs between 2006 and 2011, and 251 reefs between 2000 and 2012 for outbreak detection. Similarly, Hock et al. (2017) find that reefs predicted by dispersal models to experience high larval settlement had significantly higher COTS densities, albeit only for data collected in the Cairns–Cooktown region between 2013 and 2015. In contrast, our analyses consider the outbreak histories of 373 reefs, informed by data from 1983 to 2025.

Based on the same larval dispersal predictions, Matthews et al. (2020) demonstrate that the strength of connections to reefs that have experienced an outbreak is a strong predictor of a reef's susceptibility to outbreaks. However, along with the studies discussed above (Hock et al. 2014, 2017), this approach does not directly calculate larval settlement levels. Furthermore, these studies did not apply any metrics that account for the variation in the physical size of source reefs, which can vary significantly. Such differences would impact the quantity of larvae produced by each outbreaking reef, as COTS outbreaks are defined by population density rather than number of individuals. Additionally, they do not account for the spatial distribution of sampling effort, which along with source reef size are addressed in our work. While not based on survey data, these issues were addressed in a simulation study by Skinner et al. (2025) who directly calculate COTS larval settlement on the GBR, finding it negatively impacts COTS control benefits in forecasted future scenarios.

Finally, previous studies were limited by both the knowledge of COTS larval biology and computational power available at the time. Regarding the former, a lack of empirical data necessitated the approximation of larval competency and mortality rates in previous COTS dispersal models. We address these limitations by fitting competency and mortality functions to experimental data from Pratchett et al. (2017b), and account for uncertainty in the overall modelling process using an ensemble modelling approach. For the latter, previous studies applied hydrodynamic models with horizontal resolutions of approximately 4 km (Hock et al. 2014, 2017), which is coarse relative to the size, spacing, and geometry of reefs on the GBR. At this resolution, it is particularly difficult to resolve the fine-scale current structures around individual reefs that are thought to be responsible for much of local retention (Saint-Amand et al. 2023). To a lesser extent, the same limitation reduces the accuracy with which inter-reef dispersal can be predicted (Saint-Amand et al. 2023), especially for closely spaced reefs embedded within a dense reef matrix. Advances in computational power have since enabled the development of models at higher spatial resolutions, such as those applied in our work. While increasing resolution does not eliminate these challenges entirely, it is likely to mitigate them by better resolving flow features around each reef, thereby improving predictions of both local retention and inter-reef connectivity. We also apply multiple hydrodynamic models, as models with differing yet defensible architectures can perform similarly in flow field validation yet provide divergent COTS dispersal predictions (Choukroun et al. 2025).

Regardless of improvements to dispersal models, accurately capturing larval dispersal patterns remains a challenge. For example, due to computational limitations only

5 spawning seasons were modelled, which will likely fail to capture all possible dispersal patterns given their significant temporal variability (Harrison et al. 2020; Stewart and Bode 2025). Another limitation is that we do not consider spatiotemporal variability in environmental conditions such as temperature and nutrient concentration, despite their influence on the mortality and development of COTS larvae (Fabricius et al. 2010; Kamya et al. 2014; Lamare et al. 2014; Wolfe et al. 2015, 2017; Pratchett et al. 2017b; Uthicke et al. 2018).

The extent of these limitations would be better understood, were it possible to perform direct validation. Unfortunately, they are no genetic parentage datasets that could be utilised to test model predictions (Bode et al. 2019), and COTS population genetics across the GBR are too homogeneous to facilitate comparisons to dispersal models (Harrison et al. 2017). Additionally, a method equivalent to otolith microchemistry—commonly applied in fish to trace natal origins (Jones et al. 1999)—has yet to be developed for the species. Despite the lack of direct validation, this work contributes to the growing body of evidence that modelled COTS dispersal patterns can be related to COTS density observations (Hock et al. 2014, 2017; Matthews et al. 2020), constituting an approximate form of validation.

Such limitations in our dispersal model may explain the lack of significant differences in network-theoretic metrics between outbreak and non-outbreak reefs, as well as the overlap in predicted levels of larval settlement (Fig. 6). The latter, however, could also be an indication that larval settlement is not the sole determinant of outbreak formation. Instead, it is likely post-settlement juvenile and adult mortality play a role, perhaps driven by the availability of juvenile and adult food sources (crustose coralline algae and coral, respectively; Yamaguchi 1974). Additional factors may include the availability of suitable settlement substrate (Wilmes et al. 2020), environmental conditions such as nutrient content and temperature, and exposure to disturbances such as heatwaves and cyclones (Matthews et al. 2020). In this sense, the substantial overlap in larval settlement between outbreak and non-outbreak reefs is unsurprising, as COTS population dynamics are likely to be driven by multiple interacting factors (Wooldridge and Brodie 2015; Pratchett et al. 2017). Finally, our predictive models of COTS densities retain unexplained variance (Table 2), and despite their clear utility, the manta tow surveys they are trained upon are subject to observer error (Fernandes et al. 1990; Chandler et al. 2023).

A key assumption made in our estimation of larval settlement is that there is no density dependence on the production of larvae. While observational and modelled experiments demonstrate a relationship between distance and fertilisation success for COTS (Babcock and Mundy 1992; Babcock et al. 1994; Rogers et al. 2017), the relationships between density, aggregation, and fertilisation success have yet to be empirically quantified. For similar reasons, we produce estimates of larval settlement, not recruitment. While the latter would be a better predictor of adult COTS populations, the relationship between settler density and recruitment has also not been empirically established for COTS (Pratchett et al. 2017). These relationships are likely nonlinear but monotonic, meaning that increasing settlement will increase recruitment, but not necessarily in direct proportion (e.g. doubling settlers may not double recruits). Replacing settlement with recruitment would probably have the largest impact on the effect sizes we estimate, though it is possible it could also affect the statistical significance of differences between groups. Another limitation of this work is the use of long-term COTS density estimates when estimating larval settlement, given the transient nature of outbreaks. However, attempts to hindcast COTS densities at a yearly frequency revealed poor accuracy that would compromise our ability to draw defensible conclusions.

Our results reinforce the conclusion that while larval dispersal patterns are not the sole cause of COTS outbreaks, they still play a pivotal role. Models of dispersal are therefore critical to understanding and predicting COTS populations, facilitating more effective COTS control decision-making. For example, our results strongly suggest a benefit of targeting reefs with a high risk of spreading COTS larvae, given the potential to suppress outbreaks at reefs they are connected to via dispersal. This presents a potential mechanistic explanation for the findings of Matthews et al. (2024), who report regional benefits from COTS culling even at reefs without active COTS control. More generally, our work reaffirms links between larval dispersal predictions and population dynamics, and highlights their essential role in guiding efforts to preserve the world's coral reefs in the face of continuing existential threats.

Appendix A Covariates List

Table 6 List of predictors used in our model and their associated sources and citations

Code	Description	Units	Years	Source	COTS Reference
coralHabProp	Proportion of reef predicted to be coral habitat, with missing values imputed using a spatial KNN and GBR average	0–1	2018	Roelfsema et al. (2021)	
x	Longitude of reef centroid	°			Vanhatalo et al. (2016)
y	Latitude of reef centroid	°			Vanhatalo et al. (2016)
weightedInStrength	Sum of incoming dispersal strengths weighted by area of source reef	N/A	N/A	Calculated using COTS dispersal models Choukroun et al. (2025)	
inDegree	Number of nonzero incoming dispersal strengths	N/A	N/A	Calculated using COTS dispersal models Choukroun et al. (2025)	
cotsPerTowMed-Imput	Imputed median observed COTS density using a spatial KNN, only used when estimating median COTS density	COTS per manta tow	1986–2025	Calculated using COTS manta tow data	
cotsPerTowMean-Imput	Imputed mean observed COTS density using a spatial KNN, only used when estimating mean COTS density	COTS per manta tow	1986–2025	Calculated using COTS manta tow data	
cotsPerTowMax-Imput	Imputed maximum observed COTS density using a spatial KNN, only used when estimating maximum COTS density	COTS per manta tow	1986–2025	Calculated using COTS manta tow data	
totCulled	Total number of COTS culled from a reef	COTS	1986–2025	Calculated using COTS culling data	Matthews et al. (2024)
bottomTimeTot	Total culling time at a reef	minutes	1986–2025	Calculated using COTS culling data	Matthews et al. (2024)
cpueMean	Mean catch per unit effort during COTS culling, averaged across all years of culling	COTS per minute	1986-2025	Calculated using COTS culling data	Matthews et al. (2024)
shelfPos	Shelf position—inner, outer, and mid	categorical	N/A	Matthews et al. (2020)	Vanhatalo et al. (2016)
dist2Shore	Distance from shore, related to crustose coralline algae abundance	km	N/A		Vanhatalo et al. (2016) Fabricius and De'ath (2001)
cycImpactMean	Mean yearly cumulative wind speed experienced by reefs due to cyclonic activity	mh s^{-1}	1980–2024	BoM (2025)	
cycImpactSd	As above, but the standard deviation	mh s^{-1}	1980–2024	BoM (2025)	
cycImpactMax	As above, but the maximum	mh s^{-1}	1980–2024	BoM (2025)	
cycImpactMin	As above, but the minimum	mh s^{-1}	1980–2024	BoM (2025)	
rubbleProp	Proportion of reef predicted to be rubble, with missing values imputed using a spatial KNN and GBR average	0–1	2018	Roelfsema et al. (2021)	Wilmes et al. (2020)
chlAMean	Mean surface Chlorophyll *a* concentration in a 110 km radius of each reef between December and February inclusive	µg L^{-1}	2002–2025	NASA (2025)	Fabricius et al. (2010) Uthicke et al. (2018) Wolfe et al. (2015, 2017) Pratchett et al. (2017b)

Table 6 (continued)

Code	Description	Units	Years	Source	COTS Reference
chlASd	As above, but the standard deviation	$\mu g\ L^{-1}$	2002–2025	NASA (2025)	As above
chlAMax	As above, but the maximum	$\mu g\ L^{-1}$	2002–2025	NASA (2025)	As above
chlAMin	As above, but the minimum	$\mu g\ L^{-1}$	2002–2025	NASA (2025)	As above
sstMean	Mean sea surface temperature in a 110 km radius of each reef between December and February inclusive	°C	1981–2025	NOAA (2025b)	Caballes et al. (2017) Lamare et al. (2014) Kamya et al. (2014)
sstSd	As above, but the standard deviation	°C	1981–2025	NOAA (2025b)	As above
sstMax	As above, but the maximum	°C	1981–2025	NOAA (2025b)	As above
sstMin	As above, but the minimum	°C	1981–2025	NOAA (2025b)	As above
dhwMean	Mean yearly degree heating weeks experienced by a reef	DHW	1986–2025	NOAA (2025a)	Hughes et al. (2017)
dhwSd	As above, but standard deviation	DHW	1986–2025	NOAA (2025a)	Hughes et al. (2017)
dhwMax	As above, but the maximum	DHW	1986–2025	NOAA (2025a)	Hughes et al. (2017)
dhwMin	As above, but the minimum	DHW	1986–2025	NOAA (2025a)	Hughes et al. (2017)
area	Area of a reef	m^2	N/A		
aveDepth	Average depth of a reef	m	N/A	Geoscience Australia (2017)	Wilmes et al. (2020) Doll et al. (2023)

Additional predictors from Matthews et al. (2020) were also included and are detailed in Appendix B, along with the estimates gathered from spatially constrained K-nearest neighbours estimators. Further details on some covariates are included in Supplementary Materials

Appendix B Matthews et al. (2020) Covariates list

Table 7 List of predictors used by Matthews et al. (2020) and their associated sources that we use in our models

Type	Code	Description	Units	Years	Source	COTS Reference
Env	o2Ave	Average oxygen	mLL^{-1}	1960–2006	Huang et al. (2010) Matthews et al. (2019)	Lamare et al. (2014) Hardy et al. (2014)
Env	no3Ave	Average nitrate	μM	1960–2006		Birkeland and Lucas (1990)
Env	salAve	Average salinity	PSU	1960–2006		Lucas (1973) Allen et al. (2017) Caballes et al. (2017)
Env	salSR	Seasonal range salinity	PSU	1960-2006		
Env	waveStress	Percentage of time for which the bed shear stress was > 0.4 Pa Wave exposure proxy	%	2010		Moran (1988)
Env	mud	percentage of a seabed sediment sample that is < 63 μm in diameter	%	1960–2009		Wolanski et al. (2003)
WQ	floodPrim	Relative primary (representing turbid, sediment dominated plume) flood plume frequency (weeks occurred/total weeks) during wet season (max = 26)	0–1	2000–2014	Devlin et al. (2012) Matthews et al. (2019)	Fabricius et al. (2010) Wolfe et al. (2015) Wooldridge and Brodie (2015) Pratchett et al. (2017b) Brodie et al. (2017)
WQ	floodSec	Secondary chlorophyll dominated plume–relative frequency	0–1	2000–2014		
WQ	floodTer	Further extent of plume, as delineated by salinity < 34 ppt–relative frequency	0–1	2000–2014		
Cor	corHardMax	Predicted maximum coral cover	0–100%	Estimated 2018		Lucas (1984) Caballes et al. (2017a)
Dist	bleachExp	Mean exposure to 1998 and 2002 bleaching events	1–5	1998, 2002	Berkelmans et al. (2004) Matthews et al. (2019)	Hughes et al. (2018)

Variable categories are environmental (Env), water quality (WQ), coral (Cor), and disturbance (Dist). These variables were not available for all reefs, so we chose to impute missing values with a K-nearest neighbours approach (for further details, see the Supplementary Materials)

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Author contributions All authors contributed to the conception of the study and the writing of the manuscript. Biophysical dispersal modelling was conducted by SC and OS, with all subsequent analyses and visualisations conducted by OS. This work will form part of OS's PhD Thesis.

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Data availability The COTS monitoring data used in this paper are not publicly available, but can be requested from the Great Barrier Reef Marine Park Authority and the Australian Institute of Marine Science. The remaining code and data are available at https://github.com/

OwenS1919/cotsOutbreakAnalysisPaper. The majority of modelling and analysis for this paper was conducted in MATLAB (version R2023b, The MathWorks Inc. 2023), with the statistical analysis of COTS monitoring data and predictions of COTS populations conducted in R (version 4.2.3, R Core Team 2023.

Declarations

Conflict of interest The authors have no financial or non-financial conflict of interest to declare.

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