50 YEARS WITH IMPACT
Journal of Applied Ecology
1913 British Ecological Society 2013 CELEBRATING 100 YEARS

Journal of Applied Ecology 2014, **51,** 1188–1196 doi: 10.1111/1365-2664.12320

Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef

Karlo Hock[1,2]*, Nicholas H. Wolff[1], Scott A. Condie[3], Kenneth R. N. Anthony[2] and Peter J. Mumby[1]

[1]*Marine Spatial Ecology Lab, School of Biological Sciences, University of Queensland, St. Lucia, Qld 4072, Australia;* [2]*Australian Institute for Marine Science, Townsville, Qld 4810, Australia; and* [3]*CSIRO Wealth from Oceans Flagship, Hobart, Tas 7004, Australia*

Summary

1. Many ecosystems suffer systemwide outbreaks of damaging species propagating from primary outbreak sites. Connectivity patterns can identify parts of the ecosystem that help turn local outbreaks into a systemwide contagion through a series of transmission events. Here, we show that patterns of larval connectivity among reefs can help explain periodic crown-of-thorns starfish (COTS) epidemics across the Great Barrier Reef (GBR).

2. We simulated potential dispersal of COTS larvae to obtain a connectivity network of coral reefs across the entire GBR. Network analysis revealed areas of high local connectivity where any outbreaks could be amplified locally, as well as those areas with potential to cause large-scale epidemics with ecosystem-wide impacts.

3. We find that the regions where COTS epidemics are known to originate are predictable from their high local and systemwide connectivity. Extensive larval exchanges among reef clusters in these regions can start a chain reaction of COTS population build-up. The same regions also have high potential to reach and affect other parts of the GBR, thereby maximizing the likelihood that any outbreaks would eventually propagate throughout the ecosystem.

4. Hydrodynamic properties and geography of the GBR make it vulnerable to COTS epidemics. Using network analysis to identify regions with high-risk high-impact sources could help control these devastating events in future.

5. *Synthesis and applications*. The observed centre of origin for COTS epidemics (the Cooktown–Cairns region) can be predicted from its elevated short- and long-range levels of larval connectivity. Connectivity analysis of per-reef risks provides spatially explicit targets to guide surveillance and control measures that might help curtail COTS epidemics through prioritization of highly connected reefs. The analytical approach developed here for COTS connectivity can also be applied to identify well-connected patches and regions in other interconnected ecological systems.

Key-words: *Acanthaster planci*, contagion, coral cover, coral reef, dispersal, epidemic, outbreak dynamics, pest control, reef management, spatial network

Introduction

Some of the most challenging questions in management and environmental control involve the connectivity of organisms in spatially heterogeneous, fragmented habitats (Sale *et al.* 2005; Cowen, Paris & Srinivasan 2006). Connectivity, or the dispersive capability of species among habitat patches, is a key aspect of metapopulation structure, both in terms of habitat colonization and population persistence (Hastings & Harrison 1994; Hanski 1997; Hastings 2003). Systemwide models of such functional connections are often represented as networks of interconnected components. Connectivity networks have been used successfully to describe connectivity in both terrestrial and marine systems (Urban & Keitt 2001; Minor & Urban 2008; Treml *et al.* 2008; Lookingbill *et al.* 2010; Mumby *et al.* 2011; Watson *et al.* 2011, 2012) and also to understand the outbreaks of undesirable agents in systems as diverse as social groups (Meyers *et al.* 2005), computer networks (Balthrop *et al.* 2004) and transportation

*Correspondence author. E-mail: k.hock1@uq.edu.au

(Hewitt & Campbell 2007). Successful control of these outbreaks often depends on employing network-based methods in order to find priority intervention sites that could disrupt the connectivity pattern.

One of the most famous examples of an undesirable 'pest' is the crown-of-thorns starfish *Acanthaster planci* (Linnaeus), or COTS, which feeds on coral and forms plagues that beset reefs in much of the Indo-Pacific (Brodie *et al.* 2005; Pratchett *et al.* 2011; Sweatman, Delean & Syms 2011; Timmers *et al.* 2012; Baird *et al.* 2013). A recent analysis of the health of the world's largest coral reef, Australia's iconic Great Barrier Reef (GBR), found that COTS were among the most important causes of reef decline (De'ath *et al.* 2012). On the GBR, COTS populations undergo cyclical population booms that eventually spread across much of the ecosystem (Moran *et al.* 1992; Brodie *et al.* 2005; Pratchett 2005; Sweatman, Delean & Syms 2011). While high levels of COTS have likely occurred throughout the evolutionary history of the GBR, a combination of anthropogenic influences and climatic events are thought to make the impacts of COTS outbreaks more severe (Brodie *et al.* 2005; Fabricius, Okaji & De'ath 2010; De'ath *et al.* 2012), although not necessarily more frequent (Fabricius, Okaji & De'ath 2010).

For COTS populations, the term 'outbreak' has been used to characterize COTS population densities that exceed local resource availability. To distinguish between COTS outbreaks and two related processes, we also propose the following terminology: COTS 'build-up' on a single reef that may or may not lead to an outbreak, and COTS 'epidemic' in which outbreaks spread among reefs through connectivity. Crown-of-thorns starfish build-up will not necessarily cause an outbreak because demographic and physical factors on individual reefs could prevent populations from reaching sufficient density to cause significant coral damage. Similarly, a build-up and outbreaks of COTS on individual reefs will not necessarily entrain an epidemic without connectivity.

Several hypotheses have been proposed to understand processes that lead to COTS outbreaks, alternatively emphasizing larval processes (Brodie 1992; Brodie *et al.* 2005; Fabricius, Okaji & De'ath 2010) vs. adult behaviour, demography and reproduction (Reichelt *et al.* 1990; Pratchett 2005). Rather than influencing the debate over the causation of outbreaks on individual reefs, the aim of this study is to provide insights into why large-scale COTS epidemics begin in specific locations and why they might spread from there. While factors that contribute to outbreaks may also affect the propagation of COTS epidemics (e.g. Brodie 1992; Brodie *et al.* 2005), little is known about how connectivity patterns contribute to differential COTS risks.

In the past four decades, COTS epidemics have followed a well-documented pattern, with two focal areas of initiation (Kenchington 1977; Moran *et al.* 1992; Sweatman, Delean & Syms 2011). Outbreaks that preceded major COTS epidemics generally arose in the Cooktown–Cairns area of the northern GBR and subsequently spread northward and southward (Moran *et al.* 1992; Fabricius, Okaji & De'ath 2010; http://www.aims.gov.au/docs/research/biodiversity-ecology/threats/cots-animation.html). Crown-of-thorns starfish epidemics in the Swains region of the southern GBR may have started independently from these major epidemics, but did not seem to spread to other regions of the GBR (Sweatman, Delean & Syms 2011). Population genetic studies have consistently demonstrated that COTS populations on the GBR exhibit high homogeneity and high gene flow (e.g. Nash, Goddard & Lucas 1988; Benzie & Wakeford 1997; Yasuda *et al.* 2009). This suggests that connectivity among reefs leads directly to the exchange of COTS larvae, causing or at least contributing to outbreaks on reefs downstream. While it is possible that other particles or dissolved substances are also transported along with COTS larvae, some of which could also indirectly contribute to the likelihood of COTS outbreaks, here we consider advective transport primarily as a proxy measure of the outbreak risk from connectivity to the larval sources of COTS, that is, the spread of outbreaks from one reef to another.

Connectivity patterns will likely influence the progression of COTS epidemic at metapopulation scales. Using simulated dispersal to link potential source reefs with probable destinations (sinks) leads to the construction of a network of possible exchanges between reefs across the GBR. Assuming that COTS populations are recruitment limited – which is virtually mandatory for initial colonization – then all else being equal, those reefs receiving the greatest influx of larvae are also likely to experience greater COTS recruitment (cf. Calabrese & Fagan 2004). Analysis of connectivity for the entire GBR system will then pinpoint reefs and regions that are likely to experience major COTS build-ups as well as those that have the potential to create major COTS epidemics by having links to many reefs in both immediate surroundings and more distant regions. Understanding these risks will be critical for monitoring, prevention and targeted management of COTS epidemics.

To determine the role of connectivity in identifying the risks and impacts of COTS build-up and epidemics, we simulated potential larval dispersal with oceanographic models to construct a connectivity network corresponding to advective transport among reefs of the GBR. We applied network analysis to these simulations results in order to pose three principal questions. First, to what extent can the connectivity of reefs explain observed patterns of outbreaks? Potential connectivity should be significantly stronger between sites where simulated advective transport suggested larval exchanges could have taken place. Secondly, are the hotspots of COTS build-up, and potentially also incipient epidemics, predictable based on their direct connectivity (i.e. which regions have well-connected reefs where outbreak and epidemic initiation may occur with or without changes in environmental conditions)? Validation of this question does not rely upon the sparse sampling data, and, while the major regions of initial COTS outbreaks are known from the literature, there was nothing in the models that would *a priori* favour those particular regions. Thirdly, can we use connectivity to identify regions with sources that can cause large-scale epidemics and potentially reach and impact on many other reefs? Reefs that can both extensively transmit COTS through direct connectivity and indirectly affect many reefs in future should have a much higher potential to engender the observed COTS epidemics. Network analysis revealed that reefs in known initiation regions possess both of these properties, even though neither the coincidence of these properties in individual reefs nor the presence of such reefs in specific network regions inevitably follows from the underlying mathematics. We conclude that the geography of the GBR, which includes the distribution of reefs in a hydrodynamic environment and location of major river systems, makes the GBR a system that is exceptionally vulnerable to large-scale COTS outbreak epidemics.

Materials and methods

DESIGNING CONNECTIVITY NETWORKS FROM POTENTIAL DISPERSAL OF COTS LARVAE ON THE GBR

Potential connectivity of the COTS on the GBR was modelled using a Lagrangian model of particles dispersing in the GBR region (the engine behind Connie2 online tool, available at http://www.csiro.au/connie2/; Condie, Hepburn & Mansbridge 2012). The current model has a number of advances over previous models (Dight, James & Bode 1990; Scandol & James 1992), in being geographically extensive, inclusive of all major driving forces such as tides, winds and offshore forcing, and operating at a high spatial and temporal resolution. The oceanographic environment corresponded to the GBR-wide conditions of 2008/9 summer spawning season, and model parameters were selected so as to resemble known properties of COTS larvae. The release events were timed so as to match with proposed COTS spawning times that occur around coral spawning events (Babcock & Mundy 1992). The dispersal of particles was simulated using a high-resolution oceanographic model in which 10 000 particles were released from each reef polygon. Time that COTS larvae spend in the water column can be highly variable (9–42 days). Since this period will be highly dependent on local conditions (e.g. Olson 1987), the modelling of which would be prohibitive, we opted for a compromise 28-day period of particle dispersal. This period captures the majority of proposed COTS larval transport, especially since many COTS larvae will still travel only short distances despite their theoretical potential for long-distance dispersal (Benzie *et al*. 1994). Capturing short-range dispersal was therefore an important aspect of the model, and as a result we included only a short period of 24 h before considering potential destinations for particles. Crown-of-thorns starfish larvae have also been shown to be roughly neutrally buoyant and passive (Benzie *et al*. 1994). Accordingly, the simulated particles were passively dispersed by hydrodynamic flows and did not exhibit buoyancy and behavioural changes. However, to account for the local effects beyond the model resolution, the particles were considered as having 'arrived' when located within 1 km of any reef polygon. Additional details are provided in Appendix S1 in the Supporting Information.

Simulated particle trajectories were used to determine potential functional links among pairs of reefs, which were then combined into a systemwide connectivity model. Specifically, potential connectivity of COTS on the GBR was represented as a directed weighted network, with reefs as nodes and the probability of dispersal as weighted edges between those nodes. To construct a network, particle trajectories were used to establish a connection of each reef source with all potential destination reefs that can be reached by larvae released from it. The number of particles that arrived at each destination reef from a source reef in a simulation represented potential functional connections among these reefs. The connections were represented as ordered pairs of reefs (i, j), with larval traffic going from reef i to reef j. In graph-theoretical terms, reef i is called in-neighbour of j, while reef j is called out-neighbour of i, with a directed edge (link) going from i to j. The amount of larval traffic in (i, j) relative to the total number of particles released from i indicated the strength and direction of this connection and therefore provided the weight for the arrow going from i to j. Bidirectional exchange was also possible, such that both (i, j) and (j, i) could exist. In such cases, both of the ordered pairs were present in the network, and traffic in both directions was represented as two separate connections in the model rather than an aggregate connection representing the net traffic between reefs. Retaining the information on direction and strength of functional connections preserved the asymmetries as well as the potential amount of larval transport between reefs without complicating the analyses since the focus was on identifying potential connections that lead to propagation of COTS epidemics rather than on population dynamics on individual reefs where such feedback loops will be important. For similar reasons, we also did not consider self-loops in our models. While self-recruitment will likely have a major impact on the population build-up on a reef, the inclusion of self-loops on the reefs was not necessary to analyse inter-reef connectivity that underlies COTS epidemics. Even though analysis of direct source–sink links can be done using simple connectivity matrices, network analysis offers important advantages by providing ways to explore the consequences of connectivity beyond direct connections that would manifest only after many dispersal steps/generations. This long-term perspective in terms of both space and time is especially important when considering reef's potential role in large-scale COTS epidemics, identifying reefs that pose the highest risk as sources of such epidemics on the GBR.

ROLE OF CONNECTIVITY IN THE DYNAMICS OF COTS OUTBREAKS

Predicting observed COTS transmissions using a connectivity model

To determine whether reefs with a higher predicted input of COTS larvae were more likely to experience an outbreak, we compiled all available field data from five summer spawning seasons between 2006 and 2011 collected by the Australian Institute of Marine Science (AIMS; for details see Appendix S2, Supporting information). This period encompasses years represented by connectivity simulations (2008/9) as well as an additional 2-year bracket. While this did not allow us capture the entire course of the COTS epidemic cycle, it potentially reduced uncertainty about interannual variations in simulated connectivity patterns.

We then used the connectivity network to identify pairs of reefs – a source and a destination connected to it – in the field data. Sources were reefs at which a COTS outbreak was observed in a survey between 2006 and 2010. The year when COTS was observed at a source was recorded as time T for that source. Destination reefs needed to have no COTS in the 2 years prior to year T of their respective source and also to have been sampled for COTS at some point after T. Seventeen unique source–destination pairs in the data satisfied these criteria (Figs 1 and S1, Supporting information).

Since functional connectivity should decrease with travel, reefs further away may be less likely to be colonized for a given connection strength. We therefore included the spatial (geographic) distance of the destination reef to its source in the analysis. To contrast this focus on advection, we also considered an alternative hypothesis for the distribution of COTS outbreaks observed in surveys. We used simple linear interpolation of field data on observed COTS outbreaks at T to predict whether the occurrence of COTS at destination reefs was simply a function of geospatial proximity and independent of oceanographic advection.

Characterizing the connectivity of the GBR: are hotspots of COTS build-up predictable?

In theory, population build-up due to connectivity – a hotspot for generation of a COTS epidemic – is most likely for reefs with many strong outgoing and incoming connections to other reefs, especially if such reefs are concentrated in one area. With all else being equal, and taking outgoing connections first, if COTS occur on reefs with these characteristics, it is likely that they will then colonize reefs directly connected to this source. To quantify this property, we calculated each reef's weighted out-degree centrality in the connectivity network: a composite measure that takes into account the number and the strength (edge weight) of reef's outgoing connections (Opsahl, Agneessens & Skvoretz 2010; see Appendix S3 for computational details; also see Fig. S2, Supporting information). Such reefs can be considered 'superspreaders' of COTS populations, analogous to the way the term is used to describe the spread of communicable diseases (Meyers *et al.* 2005). Secondly, and again with all else being equal, a reef can be at high risk of colonization from a local neighbourhood of reefs if it has many strong incoming connections. Therefore, reefs that exhibited high values of weighted in-degree centrality in the connectivity network would run a high risk of receiving COTS from other reefs in the area. Reefs predicted to have high values of both in- and out-degree will therefore be likely to both receive and transmit COTS (a superspreader that will also likely receive COTS from neighbouring reefs that may also be superspreaders etc.), creating a reinforcing feedback that generates a hotspot of COTS build-up that is amplified as more and more reefs become secondary sources. Reefs with high local connectivity that are connected to each other will therefore fuel a chain reaction of population build-up that may form the core of a future epidemic.

Characterizing the connectivity of the GBR: identifying high-impact regions

Reefs that can produce extensive COTS epidemics need to be able to reach many other reefs in the GBR connectivity network, regardless of whether the connections are direct or indirect. In graph theory, a set of all nodes that can be reached from a node in a directed network is called an out-component. An out-component of a reef in the connectivity network would therefore allow us to estimate the number of reefs to which COTS can potentially spread over time from that reef. If COTS outbreak occurs on a reef predicted to have a large out-component, then the potential exists for this outbreak to affect many reefs in future.

Analogously, some reefs may be more likely to experience an outbreak by having many reefs that can potentially affect them, perhaps through a long-term build-up of COTS. A set of all nodes from which a target node can be reached is called an in-component, and a reef with a large in-component could have a higher chance of eventually experiencing an outbreak. Regions with reefs that have large in-components will therefore be more readily affected by COTS epidemics that start in other parts of the GBR.

Finally, reefs that have large out- and in-components could be reached by and also reach many other reefs, and will therefore be at higher risk of outbreaks and potentially important for passing on COTS. Regions with many such reefs could thus be critical

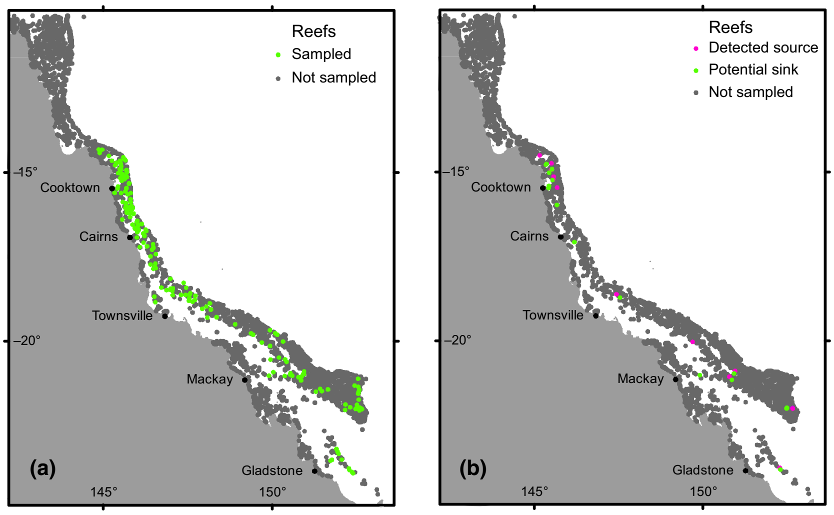

Fig. 1. Sampling for crown-of-thorns starfish in years between 2006 and 2010. (a) Green dots indicate reefs sampled in these years. (b) Identified sources (magenta) and potential destinations connected to a respective source (green) that were used in the analysis.

Table 1. Logistic regression of COTS detections on reefs connected to known sources identified at time *T*, where *T* was a year between 2006 and 2010. Response variable value of 1 = COTS population detected at destination in years after *T*; 0 = COTS population not detected at destination in years after *T*

	Likelihood ratio		
Variable	Chi^2	d.f.	*P*
Connection strength to source	6·23	1	0·013*
Interpolated COTS density at time *T*	0·55	1	0·455
Spatial distance to nearest source	6·91	1	0·009*

Whole model test: Chi^2 = 10·86, **P* = 0·013, d.f. = 3, R^2 = 0·527, N = 17.

for propagation of COTS epidemics and may present prime targets for interventions. Unlike other measures of relative importance (e.g. betweenness centrality that measures how important is the node for fragmenting the network into the unconnected clusters of nodes, as in Treml *et al.* 2008), size of reef's in- and out-components specifically identifies the total number of reefs that can reach or are reachable by a reef, and with it the portion of the ecosystem that eventually can affect or be affected by a COTS population on it (also see Fig. S2 and S3, Supporting information).

A reef's position in a connectivity network could also estimate reef's risk of experiencing COTS outbreak in future as a result of its connectivity. This was investigated by using in-degree and in-component of each node as a measure of direct and indirect connectivity, as well as in-degree of node's in-neighbours as a measure of mid-range connectivity. Simulated surface area of each reef polygon was used as a non-connectivity predictor in the analysis. These values were then used as predictors to explain historical data on detected COTS outbreaks in years between 2000 and 2012. Computational details of the network metrics used in the analyses are provided in Appendix S3, Supporting information.

Results

PREDICTING OBSERVED COTS TRANSMISSIONS USING A CONNECTIVITY MODEL

Both the strength of modelled connectivity between reefs obtained from simulations and geospatial distance to source had a significant and positive relationship with the observed probability of detectable COTS (Table 1). In contrast, linearly interpolated COTS density was not a good predictor of COTS presence in future surveys. A combination of strong connectivity in simulations and spatial proximity to the source of COTS suggests advection-based, but spatially limited, larval transport could play a role. These results also imply that COTS infestations should be seen as individual events that affect discrete and potentially distant locations in space rather than forming a contiguous 'front' that moves across the seascape.

CHARACTERIZING THE CONNECTIVITY OF THE GBR: ARE HOTSPOTS OF COTS BUILD-UP PREDICTABLE?

Reefs with many incoming connections (high in-degree centrality) were found to be distributed across the GBR (Fig. 2a). However, superspreader reefs with many outgoing connections (high out-degree centrality), and thus important for COTS build-up, were concentrated in the Cooktown–Cairns and in the Swains regions (Fig. 2b). Reefs with high values of both in- and out-degree will be potential catalysts of local cascades, amplifying the effect of local build-up. Such reefs were also predominantly found between Cooktown and Cairns, as well as in the central region of the Swains (Fig. 2c). Both of these regions have historically experienced apparently independent initiation of COTS epidemics (Sweatman, Delean & Syms 2011).

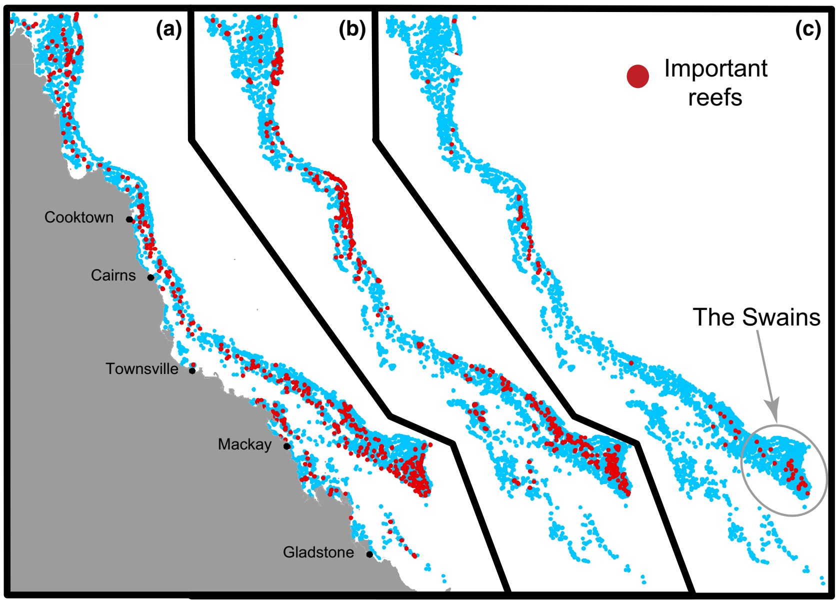

Fig. 2. Potential connectivity hotspots for crown-of-thorns starfish (COTS) build-up. (a) Top 10% of the reefs with the most incoming connections (highest in-degree centrality). (b) Top 10% of the potential superspreader reefs (highest out-degree centrality). (c) Reefs in top 10% of both in- and out-degree centrality. Areas with high concentration of reefs with many direct incoming and outgoing connections, as observed in the Cooktown–Cairns and the Swains regions, could experience amplification of COTS build-up and are potential hotspots for initiation of wider COTS epidemics.

CHARACTERIZING THE CONNECTIVITY OF THE GBR: IDENTIFYING HIGH-IMPACT REGIONS

Reefs reachable by many other reefs (large in-components), and at a potentially higher risk of long-term build-up and of being reached by COTS epidemics, were located mainly in the far north of the GBR, as well as in some coastal regions in the south (Fig. 3a). However, several were also located in other regions, such as off Townsville. Reefs potentially capable of reaching many other reefs (large out-components) were overwhelmingly concentrated in the Cooktown–Cairns region (Fig. 3b). Unlike COTS populations that occur elsewhere on the GBR, any COTS outbreaks originating in the Cooktown–Cairns region therefore stand to have a much stronger impact on the rest of the ecosystem due to their potential to eventually reach many other reefs. Reefs with large in- and out-components, that is, those that would be at risk of both receiving and transmitting COTS, have been identified around Cairns and around Forbes Islands in the far northern GBR (Fig. 3c).

The total number of reefs that can reach a reef, that is, the size of its in-component calculated from simulations, was a significant predictor of COTS detected in surveys (Table 2), while no effect was detected for direct or intermediate connectivity of reefs. This result suggests that a reef reachable from many other reefs could experience a greater risk of COTS outbreaks, highlighting such reefs as significant sinks in the ecosystem.

Discussion

Outbreaks of COTS are often highly localized events, with individuals in high abundance on a particular reef but absent from adjacent reefs (Pratchett 2005; Sweatman, Delean & Syms 2011). We found that high-resolution models of oceanographic advection had significant explanatory power in predicting whether a reef would become colonized by COTS from potential sources that can reach it: reefs with significant connections to known sources of COTS were more likely to become infested in future. Nevertheless, while similar oceanographic models have been used to predict connectivity in seascapes at different scales in several marine ecosystems (Bode, Bode & Armsworth 2006; Cowen, Paris & Srinivasan 2006; Treml *et al.* 2008; Watson *et al.* 2012), finding a demographic relationship between a model of potential larval flux and observed patterns of colonization/local outbreaks is challenging. Most tests of the efficacy of larval dispersal models do not focus on demographic processes within single generations (as we attempted); rather, they use genetic data to compare predicted and observed gene flow which integrates over multiple dispersal events (Galindo, Olson & Palumbi 2006; Foster *et al.* 2012). There is also a question of scale: the exchanges that occur over shorter, and possibly ecologically meaningful, distances in a system like the GBR (e.g. Benzie & Wakeford 1997) might not work over larger spatial and temporal scales (Timmers *et al.* 2012). Moreover, the data on the abundance of COTS are notoriously difficult to collect (Sweatman *et al.* 2008; Sweatman, Delean & Syms 2011) and only a subset of the possible larval sources to a reef ends up being surveyed, thereby offering an incomplete view of COTS risk from reefs that can reach it. Yet, despite these potential limitations, we demonstrate here that predicted connectivity of a reef to sources of COTS could influence the risks of a future outbreak.

Further analysis of connectivity patterns revealed that the two historical hotspots for initiation of COTS epidemics – Cooktown–Cairns region and the Swains (Moran *et al.* 1992; Sweatman, Delean & Syms 2011) – had high local connectivity that could engender future COTS

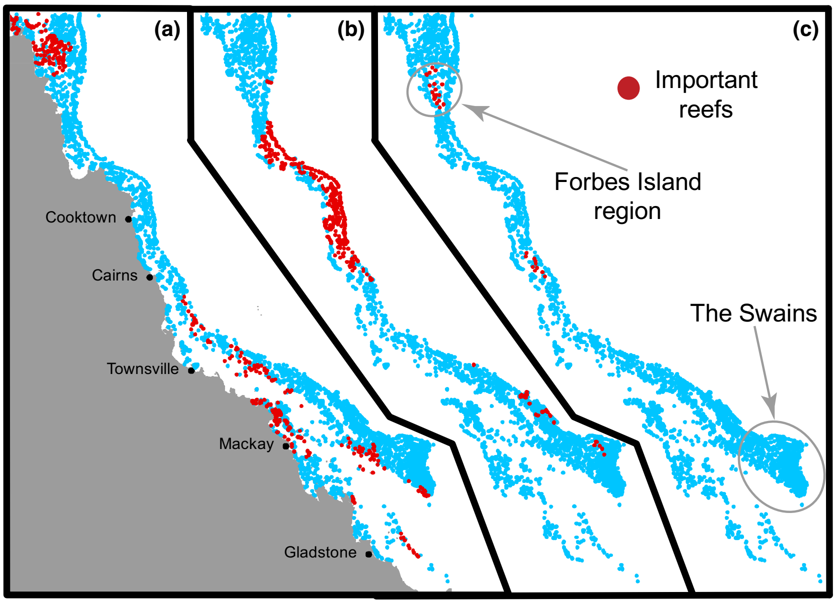

Fig. 3. Reefs important for large-scale crown-of-thorns starfish epidemics. (a) Top 10% of the reefs with largest in-components. (b) Top 10% of the reefs with largest out-components. (c) Reefs in top 20% in terms of both in- and out-component size (no reefs were in top 10% in both categories, so the criteria had to be relaxed). While reefs reachable from most other reefs were located in fringe areas, reefs with the highest potential impact capable of reaching many other reefs were concentrated around Cooktown and Cairns. Reefs that are both very reachable and can reach many other reefs were also located around Cairns, as well as in the region around Forbes Island in northern GBR.

Table 2. Logistic regression of COTS outbreaks on reefs sampled between 2000 and 2012 with characteristics of reef position in a connectivity network as predictor variables. Response variable value of 1 = incipient COTS outbreak detected at reef; 0 = incipient COTS outbreak not detected at reef

Variable	Likelihood ratio		
	Chi^2	d.f.	*P*
In-component	9·58	1	0·002*
Weighted in-degree	0·34	1	0·562
Weighted in-degree of in-neighbours	0·26	1	0·608
Reef size	0·15	1	0·697

Whole model test: $Chi^2 = 9{\cdot}85$, $*P = 0{\cdot}043$, d.f. = 4, $R^2 = 0{\cdot}04$, N = 251.

epidemic by amplifying the effects of COTS build-up irrespective of distinct environmental conditions. Moreover, our model was inclusive of, rather than exclusive to, COTS larval transport and therefore did not preclude the possibility that other particles or dissolved substances like nutrients or chemical cues are being transported as well, as any such transport would be amplified by strong advection. These regions could therefore be a major source of COTS for multiple, potentially synergistic, reasons, with connectivity driving the amplification of populations beyond individual reefs. Identifying highly connected reefs can help highlight the reefs where COTS would pose a potential threat due to population build-up and therefore also help direct the efforts aimed at curbing any causes of such build-up.

The Cooktown–Cairns region also exhibited the highest concentration of reefs that could impact the rest of the ecosystem in the long term as well as at a large scale. While outbreaks can in theory start anywhere on the GBR, connectivity patterns imply that those that do start in the Cooktown–Cairns region will not only be amplified locally, but also have systemwide impact by spreading to many other reefs. Moreover, reefs that were potentially critical for build-up and propagation of COTS epidemics were located around Cairns (Fig. 3c). This again corresponds well with historical records: before 1986, when an extensive sampling programme was introduced, the COTS epidemics were first recorded around Cairns in 1962 and 1979 (Moran *et al.* 1992). Such reefs could form essential bottlenecks and become priority locations for COTS removal with the goal of curtailing further propagation. As evident from analyses of historical outbreak records, connectivity patterns may also help explain why some reefs tend to experience more COTS outbreaks over time.

Despite insights into the connectivity contributions to observed patterns of COTS outbreaks, our results incorporate several key assumptions. While the specifics of the exchanges between reefs will undoubtedly vary seasonally and annually (Bode, Bode & Armsworth 2006; Treml *et al.* 2008; Watson *et al.* 2011), by selecting a relatively high-resolution oceanographic model spanning the entire GBR, we made an implicit trade-off between resolving spatially detailed oceanographic phenomena and a longer time series of coarse model predictions. In turn, we had to assume that the major characteristics of the connectivity of individual reefs, such as the presence or absence of links, are at least relatively persistent over several seasons. We also had to assume that the broad-scale sampling used to assess adult COTS populations accurately described historical outbreak patterns and local COTS abundance despite the absence of more detailed information on condition and age structure in developing outbreaks (Miller & Müller 1999; Sweatman, Delean & Syms 2011). While not all of these reefs were necessarily a part of a major COTS epidemic, not limiting the observations to outbreaks that are a part of a major COTS epidemic potentially makes our results more generalizable by implying that advection matters for any source–sink pair. Finally, we did not explicitly model population dynamics, focusing instead on identifying the regions with the highest potential for larval exchange under favourable conditions rather than attempting to precisely predict those conditions (Calabrese & Fagan 2004).

Even if these assumptions preclude exact fine-scale predictions, the model results should be robust enough to detect major effects of connectivity on COTS epidemics and therefore regions of potential interest for control efforts. Crown-of-thorns starfish control measures are both resource- and labour-intensive (Fabricius, Okaji & De'ath 2010; Rivera-Posada *et al.* 2012), restricting the scope of their application. Connectivity analysis alleviates this problem by providing specific and spatially explicit intervention targets where monitoring and control efforts can be applied for maximum effect and also proactively target growing COTS populations and developing outbreaks rather than reactively managing ongoing and escalated outbreaks. Connectivity-based assessment of per-reef risks can further guide sampling efforts, help with planning an early warning system that would look for signs of a developing COTS epidemic, and identify the priority sites for management in less accessible areas such as the northern GBR (Moran *et al.* 1992). Moreover, since these connectivity patterns could provide some insight into the connectivity of other species, the regions that warrant extra attention due to COTS build-up and eventual epidemic spread could be valuable for conservation of larval sources of other species as well. Since the mathematical underpinnings of performed connectivity analyses are ubiquitous and system-independent, identifying well-connected patches and regions through connectivity analysis may also help us understand why some ecological systems, both marine and terrestrial, undergo systemwide epidemic infestations, whereas others that potentially lack the type of connectivity reinforcement proposed for the GBR do not.

In conclusion, it appears that the geographical structure of the world's largest coral reef system, in terms of its hydrodynamic properties and distribution of coral reefs, pre-disposes it to being very vulnerable to epidemic COTS infestations. A major emergence of COTS on the GBR will be likely to occur in regions of dense inter-reef connectivity. Successful generation of COTS epidemics is most likely once it occurs on a reef that can reach an extensive network of other reefs. Unfortunately for the GBR, it appears that the area of major COTS outbreak generation (especially Cooktown–Cairns region in the wet tropics) also happens to be the most dangerous site for an outbreak to become a large-scale epidemic of the wider reef system. Controlling COTS outbreaks in these critical regions is therefore likely to remain a priority for coral reef management on the GBR.

Acknowledgements

This study was supported by a SIEF John Stocker fellowship to K.H., an ARC Laureate fellowship to P.J.M., and a NERP grant to P.J.M. and K.R.N.A. that also supported N.H.W. Crown-of-thorns starfish outbreak data provided by the Australian Institute for Marine Science. Oceanographic data provided through the eReefs project (http://www.ereefs.org.au). Reef coordinates provided by the Great Barrier Reef Marine Park Authority.

Data accessibility

Reef monitoring and outbreak data: http://www.aims.gov.au/docs/research/monitoring/reef/latest-surveys.html.

Connie2 online tool: http://www.csiro.au/connie2/.

Reef coordinates available free of charge from: http://www.gbrmpa.gov.au/resources-and-publications/spatial-data-information-services.

References

Babcock, R. & Mundy, C. (1992) Reproductive biology, spawning and field fertilization rates of *Acanthatser planci*. *Marine and Freshwater Research*, **43**, 525–533.

Baird, A.H., Pratchett, M.S., Hoey, A.S., Herdiana, Y. & Campbell, S.J. (2013) *Acanthaster planci* is a major cause of coral mortality in Indonesia. *Coral Reefs*, **32**, 803–812.

Balthrop, J., Forrest, S., Newman, M.E.J. & Williamson, M.M. (2004) Technological networks and the spread of computer viruses. *Science*, **304**, 527–529.

Benzie, J. & Wakeford, M. (1997) Genetic structure of crown-of-thorns starfish (*Acanthaster planci*) on the Great Barrier Reef, Australia: comparison of two sets of outbreak populations occurring ten years apart. *Marine Biology*, **129**, 149–157.

Benzie, J.A.H., Black, K.P., Moran, P.J. & Dixon, P. (1994) Small-scale dispersion of eggs and sperm of the crown-of-thorns starfish (*Acanthaster planci*) in a shallow coral reef habitat. *Biological Bulletin*, **186**, 153–167.

Bode, M., Bode, L. & Armsworth, P.R. (2006) Larval dispersal reveals regional sources and sinks in the Great Barrier Reef. *Marine Ecology Progress Series*, **308**, 17–25.

Brodie, J.E. (1992) Enhancement of larval and juvenile survival and recruitment in *Acanthaster planci* from the effects of terrestrial runoff - a review. *Australian Journal of Marine and Freshwater Research*, **43**, 539–554.

Brodie, J., Fabricius, K., De'ath, G. & Okaji, K. (2005) Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Marine Pollution Bulletin*, **51**, 266–278.

Calabrese, J.M. & Fagan, W.F. (2004) A comparison-shopper's guide to connectivity metrics. *Frontiers in Ecology and the Environment*, **2**, 529–536.

Condie, S., Hepburn, M. & Mansbridge, J. (2012) *Modelling and visualisation of connectivity on the Great Barrier Reef*. Proceedings of the 12th International Coral Reef Symposium. Cairns Australia.

Cowen, R.K., Paris, C.B. & Srinivasan, A. (2006) Scaling of connectivity in marine populations. *Science*, **311**, 522–527.

De'ath, G., Fabricius, K.E., Sweatman, H. & Puotinen, M. (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 17995–17999.

Dight, I.J., James, M.K. & Bode, L. (1990) Modeling the larval dispersal of *Acanthaster planci*. 2. Patterns of reef connectivity. *Coral Reefs*, **9**, 125–134.

Fabricius, K.E., Okaji, K. & De'ath, G. (2010) Three lines of evidence to link outbreaks of the crown-of-thorns seastar *Acanthaster planci* to the release of larval food limitation. *Coral Reefs*, **29**, 593–605.

Foster, N.L., Paris, C.B., Kool, J.T., Baums, I.B., Stevens, J.R., Sanchez, J.A. *et al.* (2012) Connectivity of Caribbean coral populations: complementary insights from empirical and modelled gene flow. *Molecular Ecology*, **21**, 1143–1157.

Galindo, H.M., Olson, D.B. & Palumbi, S.R. (2006) Seascape genetics: A coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology*, **16**, 1622–1626.

Hanski, I. (1997) *Metapopulation dynamics*. Academic Press, From concepts and observations to predictive models.

Hastings, A. (2003) Metapopulation persistence with age-dependent disturbance or succession. *Science*, **301**, 1525–1526.

Hastings, A. & Harrison, S. (1994) Metapopulation dynamics and genetics. *Annual Review of Ecology and Systematics*, **25**, 167–188.

Hewitt, C.L. & Campbell, M.L. (2007) Mechanisms for the prevention of marine bioinvasions for better biosecurity. *Marine Pollution Bulletin*, **55**, 395–401.

Kenchington, R.A. (1977) Growth and recruitment of *Acanthaster planci* (L) on Great Barrier Reef. *Biological Conservation*, **11**, 103–118.

Lookingbill, T.R., Gardner, R.H., Ferrari, J.R. & Keller, C.E. (2010) Combining a dispersal model with network theory to assess habitat connectivity. *Ecological Applications*, **20**, 427–441.

Meyers, L.A., Pourbohloul, B., Newman, M.E.J., Skowronski, D.M. & Brunham, R.C. (2005) Network theory and SARS: predicting outbreak diversity. *Journal of Theoretical Biology*, **232**, 71–81.

Miller, I. & Müller, R. (1999) Validity and reproducibility of benthic cover estimates made during broadscale surveys of coral reefs by manta tow. *Coral Reefs*, **18**, 353–356.

Minor, E.S. & Urban, D.L. (2008) A graph-theory framework for evaluating landscape connectivity and conservation planning. *Conservation Biology*, **22**, 297–307.

Moran, P., De'ath, G., Baker, V., Bass, D., Christie, C., Miller, I., Miller-Smith, B. & Thompson, A. (1992) Pattern of outbreaks of crown-of-thorns starfish (*Acanthaster planci L.*) along the Great Barrier Reef since 1966. *Marine and Freshwater Research*, **43**, 555–567.

Mumby, P.J., Elliott, I.A., Eakin, C.M., Skirving, W., Paris, C.B., Edwards, H.J. *et al.* (2011) Reserve design for uncertain responses of coral reefs to climate change. *Ecology Letters*, **14**, 132–140.

Nash, W., Goddard, M. & Lucas, J. (1988) Population genetic studies of the crown-of-thorns starfish, *Acanthaster planci* (L.), in the Great Barrier Reef region. *Coral Reefs*, **7**, 11–18.

Olson, R.R. (1987) In situ culturing as a test of the larval starvation hypothesis for the crown-of-thorns starfish, *Acanthaster planci*. *Limnology and Oceanography*, **32**, 895–904.

Opsahl, T., Agneessens, F. & Skvoretz, J. (2010) Node centrality in weighted networks: generalizing degree and shortest paths. *Social Networks*, **32**, 245–251.

Pratchett, M.S. (2005) Dynamics of an outbreak population of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995–1999). *Coral Reefs*, **24**, 453–462.

Pratchett, M.S., Trapon, M., Berumen, M.L. & Chong-Seng, K. (2011) Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia. *Coral Reefs*, **30**, 183–193.

Reichelt, R.E., Greve, W., Bradbury, R.H. & Moran, P.J. (1990) *Acanthaster planci* outbreak initiation: a starfish-coral site model. *Ecological Modelling*, **49**, 153–177.

Rivera-Posada, J., Owens, L., Caballes, C.F. & Pratchett, M.S. (2012) The role of protein extracts in the induction of disease in *Acanthaster planci*. *Journal of Experimental Marine Biology and Ecology*, **429**, 1–6.

Sale, P.F., Cowen, R.K., Danilowicz, B.S., Jones, G.P., Kritzer, J.P., Lindeman, K.C. *et al.* (2005) Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology & Evolution*, **20**, 74–80.

Scandol, J.P. & James, M.K. (1992) Hydrodynamics and larval dispersal - a population model of *Acanthaster planci* on the Great Barrier Reef. *Australian Journal of Marine and Freshwater Research*, **43**, 583–596.

Sweatman, H., Delean, S. & Syms, C. (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. *Coral Reefs*, **30**, 521–531.

Sweatman, H., Cheal, A., Coleman, G., Emslie, M., Johns, K., Jonker, M., Miller, I. & Osborne, K. (2008) Long-term monitoring of the Great Barrier Reef, Status report. Number 8, 2008. *Long-Term Monitoring of the Great Barrier Reef Status Report*, **8**, i-x, 1–369

Timmers, M.A., Bird, C.E., Skillings, D.J., Smouse, P.E. & Toonen, R.J. (2012) There's no place like home: crown-of-thorns outbreaks in the Central Pacific are regionally derived and independent events. *PLoS One*, **7**, 000–000.

Treml, E.A., Halpin, P.N., Urban, D.L. & Pratson, L.F. (2008) Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology*, **23**, 19–36.

Urban, D. & Keitt, T. (2001) Landscape connectivity: a graph-theoretic perspective. *Ecology*, **82**, 1205–1218.

Watson, J.R., Siegel, D.A., Kendall, B.E., Mitarai, S., Rassweiller, A. & Gaines, S.D. (2011) Identifying critical regions in small-world marine metapopulations. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, E907–E913.

Watson, J.R., Kendall, B.E., Siegel, D.A. & Mitarai, S. (2012) Changing seascapes, stochastic connectivity, and marine metapopulation dynamics. *The American Naturalist*, **180**, 99–112.

Yasuda, N., Nagai, S., Hamaguchi, M., Okaji, K., Gerard, K. & Nadaoka, K. (2009) Gene flow of *Acanthaster planci* (L.) in relation to ocean currents revealed by microsatellite analysis. *Molecular Ecology*, **18**, 1574–1590.

Received 16 May 2014; accepted 11 July 2014
Handling Editor: Quentin Paynter

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details of oceanographic models and particle tracking simulations.

Appendix S2. Data on historical COTS population abundances and outbreaks on the GBR reefs.

Appendix S3. Calculation details for centrality metrics.

Fig. S1. Destination reefs with detected COTS outbreaks**.**

Fig. S2. Centrality metrics in an example network.

Fig. S3. Relative size of in- and out-components of the GBR reefs.