

Complex Systems: From Biology to Computation

edited by

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IOS Press

1993

Amsterdam • Oxford • Washington • Tokyo

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ISBN 90 5199 117 7

Library of Congress Catalogue Card Number: 92-55077

Publisher:

IOS Press
Van Diemenstraat 94
1013 CN Amsterdam
Netherlands

Distributor in Australia and New Zealand:

DA Books
648 Whitehorse Road
Mitcham, VIC 3132
Australia

Distributor in the USA and Canada:

IOS Press, Inc.
Postal Drawer 10558
Burke, VA 22009-0558
USA

Distributor in Japan:

Kaigai Publications Ltd.
21 Kanda Tsukasa-Cho 2-Chome
Chiyoda-Ku
Tokyo 101
Japan

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PRINTED IN AUSTRALIA

Cover:

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Recovery of Model Coral Communities: Complex Behaviours from Interaction of Parameters Operating at Different Spatial Scales

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Abstract.

Because scientists tend to define questions that are commensurate with established and tractable methods of analysis, ecologists concerned with the dynamics of communities and ecosystems have given too little attention to phenomena at large spatial scales and to parameters that have a spatial context. Cellular automata (CA) are a useful tool for study of parameters that have a spatial component and for analysis of system behaviours over a range of spatial scales, and thus for identifying the emergent properties of communities and ecosystems.

We illustrate this with simple CA models of a system of coral reefs that includes corals of 2 types of life-history, viz. broadcast spawning corals which release gametes and brooding species which release larvae that can settle almost immediately. We examine the influence on system recovery after large-scale disturbances of 3 parameters that manifest at different spatial scales, viz. reef density (a parameter affecting large scale connectivity), local hydrodynamic retention of larvae around individual reefs (meso scale), and the feeding behaviour of crown-of-thorns starfish (small scale).

The results indicate that recovery depends on the system level properties of overall connectivity and among-reef variance in coral cover. Also, there are strong interactions among parameters. For example, recovery is less dependent on reef density when retention of larvae is high, but brooding species are generally less sensitive to reef density than are broadcasters. Conversely, the degree of larval retention is less important to recovery when reef density is high. At high levels of disturbance recovery of broadcasting corals is more sensitive than that of brooders to starfish feeding behaviour, particularly if inter-reef distances are short. There are also thresholds in the qualitative pattern of recovery. The usual pattern of dominance of broadcasting over brooding species can be reversed if poorly connected reefs with low levels of larval retention suffer high levels of disturbance. For either type of life-history there are levels of disturbance from which the system does not recover. The values of these thresholds depend on all parameters we examined, including the life-history type.

1. Introduction

Ecologists concerned with dynamics of communities and ecosystems are unlikely to be able to derive all system level processes from investigations of processes at small spatial and temporal scales. This is because important patterns and processes identified

at some scales may be hidden or non-existent at others [1]. Thus communities and ecosystems are likely to manifest emergent properties that are not predictable from knowledge of their component parts in isolation. Conversely, patterns that manifest at small scales may be influenced to a large degree by system-level parameters. It follows that to answer most questions about community structure at large spatial (system-level) and temporal scales, and some questions that focus at smaller scales, ecologists must design projects to consider system-level parameters. However, it is difficult and often impossible to monitor ecosystems, manipulate them experimentally or replicate them at the system scale. Hence it is not surprising that ecologists have given too little attention to system-level phenomena. A more subtle problem is the epistemological one that many system-level behaviours and properties may be unknown. Seeking an undefined phenomenon of uncertain existence is difficult and may even be seen as risky in a competitive environment of "results-based" research.

One approach to the study of system-level phenomena that circumvents these problems is modelling. Whereas more traditional approaches to modelling communities and ecosystems usually do not explicitly include spatial phenomena, the formalism of cellular automaton (CA) models [2] allows examination of parameters with a spatial component. Parameters can be defined which incorporate different spatial (e.g. 10^{-3} – 10^6 m) and temporal (e.g. 10^0 – 10^5 days) scales, and thus CA modelling is a useful alternative to complement field based research.

The system-level behaviours of systems of coral reefs, and the influence of system level properties on the community dynamics on individual reefs, is poorly understood, but such information is likely to be vital to their effective management. Although it is well recognised that parameters operating at different scales influence community structure on coral reefs [3], e.g. dispersal by large scale ocean circulation [4] and selectivity of substrata by settling larvae which manifests at scales of 0 – 10^{-3} m [5, 6], the consequences of interactions of parameters that operate at different scales is little studied. Johnson and Preece [7] modelled recovery of coral following disturbance by crown-of-thorns (COT) starfish on a system of reefs [8] and found interactions between parameters operating at three different spatial scales (i.e. the relative importance of any one parameter to recovery of coral cover often depended on the levels of other parameters and the dependence of recovery time on the extent of disturbance was sensitive to particular combinations of parameters).

The three parameters they considered were:

1. the ability of juvenile corals (less than two years old) to survive the disturbance event. In the context of outbreaks of COT starfish this parameter describes whether starfish feed on small colonies. Empirical data indicate that starfish largely avoid corals less than 30 mm diameter [9],
2. the degree of hydrodynamic retention of particles around individual reefs (meso-scale), and
3. the large scale connectivity of the system, which is a function of large scale water circulation (direction and velocity), distances between reefs, and the life-history characteristics of larvae.

However, Johnson and Preece [7] considered only a single hypothetical "average" coral species and thus could consider only coral cover but not community structure in the sense of changes in the relative abundances of species.

In this paper we extend the models of Johnson and Preece [7] to include coral with two distinct life-histories, viz. broadcast spawning corals which release their gametes externally and whose larvae require development times of 4–6 days before they can settle and metamorphose, and coral that brood planula larvae which usually settle within one day of release [10].

Although these simple qualitative CA models were developed initially to examine disturbances by COT starfish, they can be applied generally to the gamut of anthropogenic factors that reduce coral cover [11, 12]. The models are not calibrated to any particular reef system but are intended to be exploratory and help focus future research about large scale properties and behaviours, and interactions among parameters that operate at different scales. Although this work concerns a marine ecosystem, the concepts of patchiness (spatial layout of reefs), disturbance and connectivity are equally relevant to some terrestrial habitats that have been fragmented by anthropogenic activities.

2. Methods

2.1. General

Eight cellular automaton models representing all combinations of two levels of each of the parameters of reef density (or inter-reef distance), degree of larval retention, and survivorship of pre-disturbance recruits are compared. In general, each model consists of a grid of cells representing a matrix of equidistant reefs separated by deep water (see [7]). Reefs exist in one of six qualitative states of coral cover (C_0 – C_5 : C_0 = no coral cover, C_5 = maximum coral cover), and annually produce an amount of larvae in proportion to their coral cover (L_1 – L_5 ; C_0 produce no larvae). The larvae are dispersed by water currents. For each reef, a record is kept of coral cover of both life-history types (i.e. broadcast spawning and brooding species). Larvae produced by each type can disperse in the system independently of one another.

The behaviour of the system is assessed in terms of the average coral cover of each life-history type on all reefs in the system. This response is estimated as the mean of Monte Carlo simulations of each model ($n = 10$ runs per simulation). A reef is considered to have recovered when the average coral cover of the system is ≥ 4 .

2.2. Spatial parameters

Each of the three parameters could occur at one of two levels.

2.2.1. Reef density (large scale)

Reef density refers to the number of reefs in the system and defines the inter-reef distance. Reefs occur at either high density (440 reef cells distributed evenly in the system of 3960 cells, with each reef separated by two “water” cells) or at low density (120 reefs separated by an inter-reef distance of 5 “water” cells). If each cell is assumed to have the dimensions of 5×5 km, the model system could be viewed as a crude caricature of the central sector of the Great Barrier Reef (GBR) which has experienced two series of outbreaks of COT starfish in the past 3 decades [13].

2.2.2. Larval retention (meso scale)

The degree of larval retention defines the probability of water-borne particles being retained on a reef over a 24 hour period due to meso-scale hydrodynamic circulation around individual reefs. In the model, larval retention is set either at zero (in which case the distribution of flow is set as 0:10:5:5:1:1:1:1:1 for stationary:S:SE:SW:N:E:W:NE:NW) or at a rate of retention of 13% of particles per week (i.e. distribution of flow set as 75:10:5:5:1:1:1:1:1 for stationary:S:SE:SW:N:E:W:NE:NW). The non-zero retention rate is derived from Black's [14] estimates of retention around reefs of average shape and size in average weather conditions in the central section of the GBR.

In deep water cells between reefs there is no retention of larvae so they are dispersed according to the same probabilities as for zero retention on reefs (just mentioned). Thus, in inter-reef areas larvae move one cell per day and although they may be transported in any direction, the net flow is southwards in accordance with the residual circulation in the central sector of the GBR.

2.2.3. Survival of juvenile corals (small scale)

The survival of juvenile corals recruited in the two years prior to the disturbance events essentially describes the feeding behaviour of COT starfish (starfish usually avoid small corals less than 3 cm diameter) [9]. To generate pre-disturbance recruitment, the model is run for two years with initial coral cover for all species on all reefs set at the maximum possible. The amount of larvae that settled on each reef in these two years before the disturbance event is recorded.

2.3. Coral life-history parameters

Differences in the life-histories of the two types of corals is an important comparison in the model. The parameters that describe the two life-history types act overall on an annual time-step. The two coral life-history types do not interact with one another. The parameters are:

2.3.1. Production of larvae

The model year commences with an annual release of larvae into the system. This is accurate for broadcast spawning corals which on the GBR generally produce larvae in an annual spawning event [15]. However, for species that brood larvae, the model uses the sum of all releases of larvae occurring in one year. This is justified in that Richmond [16] estimated that the sum of brooded larvae produced by *Pocillopora damicornis* in one year is equivalent to the amount of larvae produced in the single annual spawning of the broadcasting species *Acropora tenuis*.

2.3.2. Dispersal of larvae

Larvae are moved in the system by water currents as described in Section 2.2.2 on larval retention. If larvae arrive at a reef but are not competent to settle, they continue to be dispersed in the system.

2.3.3. Settlement and mortality of larvae

All larvae are competent to settle up to a maximum of 10 days. From day 6 to 10 there is a decline in the competency of larvae to settle, which is analogous to a daily mortality rate of one larval class per day from day 6 onwards (i.e. $L_n \rightarrow L_{n-1}$ each day, for each species).

Although competent up to 10 days old, the larvae of broadcast spawning corals require time to develop in the plankton and are not competent to settle until 5 days after spawning [17].

For brooding corals, 25% of larvae are deemed competent to settle on their natal reef within 24 hours of release. This estimate of the proportion competent to settle within one day of release is likely to be conservative [18]. Brooded larvae that do not settle on day 1 settle on any reef they contact subsequently.

2.3.4. Background mortality of corals

The annual rate of background mortality for each life-history type is calculated from estimates of life expectancy, being 15 years for a broadcast spawning coral and 10 years for brooding species, representing typical species of the *Acroporidae* and *Pocilloporidae* respectively [19]. Background mortalities are expressed as an annual probability of coral cover on each reef being reduced by one class for each species. These are $Pr = 0.33$ for the broadcast spawning coral (5 classes in 15 years), and $Pr = 0.5$ for the brooding coral (5 classes in 10 years).

2.3.5. Coral growth

Because the model represents coral cover in six qualitative states rather than as a continuum, growth occurs as increments in reef state. The rate of increments depends on the life-history type and history of larval settlement on each reef. The greater the amount of larvae settling in any one year, the greater the growth rate (i.e. probability of increment; see Table 1) and total cover achievable from that settlement event (i.e. total number of increments attributable to that settlement; Table 1).

Probabilities of increments for broadcast spawning corals were estimated assuming complete recovery of cover (i.e. to C_5) of a devastated reef (cover = C_0) in 25 years after seeding with the maximum amount of larvae (i.e. larval class = L_5). Since empirical data on average annual growth rates [18] indicate a ratio of 5:2 for broadcast (*Acroporidae*) to brooding (*Pocilloporidae*) corals based on area, the probabilities of increments in cover of brooding corals were scaled accordingly. The maximum time that any one annual recruitment on a reef could contribute to growth was set conservatively at 20 years (clearly, individuals can grow beyond the life expectancy of the species).

3. Results

3.1. System level properties

3.1.1. Effect of reef density — large scale

The effect of reef density (inter-reef distance) on recovery after disturbance depends on both the life-history type and the degree of larval retention.

Recovery of brooding corals is little affected by inter-reef distance provided there is retention of larvae around reefs (Figure 1: Ab, Ad, Cb and Cd). This suggests that

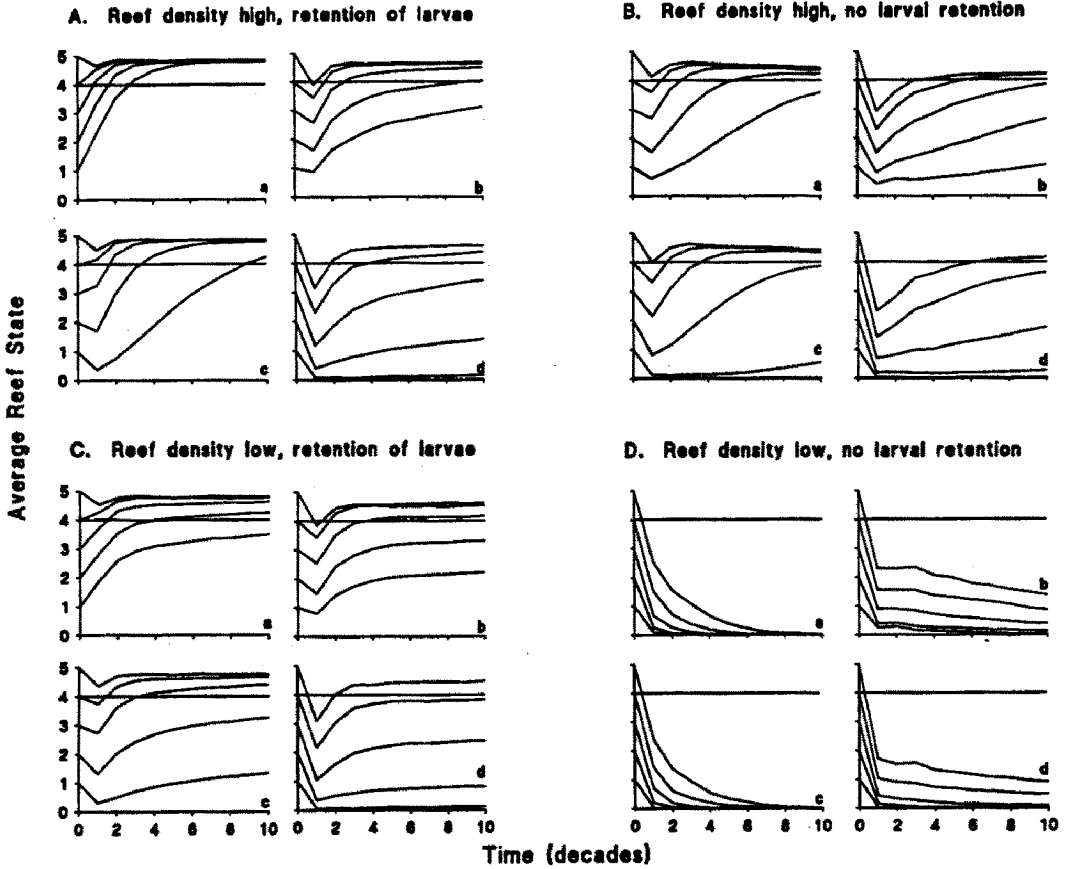


Figure 1: Recovery of coral cover following a single disturbance event affecting all reefs in the system. Trajectories show recovery from different intensities of damage under different regimes of reef density (high or low), retention of larvae (0 or 13% in 7 days) and survival or failure of pre-disturbance recruits, for two life-history types of coral. Codes a-d indicate: (a) broadcast spawning species, survival of pre-disturbance recruits; (b) brooding coral species, survival of pre-disturbance recruits; (c) broadcast spawning species, failure of pre-disturbance recruits; (d) brooding coral species, failure of pre-disturbance recruits. Coral cover for each species is deemed to have recovered when the average reef state is ≥ 4 (horizontal line).

Table 1: Parameters of coral growth (recovery) in the model: the nature of the dependency of (1) the rate of increase of coral cover (= probability of $C_s \rightarrow C_{s+1}$) and (2) the absolute amount of increase in cover (= maximum number of increments $C_s \rightarrow C_{s+1}$) on levels of annual recruitment (equivalent to amount of larval settlement). Note that growth of recruits can increase coral cover for up to 20 years after a recruitment event.

Level of larval settlement	Rate of increment = $Pr(C_s \rightarrow C_{s+1})$		Maximum number of increments $C_s \rightarrow C_{s+1}$
	Broadcast spawning corals	Brooding corals	
L_5	0.3	0.12	5
L_4	0.24	0.096	4
L_3	0.18	0.072	3
L_2	0.12	0.048	2
L_1	0.06	0.024	1

under these circumstances exchange of larvae among reefs is relatively unimportant, regardless of inter-reef distance. In contrast, for broadcast spawning corals under conditions of high retention of larvae around reefs, recovery rates decline noticeably with increasing distance between reefs (cf. Figure 1: Aa, Ac vs. Ca, Cc). This effect is more pronounced if recent recruits do not survive the disturbance (Figure 1Cc).

If there is no retention of larvae (Figure 1: Ba, Bc, Da, Dc, Bb, Bd, Db and Dd), the negative effect on recovery of increasing inter-reef distances (lower reef densities) is dramatic for both life-history types (Figure 1: Da, Dc, Db and Dd), particularly for the broadcast spawning corals which cannot persist with zero larval retention at low reef densities.

3.1.2. Variance in reef state

A notable feature of many of the models is dissimilar recovery trajectories of systems, which differ only in the initial amount of damage they sustained, from points of identical average reef state (ARS). For example, in Figure 1Ca the system recovering from an initial state of $ARS = 1$ recovers at a much slower rate from the point where $ARS = 3$ than other systems at $ARS = 3$ that did not suffer as much damage. Similarly, in Figure 1Cd average coral cover in the undamaged system declines to a point where $ARS = 3.5$ but then recovers (i.e. attains $ARS > 4$), but other systems in the same model that do experience damage and also attain $ARS = 3.5$ do not recover (trajectories are asymptotic at $ARS < 4$). Even though systems in the same model may attain identical ARS, because the initial amount of damage is different they differ in the variance and range in reef state. For systems of identical ARS the variance in ARS is greater in those suffering greater amounts of damage.

3.2. Effect of retention of larvae around reefs — meso-scale

Not surprisingly, larval retention has the most dramatic effect on recovery trajectories when inter-reef distances are large (e.g. Figure 1: Da, Db vs. Ca, Cb). In high reef density systems, the effect of larval retention depends on the level of disturbance and

whether the recent recruits survive the disturbance (e.g. Figure 1: Ad vs. Bb). If recruits are unaffected by the disturbance, then both types of corals show a quantitative reduction in recovery rate with decreasing retention of larvae, but the qualitative behaviours are similar for both levels of retention (e.g. Figure 1: Ba, Bb vs. Aa, Ab). In contrast, if recent recruits do not survive there is a threshold of disturbance for the brooding corals from which they cannot recover, irrespective of levels of retention of larvae (Figure 1: Ad and Bd). If there is no retention of larvae and new recruits do not survive, the threshold for "non-recovery" of the brooding corals occurs at lower amounts of disturbance (e.g. higher initial average reef state, Figure 1Bd), and the broadcast spawning corals also display such a threshold (Figure 1Bc).

3.3. Effect of susceptibility of recruits to disturbance — small scale

The susceptibility of recruits to disturbance has more effect on the brooding corals than the broadcast spawning corals. Brooding corals show particular sensitivity to survivorship of recent recruits when damage is high, to the extent that the recovery rate can be zero if recent recruits do not survive the disturbance (e.g. Figure 1: Ad, Bd and Cd). The broadcast spawning corals are generally less sensitive to this parameter, although in high density reef systems with no retention, recovery from high levels of damage is noticeably sensitive to the survival of recent recruits (cf. Figure 1: Ba and Bc).

3.4. Coral life-history

In all models except in those of low reef density and zero larvae retention, the cover of broadcast spawning species is greater than that of brooding corals. This reflects the general structure of most real communities on reefs in the GBR [20], and in the models is the result of growth and mortality rates which allow faster recovery of the broadcast spawning species. However, in systems with low levels of larval retention and large inter-reef distances (Figure 1: Da, Dc, Db and Dd), the broadcast spawning corals cannot exist, and cover of brooding corals declines but is still present after 100 years. Subsequent models with similar parameter values (not covered in this paper) show that a slight increase in life expectancy (of brooding corals by 3 years to 13 years), or an increase in their settlement rates in the first 24 hours (from 25% to 50%) allows cover of brooding corals to increase after any level of damage. Thus, in contrast to systems in which inter-reef distances are small or in which reefs retain larvae in their vicinity, brooding corals can dominate communities on isolated reefs that tend not to retain larvae.

4. Discussion

4.1. Interactions among parameters at different scales

When there are interactions among parameters of different spatial scales, study of single parameters in isolation on any scale may be inadequate to predict system level responses. In this study we have demonstrated that the sensitivity of the system to any one of small scale (COT feeding behaviours), meso-scale (hydrodynamic retention around reefs) or large scale (reef density) parameters depends on the level of the other parameters in the model. Although it is rarely, if ever, possible to include all parameters relevant to a question in any one study, it is important that when two or more parameters are considered simultaneously the project design includes examination of their interaction.

4.2. Emergent behaviours

Several of the temporal trajectories demonstrate complex patterns not readily predictable from consideration of individual parameters. Two significant emergent properties are:

1. the existence of threshold levels of damage such that corals recover if the amount of damage is less than the threshold (albeit at different rates depending on the precise amount of damage) but either decline or persist indefinitely at low levels if the threshold is attained or exceeded, and
2. dependence of the pattern of recovery on the variance in reef state for a given average reef state.

The latter property is discussed in Section 4.3.3. For brooding corals there are several examples of qualitatively different trajectories (i.e. positive vs. zero slope) in the same model, where the threshold is evident at some level of damage between initial average reef state equal to 1 (the most intense damage) and average reef state equal to 2 (Figure 1: Ad, Bd and Cd). Broadcasting corals either always increased or decreased in cover over 100 years (depending on the model) regardless of the level of damage. However, in some models for broadcast spawners recovery rates showed dramatic declines for small increases in disturbance (Figure 1Bc).

4.3. Importance of system-level parameters

4.3.1. Connectivity: broadcast spawning corals

When distances between reefs are small, broadcast spawning corals always recover from disturbance, albeit at varying rates depending on other parameters (Figure 1: Aa, Ac, Ba and Bc). Clearly a highly connected system facilitates sufficient settlement of highly dispersed larvae of broadcast spawning corals. In contrast, in systems of reefs at low densities the response of the system to damage depends to a large degree on the amount of larval retention. If larvae are retained around reefs (13% per week in the models), then the trend is towards recovery (Figure 1: Ca and Cc), otherwise there is a decline (Figure 1: Da and Dd). Not surprisingly, these results imply that self seeding of natal reefs is essential for recovery when the distance between reefs is large. In other words, there is a higher risk of local extinction as a result of disturbance with increasing isolation of reefs.

4.3.2. Connectivity: brooding corals

Recovery of brooding corals depends on interactions among several parameters. When a proportion of larvae are retained on their natal reef and new recruits survive the disturbance event, the models suggest that for most levels of disturbance the system will recover irrespective of the connectivity of the system (Figure 1: Ab and Cb). This indicates that self seeding onto natal reefs is high and that connectivity between reefs is limited even when inter-reef distances are short.

If larvae are not retained on their natal reef but are dispersed (i.e. there is greater potential for connectivity within the system), brooding corals recover only when the level of damage is low and the density of reefs is high. This suggests a reliance of brooding corals on self seeding for maintenance of populations, even when reefs are in close proximity. Since individual reefs are relatively independent of one another (low

connectivity between reefs) for this type of life-history, communities of brooding corals are likely to be more vulnerable to intense damage than their broadcasting counterparts.

4.3.3. Variance in reef state

An important property of the system is the variance in coral cover among reefs within the system. This is indicated by dissimilar patterns of recovery of systems with the same average reef state but divergent variances in reef state as a result of different initial levels of disturbance (Figure 1: Ca and Cd). The trajectories associated with higher variances in coral cover are asymptotic at lower levels of coral cover. This suggests that at a regional scale there are areas within the system that recover and others that do not, and that recovery of the system is limited by patchiness in recovery at the regional scale. Changes in the variance of coral cover among reefs for different intensities of damage suggest that at the system scale there are corresponding changes in connectivity among groups of reefs related to availability of larvae, i.e. at some levels of damage there are groups of reefs that are relatively isolated from others in the system with respect to larvae even when physical distances between reefs do not vary.

4.4. Founder effects in community structure

On relatively isolated reefs there is a strong potential for founder effects in community structure as a result of species' differential susceptibility to disturbance or differential ability to recover. When inter-reef distances are large, there is a threshold level of larval retention below which cover of broadcasting corals declines regardless of whether reefs experience damage or not (cf. Figure 1: Ca, Cc vs. Da, Dc). The exact value of the threshold is likely to vary with the amount of damage. In contrast, on isolated reefs brooding species can maintain their cover and recover from damage even if there is no retention of larvae after 24 hours, depending on their life-history parameters (e.g. recovery occurs if there is 25% settlement on natal reef within 24 hours and life expectancy = 13 years or if 50% settlement within 24 hours and life expectancy = 10 years; see Section 3.4, Figure 1: Da, Dc vs. Db, Dd). It follows that when reefs are relatively isolated from one another, there are levels of disturbance from which brooding corals will recover or at least maintain their presence but broadcasting species will not. This situation will see a shift in community structure from domination by broadcasting species to domination by brooding species. These "founder effects" in community structure after damage would be exacerbated if disturbance events selectively targeted broadcasting species (e.g. if coral predators demonstrated preference for broadcasting species).

4.5. Implications for management

Under most conditions of the models, the brooding corals are susceptible to high levels of damage, and consequently they are more likely to become locally extinct after damage events. Broadcast spawning corals are more robust to disturbance except on isolated reefs with low levels of larval retention. Clearly, isolated reefs or isolated groups of reefs require different management practices to those embedded in a large network of hydrodynamically connected reefs.

An important result is the identification of threshold levels of disturbance beyond which, for some combinations of parameters, there is a risk of some communities remaining degraded indefinitely in a state of low cover and (potentially) low diversity.

For effective and informed management of real coral reefs there is a need to determine these thresholds for particular systems or reefs.

4.6. Limitations of models

Although these models may be viewed as a crude caricature of the central sector of the GBR they are too simplistic for results to be of direct relevance to current issues of management of the GBR. Future developments of the models will attempt to tailor the framework and parameters of the models more closely to the GBR system. This would include representing the real sizes, shapes and spatial relationships of reefs (i.e. not as a uniform grid of identical sized reefs), including several species of corals of particular life-history types, and including empirical data of hydrodynamic circulation at different scales. It will be important to examine the responses to several other dimensions of disturbance (e.g. frequency, duration, spatial patchiness, selectivity, seasonal timing), interactions among different coral species, and to include asexual recruitment (by fragmentation) of corals and growth of colonies unaffected by disturbance events in assessments of coral recovery.

5. Conclusions

In ecological systems, experimentation on large scales is often impractical or impossible. Modelling with cellular automata is a useful tool to study ecosystems at small or large scales where consideration of spatial components is important. In the example given here, interaction of parameters at three different spatial scales highlighted emergent system level properties, which could not be identified by considering scales smaller than the whole system. CA models can be tested through existing monitoring programmes, and may become an important predictive tool for managers.

As a final comment it is worth noting that much of the theory about patchiness and fragmentation of habitat and ecosystems is based on terrestrial systems but applies equally well to some marine systems. Conversely, the principles demonstrated in our simple and preliminary models are relevant to terrestrial environments, and can be scaled to ecosystems of any size. This work, when properly expanded, is likely to be of use in conservation science, particularly in highlighting priority areas for research and management action.

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