

Damage, Scale and Recovery in Model Coral Communities: The Importance of System State

CRAIG R. JOHNSON AND ANN L. PREECE

Department of Zoology, University of Queensland, St Lucia, QLD 4072, Australia

Abstract. Spatial models indicate that recovery of coral cover after damage events depends on large-scale system-level properties as well as those that define parameters at much smaller scales. Monte Carlo simulation studies showed that recovery on individual reefs and in the system as a whole depended on the large-scale pattern of disturbance in the system, so that 2 systems of identical average reef state (= coral cover) but of different variance in reef state may demonstrate dissimilar abilities to recover. The models showed that the relationship between recovery rate and spatial extent of damage depends on (1) the effective connectivity of the system (a system-level property), which affects availability of larvae for recruitment, and the relative magnitudes of (2) larval retention (self-seeding) around individual reefs, (3) background mortality rates of coral and (4) the susceptibility of newly recruited corals to the disturbance. Recovery rates may be highly dependent or largely independent of the spatial scale of damage depending on values of these parameters, and may vary with the intensity of damage. At high reef densities coral recovery rates are sensitive to survival of recent pre-damage recruits if coral life expectancy is relatively short (25 y), but the degree of self-seeding is relatively unimportant. In contrast, if the density of reefs is low and there is no self-seeding, coral does not recover at all but either stabilises at reduced cover or declines, depending on its life expectancy (i.e. background rate of mortality). If reef density is low and there is some larval retention (13% over 7 d), then recovery depends largely on survival of pre-damage recruits and the rate of background mortality is less important.

Introduction

Coral communities are subject to several phenomena that can cause significant reductions in both

coral cover and diversity at large spatial scales, e.g. cyclones, eutrophication, bleaching events, and predation. A spectacular example in the scale of its deleterious effect is the coral eating starfish *Acanthaster planci*. Damage to coral communities by *A. planci* can be particularly extensive in systems of reefs in which hydrodynamic connectivity is high, as has been observed in the Ryukyu Is. in Japan (Yamaguchi 1986) and on the Great Barrier Reef (GBR) in Australia (see Johnson 1992a). In the central one-third sector of the GBR (ca. 15–20°S) it is estimated that outbreaks of starfish have affected about two-thirds of reefs over the period 1962–1991 (Moran et al 1988; Reichelt et al 1990).

An understanding of the recoverability of reefs after large scale disturbances and, more importantly, the causal mechanisms that underlie the recovery process, is fundamental to prediction of the dynamics and stability properties of reef systems. Monitoring in real systems and modelling in artificial ones has yielded useful insights; empirical observation provides valuable information on spatial pattern and rates of coral recruitment and growth after disturbance, and can help to identify key parameters and processes that operate at local scales (e.g. Wallace et al 1986; Colgan 1987; Endean et al 1988; Done et al 1988; Cameron et al 1991). Modelling is particularly useful in that it can address large spatial and temporal scales and enables systematic study of the sensitivity of recovery to variation in selected parameters (e.g. Done 1987, 1988, Bradbury et al 1990, van der Laan and Bradbury 1990). Collectively, these studies have indicated that times for recovery of community structure may be large (but see Colgan 1987), and depend on the life history parameters of coral species (rates of recruitment, growth and background mortality), and intensity and frequency of damage. However, most work has focussed on local and meso scales and

scant attention has been given to system level phenomena.

Characteristics of disturbance at the scale of whole systems of reefs and the connectedness of the system via hydrodynamic dispersal of coral larvae are 2 system level parameters whose influence on recovery has not been investigated. Both are likely to be significant in defining global recoverability as well as that of individual reefs in circumstances in which the system is not saturated with coral larvae. In previous large scale spatial models of the GBR it has been assumed that coral larvae are saturating (Bradbury et al 1990; van der Laan and Bradbury 1990). This assumption was based on observations of mass spawning of corals and the formation and subsequent dispersal of surface slicks of spawn (Babcock et al 1986; Bull 1986; Oliver and Willis 1987; Willis and Oliver 1988). However, empirical data indicate differential availability of coral spat over large spatial and temporal scales (Fisk and Harriot 1990; Harrison and Wallace 1990; Sammarco 1991; V. Harriot pers. comm.). Moreover, at some scale the availability of larvae must be a function of the amount of live coral in the system. To press this point using a trivial extreme, if the intensity and spatial extent of disturbance is sufficiently great to destroy all corals in the system then global availability of larvae will be zero. If intense disturbance affects most corals on a reef, then, by definition, recovery will depend largely on recruitment from settlement of larvae and not on coral remnants (e.g. Colgan 1987, Done et al 1988). Thus, given some level of background mortality there must exist some amount of disturbance from which global recovery of corals is not possible. Beyond this critical level of disturbance, the system may remain in a degraded state indefinitely. For any system of reefs, the question arises as to what this critical level might be.

For an individual reef, we suggest that the critical level of disturbance will depend on its connectivity with others in the system as well as the global level of disturbance. Connectivity will be a function of hydrodynamic processes, longevity of competent planktonic larvae and distance to other reefs. Important hydrodynamic processes to consider are the velocity and direction of currents at large spatial scales, and the degree of local retention of water masses (containing larvae) around reefs. Both empirical observation (cf. Bull 1986; Willis and Oliver 1988; Sammarco and Andrews 1988, 1989) and results of analytical and numerical models (Black et al 1990, 1991) indicate that many reefs may be self-seeding to some degree, and that under certain conditions, may be largely self-seeding. Black et al (1990) suggested that many kinds of reefs may re-

tain $\geq 10\%$ of particles after 8 d, and concluded that particles can remain on or adjacent reefs in common weather conditions for several weeks. Existing large scale models assume that there is no self-seeding of reefs (Bradbury et al 1990; van der Laan and Bradbury 1990).

In this paper we use a cellular automaton model to investigate the recovery of corals after single disturbance events in a hydrodynamically connected system of reefs. We examine the influence on the rate of coral recovery of (1) the intensity of damage to corals, (2) the spatial extent of damage to corals, (3) background rates of mortality of corals, (4) the susceptibility of newly recruited corals to disturbance events (in the example of damage by *A. planci*, this parameter defines aspects of feeding behaviour of the starfish), and (5) the connectivity of the reef system as determined by the density of reefs and degree of larval retention around them.

Materials and Methods

The automaton generates temporal changes in a spatial matrix of cells in which the spatial information, or state, of a cell at time $t+1$ is determined by the state of that cell and its 8 immediate neighbours (the Von Neuman neighbourhood) at time t . If each cell is treated as having dimensions of 5×5 km, the model can be viewed as a simple caricature of the central sector of the GBR.

Since the objective was to use a simple model to explore concepts by examining qualitative responses to parameters, parameters were not calibrated to enable quantitative predictions. The model considers only coral cover and does not include a range of coral life history types. Instead, life history parameters describe an 'average' broadcast spawning coral between the extremes of opportunistic species (e.g. Acroporidae) and those with much lower rates of recruitment and growth (e.g. Faviidae). An outline of the model and its parameters is given below:

The spatial system: The model is based on a matrix of $33 \times 120 = 3960$ cells which exist either as reefs or as deepwater between reefs. All reefs are of identical size and are arranged in a regular grid at either 'high density' (a total of $11 \times 40 = 440$ reefs distributed evenly with 2 'water' cells between neighbouring reefs) or 'low density' ($6 \times 20 = 120$ reefs in total with 5 'water' cells separating adjacent reefs). No reefs occur in the perimeter of the system.

Coral cover: Reefs exist in 1 of 6 possible qualitative states of coral cover (C_0 – C_5) with C_0 = no coral and C_5 = maximum cover.

Disturbance regime: Two of the 6 'dimensions' of disturbance delineated by Chapman and John-

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 $C_i \rightarrow C_{i+1}$) and (2) the absolute amount of increase in cover (=maximum number of increments $C_i \rightarrow C_{i+1}$) on levels of annual recruitment (equivalent to amount of larval settlement). Note that growth of recruits can increase coral cover for up to 25 y after a recruitment event.

Level of settlement	Rate of increments = $\text{pr}(C_i \rightarrow C_{i+1})$	Maximum number of increments $C_i \rightarrow C_{i+1}$
L_3	0.25	5
L_4	0.20	4
L_3	0.16	3
L_2	0.12	2
L_1	0.08	1

son (1990) were considered, viz. spatial scale and intensity. The extent of disturbance is set as a proportion of the total number of reefs. When <100% of reefs are damaged, damage always occurs in a patch of adjacent reefs located centrally in the system (i.e. the distribution of damage is contagious) and bounded by undamaged reefs. Intensity is set by the amount that coral cover is reduced from the maximum (state C_3). However, disturbance is limited in its effect and cannot reduce coral cover to <state= C_1 , i.e. the most intense disturbance does not affect all corals on a reef.

Hydrodynamics and dispersal of coral larvae: Reefs produce coral larvae in proportion to coral abundance such that reefs in state C_0 – C_3 produce larvae in amounts L_0 – L_3 respectively. Spawning occurs synchronously on all reefs on one occasion each year. Clouds of larvae move about in the system depending on the direction of water currents and the degree of hydrodynamic retention around reefs. In keeping with the situation in the central sector of the GBR at the time of coral spawning (Andrews and Furnas 1986; Williams et al 1984; Wolanski and Pickard 1985), larvae not intersecting a reef can be dispersed in any direction but the net flow is southward (flow is distributed as 0:10:5:5:1:1:1:1:1 for stationary: S:SE:SW:E:W:NE:NW:N respectively). Movement of a parcel of larvae that intersects a reef depends on the degree of larval retention (which may lead to self-seeding). Larval retention is set at either zero, in which case larvae are dispersed according to the flow distribution when they are away from reefs, or at a level at which on average 13% of particles are retained after 7 d. For this level of retention the distribution of flow is set as 75:10:5:5:1:1:1:1:1 for stationary: S:SE:SW:E:W:NE:NW:N respectively. This amount of retention corresponds with that estimated by Black et al (1990) for the majority of reef

morphologies demonstrated in the central sector of the GBR.

Competency and longevity of coral larvae and coral recruitment: We assumed that recruitment depends on sexual production of larvae and that recovery via asexual recruitment (via fragmentation or partial mortality of intact colonies that leaves several remnants) is unimportant (see Discussion for analysis of this assumption). In concordance with field observations (Babcock and Heyward 1986, Bull 1986, Babcock unpub. data) larvae are deemed incompetent to settle until 4 d after spawning. The number of competent larvae begin to decline from 6 d after spawning at a rate of one larval class per day (i.e. $L_6 \rightarrow L_{6-1}$ per day due to predation, regression, overcompetency, etc.) so that there are no competent larvae in the system 10 d after mass spawning. Declining competency on this time scale parallels the behaviour of spawned larvae in experiments in the field (Babcock, unpub. data). Competent larvae that intersect a reef recruit to that reef.

Survival of pre-disturbance recruits: Corals recruited as a result of larval settlement in the 2 y prior to a disturbance event are deemed to either survive or not survive the disturbance. If pre-disturbance recruits survive the disturbance they contribute to subsequent coral growth and recovery.

Coral growth and recovery: Coral growth is realised by annual increments of the coral cover state, i.e. $C_i \rightarrow C_{i+1}$. The rate of coral growth on a reef is ultimately dependent on the amount of larvae that settle on it. Recruits of any one year can influence coral growth for up to 25 y, thus the state of any one reef can increment $C_i \rightarrow C_{i+1}$ several times in any one year depending on its history of larval settlement over the previous 25 y. The greater the magnitude of a recruitment the greater the rate of increase of cover and the greater the absolute amount of cover that can be attributable to that recruitment. Thus, the rate of increments in cover and the maximum number of times that a particular settlement event can subsequently lead to an increment in coral cover is dependent on the amount of larvae that settle each year (Table 1). Probabilities were determined assuming that growth of recruits following maximum settlement of larvae (i.e. at level L_3) in one year would lead to complete recovery of cover of a devastated reef (i.e. $C_0 \rightarrow C_3$) in 20 y.

Note that because overall growth of coral on a reef depends on its history of coral recruitment over the previous 25 y, coral recovery depends indirectly on C_i . However, since the level of recruitment in any one year influences both the rate of recovery and total cover achievable, the overall potential for

growth and recovery (in terms of both growth rate and total cover of coral achievable) of a reef at any point in time also depends on its precise recruitment history. Thus, for example, the model distinguishes between two reefs of identical state (e.g. C_2) where one is dominated by fewer but larger and older colonies (lower potential for further growth) and the other by a larger number of smaller, more recently recruited colonies (higher potential for further growth).

Background coral mortality (independent of disturbance): Rates of mortality are based on conservative life expectancies of either 25 y (high background mortality) or 50 y (low background mortality). Mortality schedules are implemented by setting probabilities of annual decline in reef state from C_i to C_{i-1} . For a life expectancy of 25 y, $\text{pr}(C_s \rightarrow C_{s-1}) = 0.2$, and for a life expectancy of 50 y, $\text{pr}(C_s \rightarrow C_{s-1}) = 0.1$.

Simulation structure: Recovery of coral cover was examined following single events of disturbance. Two series of simulations were conducted in which the intensity and spatial magnitude of disturbance were varied systematically. In the first, all reefs in the system were affected similarly and were reduced to a uniform coral cover (any of states C_1 – C_4). 'Recovery' from state = C_s examined the ability of reefs to maintain coral cover in the absence of disturbance. The recovery trajectory is defined as the change in average reef state with time. Since coral cover normally fluctuates even in the absence of (known) significant disturbance events, complete recovery of the system is defined arbitrarily as return to an average reef state ≥ 4 .

The second series examined the relationship between the time for recovery after disturbance and the spatial extent of damage (=proportion of reefs affected). Recovery was defined arbitrarily as attaining an average reef state ≥ 4 (considering damaged reefs only). Groups of contiguous reefs were disturbed by reducing their coral cover to state = C_1 . The number of reefs in the system damaged in this way was varied from a single reef to 100% of reefs. Heavy damage to a subset of reefs is broadly analogous to the effect of outbreaks of *Acanthaster* on reef systems (Birkeland and Lucas 1990). The subset of reefs damaged was symmetrical around the central point of the system.

Both series of simulations examined systematically the influence on recovery of the 16 possible combinations of (1) high/low reef density, (2) high/low rates of background coral mortality, (3) larval retention 0%/13% per 7 d, and (4) survival/no survival of corals recruited 2 y prior to disturbance. Results (recovery trajectories) are given as means

calculated from Monte Carlo simulations (20 runs per simulation).

Results

Behaviour of the model indicated that recovery of coral cover after disturbance can depend on the spatial scale and intensity of disturbance, the variance in intensity of disturbance throughout the system, distance between neighbouring reefs, amount of larval retention around reefs (self-seeding), rate of background mortality of corals, and survivorship of pre-disturbance recruits. However, the effect on recovery of any 1 of these parameters was dependent on the levels of the others.

Effects of intensity and spatial extent of disturbance: Not surprisingly, times to recovery of coral cover increased with intensity of disturbance (Fig. 1). However, depending on values of other parameters, rates of recovery (=slopes of lines in Fig. 1) were either dependent or independent of the intensity of disturbance. For example, at high reef densities and at relatively high background rates of coral mortality (i.e. coral life expectancy = 25 y), rates of recovery from intense disturbance were lower than recovery from disturbance at low and intermediate intensities if pre-disturbance recruits did not survive the disturbance event (Figs. 1B.a, 1B.b). However, if pre-disturbance recruits were not affected, the rate of recovery was similar for any intensity of disturbance (Figs. 1B.c, 1B.d).

A fundamental result is that recovery rates could be dissimilar in 2 systems after they had recovered to the *same* average reef state after disturbance at different initial intensities, even when initial rates of recovery were similar, so that coral cover recovered in 1 system but not in the other (e.g. compare recovery trajectories in Fig. 1C.b from the point where average reef state = 2 in the systems reduced initially to average reef state = 1 and = 2; see also Figs. 1B.a, 1B.b, 1D.b). This is attributable to a greater variance in coral cover among reefs (a system-level property) in systems that experience greater intensities of disturbance. High variance in reef state for a given average reef state indicates that coral cover on badly damaged reefs may remain at low levels (for some combinations of background mortality and self-seeding) so that the system does not recover.

The most rapid recovery from any intensity of disturbance occurred when reefs were self-seeding and when recent pre-disturbance recruits were not affected by the disturbance (Figs. 1A.d, 1B.d, 1C.d, 1D.d, 2A.d, 2B.d, 2C.d, 2D.d). In these circumstances, the rate of recovery was independent of the

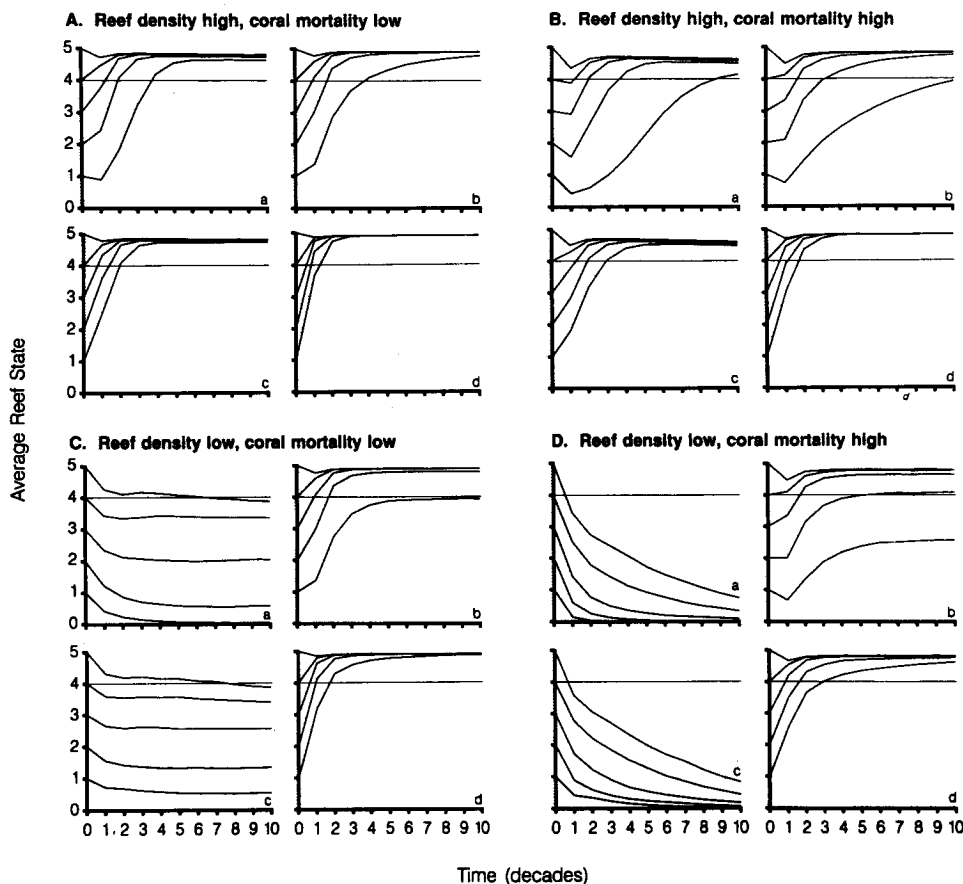


Fig. 1. Recovery of coral cover in the 100 y following a single disturbance event affecting all reefs in a system. The system is deemed to have recovered when average reef state >4 (shown by solid horizontal line). Trajectories show recovery from different intensities of disturbance under different regimes of reef density (high/low), background mortality rate of corals (high/low = life expectancies of 25 y and 50 y respectively), larval retention (0%/13% in 7 d), and survival of corals recruited in the 2 y prior to disturbance (recruits survive/fail). Codes a–d indicate: (a) no larval retention, failure of pre-disturbance recruits; (b) retention of larvae, failure of pre-disturbance recruits; (c) no larval retention, survival of pre-disturbance recruits; (d) retention of larvae, survival of pre-disturbance recruits.

spatial scale of damage, i.e. recovery times were similar whether 1% or 100% of reefs were damaged (Figs. 2A.d, 2B.d, 2C.d, 2D.d). In contrast, if pre-disturbance recruits did not survive the disturbance event on reefs which were not self-seeding, the time to recovery of damaged reefs was highly dependent on the proportion of reefs in the system that were damaged (Figs. 2A.a, 2B.a, 2C.a, 2D.a). Under these circumstances, if reefs were relatively isolated in terms of the likelihood of influx of larvae, and background coral mortality was relatively high, even if only a single reef in the system was damaged it may not recover at all (Figs. 2D.a,c). Under most circumstances recovery times were more predictable (i.e. less variable) with increasing proportion of reefs damaged. However, for isolated reefs that were not self-seeding the predictability of recovery

reduced dramatically with increasing proportion of reefs damaged (Figs. 2C.a,c, 2D.a,c).

Effects of connectivity; effective distance between reefs and larval retention: Since the average long-term current velocity and direction was constant, the effective distance between reefs was directly proportional to the absolute distance between reefs and thus to reef density. When inter-reef distances were small (high connectivity) the system always recovered eventually (Figs. 1A, 1B) and the time to recovery was considerably shorter than when connectivity was lower (cf. Figs. 2A, 2B with 2C, 2D).

The level of connectivity of the system of reefs was especially important if reefs were unable to retain the larvae they produced for longer than 1 day. Reefs did not recover at all if all reefs in the system were damaged, were not self-seeding and distances

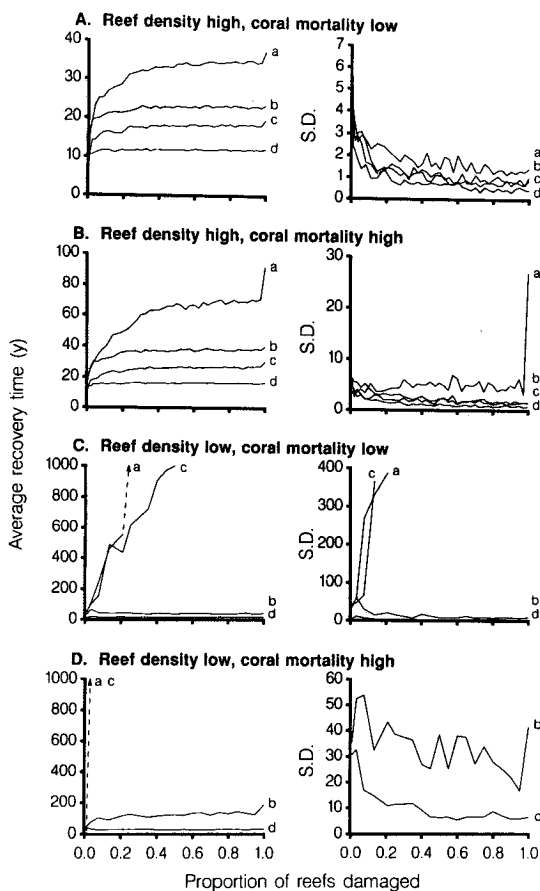


Fig. 2. Dependence of recovery time on the spatial extent of disturbance (=proportion of reefs damaged) in a system of reefs. The intensity of disturbance was identical among the subset of reefs damaged (all damaged reefs were reduced to coral state C_1). The system is deemed to have recovered when the average reef state of damaged reefs > 4 . Recovery times are estimated for different regimes of reef density (high/low), background mortality rate of corals (high/low = life expectancies of 25 y and 50 y respectively), larval retention (0%/13% in 7 d), and survival of corals recruited in the 2 y prior to disturbance (recruits survive/fail). Codes a–d indicate: (a) no larval retention, failure of pre-disturbance recruits; (b) retention of larvae, failure of pre-disturbance recruits; (c) no larval retention, survival of pre-disturbance recruits; (d) retention of larvae, survival of pre-disturbance recruits.

separating reefs were high. In these circumstances, coral cover either remained relatively constant at a reduced level or declined, depending on background rates of mortality (cf. Figs 1A.a,c with 1C.a,c; 1B.a,c with 1D.a,c); even when relatively few reefs in the system were damaged, recovery times were of the order of 100's or 1000's of years (Figs. 2C.a,c; 2D.a,c). It is noteworthy that in the absence of any disturbance, if reefs were not self-

seeding, high coral cover was maintained in a connected system but declined when the distance between reefs became too great to effect inter-reef transport of large amounts of competent coral spat (cf. Figs. 1A.a,c with 1C.a,c, and especially 1B.a,c with 1D.a,c). However, note also that in the model competent larvae are able to disperse > 1.5 times the inter-reef distance when reefs are at low density.

In contrast, if reefs manifested some degree of self-seeding due to hydrodynamic retention of larvae, and if corals that recruited in the 2 y prior to damage survived the disturbance, then recovery trajectories were little influenced by the level of connectivity and recovery was rapid (cf. Figs. 1A.d with 1C.d and 1B.d with 1D.d) and independent of the scale of disturbance in the system (Figs. 2A.d, 2B.d, 2C.d, 2D.d).

Effect of rate of background mortality: Recovery rates could (but did not always) decrease markedly as rates of background mortality of corals increased. Recovery was most sensitive to rates of background mortality when connectivity of the system was low, particularly if larval retention was zero (cf. Figs. 1C with 1D, 2C with 2D). At high levels of system connectivity, dependence of recovery rate on the intensity of disturbance was evident only at the higher rate of background mortality (cf. Figs. 1A.a with 1B.a, 1A.b with 1B.b).

Effect of survivorship of pre-disturbance recruits: Rates of recovery were always greater when pre-disturbance recruits were unaffected by the disturbance event than when they did not survive the disturbance. Recovery showed greatest sensitivity to survivorship of re-disturbance recruits at higher rates of background mortality (cf. Figs. 1B.a,b with 1B.c,d, 1D.b with 1D.d).

Summary: Overall, these results highlight several general precepts important to considerations of the recoverability of coral cover after disturbance events. These are:

- (1). Recovery of coral cover on a damaged reef, or damaged group of reefs, can depend not only on the intensity of damage to the particular reef(s) of interest but also on system-level properties such as the spatial extent and intensity of disturbance in the entire system (e.g. Figs. 2B.a, 2D.c), variance in reef state, and effective connectivity of the system. Connectivity is a function of the temporal scale of competency of larvae, velocity and direction of large scale water movement, the extent of larval retention around reefs, and distances between reefs (e.g. compare among Figs. 1A.a with 1C.a, 1C.c with 1C.d, 1D.c with 1D.d).

- (2). The rate of recovery of coral can depend on the intensity of disturbance (e.g. Figs. 1B.a, 1B.b) and its spatial scale (e.g. Figs. 2A.a, 2B.a, 2C.c), but under some circumstances may be largely independent of either the intensity (e.g. Figs. 1A.a–1A.d) or scale (e.g. Figs. 2A.d, 2B.d) of damage.
- (3). There are critical levels of disturbance beyond which systems demonstrate limited recovery and remain indefinitely in a degraded state of low coral cover even in the absence of further disturbance (e.g. Figs. 1C.b, 1D.b). In circumstances in which larval retention is zero and connectivity with other reefs is poor, recovery is slow (of the order of 10^2 – 10^3 y) or non-existent, even if only a small proportion of reefs in the system are affected (e.g. Figs. 2D.a, 2D.c, 2C.a, 2C.c).

Discussion

System-level properties and interdependence of parameters operating at different scales

When large systems of coral reefs are subject to disturbance, as can occur following outbreaks of *Acanthaster planci* (Moran 1986, Yamaguchi 1986, Johnson 1992a), the focus on recovery needs to be at the scale of the system and not just of individual reefs. Our simple qualitative model, intended to extricate concepts and not to provide quantitative predictions or critical values of parameters for any particular system, demonstrates that under some (but not all) situations recovery of coral cover on damaged reefs is highly dependent on system-level properties. The system-level properties shown to be important here are (1) the level of connectivity among reefs via larval transport, and (2) overall system state which defines the spatial extent, intensity, and distribution of intensity (=variance) of damage in the system.

A feature of biological systems is that sensitivity to a given parameter often depends on the level of others, i.e. there are interactions among parameters such that it is not the absolute values of parameters but their relative magnitudes, or balance, that is critical. In an elegant series of simulations of post-*Acanthaster* recovery of *Porites* populations on an individual reef, Done (1987, 1988) demonstrated that recovery depended on the balance of rates of recruitment, growth and background mortality of *Porites*. Our qualitative spatial model, of entirely different formulation and scale to the population models of Done, similarly underscored the impor-

tance of the balance in rates of background mortality of corals, availability of propagules for recruitment, and of survivorship of corals that recruit just prior to a damage event. It follows that the effect of factors (parameters) operating at local scales may depend on others that manifest at the scale of the system. For example, our results suggest that recovery is insensitive to large variations in rates of background mortality (local scale) providing that connectivity among reefs via transport of larvae (system scale) is high (particularly if survival of pre-disturbance recruits is high), or if reefs are self-seeding, i.e. when rates of recruitment from larval settlement are high. Clearly, the critical balance between mortality and recruitment can depend on system-level (largely hydrodynamic) properties.

Hydrodynamics, Dispersal and Recruitment

The sum of evidence from natural and model systems indicates that hydrodynamic processes at small and large scales can, and do, exert significant influence on the structure and dynamics of individual reef and reef systems by affecting the spatial movement of sexually produced larvae (Williams et al 1984; Bull 1986; Sammarco and Andrews 1988, 1989; Willis and Oliver 1988; Bradbury et al 1990; Black et al 1990, 1991; Black and Moran 1991; James and Scandol 1992; Johnson 1992b; Scandol and James 1992). Our results show clearly that if recruitment depends on settlement of larvae then the implications for recovery of reef systems, even after extensive damage, are much less serious if the effective connectivity of the system is high. Effective connectivity is a function of longevity of competent larvae, distance between reefs, and the direction and velocity of currents. Our assumption of the overriding importance of sexual vs. asexual recruitment in recovery warrants brief attention. If damage is extensive so that little or no coral remains (e.g. Colgan 1987) then, by definition, the assumption is true. Empirical data on regrowth from remnants (Done et al 1988, Endean et al 1988, Cameron et al 1991) and on the relative importance of sexual vs. asexual recruitment (Babcock 1991) indicate that the assumption is valid for some species, although it may not apply to *Porites* (Done 1988) or foliaceous corals (Hughes 1988). Certainly, significant recruitment from larvae onto dead coral skeletons after predation by *A. planci* is well documented (Wallace et al 1986), and rates of settlement of spat may increase in the presence of the algal turf that colonises dead corals (Sammarco 1980; Johnson unpub. data).

Our results raise two other important points about hydrodynamic dispersal of larvae and recruitment. First, scales of significant dispersal and significant recruitment are uncoupled. Under all conditions of the model, competent larvae were able to disperse distances greater than 1.5 times the maximum distance between adjacent reefs (i.e. at low reef density), but at low density of reefs dispersal on this scale did not effect significant recruitment leading to subsequent recovery (e.g. Fig 1C). An extreme example to emphasize the decoupling of scales of dispersal and recruitment in natural systems is the dispersal of coral on buoyant pumice over several thousand kilometres from Tonga into the GBR (Jokiel 1990); this is undoubtedly a significant dispersal but it is unlikely that sufficient coral arrives (estimated 10^3 colonies y^{-1} for the entire GBR) and establishes (unknown) on the GBR to constitute significant recruitment on ecological time scales.

The second point is that small scale hydrodynamic processes affecting local retention of larvae around reefs are critical to recruitment if effective system connectivity is low. Long the subject of debate, there is now clear evidence that some reefs can be self-seeding to some degree as a result of hydrodynamic retention of larvae (Bull 1986; Sammarco and Andrews 1988, 1989; Willis and Oliver 1988; Black et al 1990, 1991). Self-seeding is not required for recovery of coral cover if the effective system connectivity is high (Figs. 1A,1B,2A,2B), but it is likely to be the primary mechanism effecting recovery of corals (at least for species in which recruitment by means other than production of larvae is relatively unimportant) on relatively isolated reefs (Figs. 1C,1D,2C,2D). On isolated reefs, regardless of the mechanism of recruitment, there is likely to be a strong positive feedback, or founder effect, in recovery depending on species' relative abundances after disturbance. This may be particularly pronounced when species are not equally susceptible to disturbance, for example because of food preferences of predators (Birkeland and Lucas 1990; Keesing 1990) or the existence of refuges in areas of high wave energy where predators cannot feed (e.g. Colgan 1987).

Life Histories

A limitation of the model is that it does not consider different life histories and thus assesses recovery only in terms of cover but not in terms of community composition. It is acknowledged widely that return of coral cover alone does not constitute recovery, but that recovery requires a return to pre-

disturbance community structure. Since the age of first reproduction (e.g. Babcock 1991), rates of recruitment and relative importance of recruitment by production of larvae or by fragmentation (e.g. Harriot and Fisk 1988, Fisk and Harriot 1990, Harrison and Wallace 1990) and growth (cf. Pearson 1981, Done 1985, Colgan 1987, Babcock 1991, Cameron et al 1991) vary greatly among coral species, different species demonstrate different abilities to recover. Recovery can be rapid (<15 y) for species (e.g. *Acropora* spp.) with high rates of recruitment and growth (Pearson 1981, Done 1985, Colgan 1987), but for slowly growing and recruiting species, recovery from single disturbance events may be of the order of 10^2 y (Done 1988) or longer (Cameron et al 1990), even in hydrodynamically connected systems. For relatively isolated reefs, differences in life histories are likely to compound founder effects in recovery. Also, differences in larval longevity among broadcast spawning (ca. 10^1 d, Harrison and Wallace 1990, R Babcock unpub. data) and brooding (10^0 – 10^2 d, see Harrison and Wallace 1990) species infer large differences in their effective connectivities. Incorporation into future models of different life history parameters (e.g. relative importance of asexual vs. sexual recruitment; larval longevity; recruitment, growth and survival rates; differential susceptibility to disturbance) is likely to provide instructive, if complex, behaviours.

Critical levels of disturbance

An important result of the model is that there are regimes of disturbance from which for some values of life history and system parameters the system does not recover but remains in a degraded state of low coral cover indefinitely. Indeed, there must be a level of disturbance to systems of connected reefs from which recovery is unlikely on meaningful time scales (see Introduction). For particular systems of reefs, the challenge is to identify what this critical level of disturbance is likely to be. In this paper we considered 2 of the 6 'dimensions' of disturbance (intensity, spatial extent) that define the overall level and impact of disturbance (Chapman and Johnson 1990). The other dimensions (frequency, timing, duration, specificity/selectivity) need to be considered in attempting to determine critical levels. The cellular automaton is a powerful formalism in this endeavour since the spatial arrangements of real reef systems, their hydrodynamic characteristics at small and large scales, any or all dimensions of disturbance, and life history parameters characteristic of different groups of cor-

als can be incorporated into relatively simple models and calibrated to scales relevant to natural systems.

Acknowledgments. We are grateful to Jan van der Laan for advice on constructing automaton models, and to Russell Babcock for offering his unpublished data on the competency of larvae of broadcast spawning corals. Development of automaton models is supported by an ARC grant to CRJ.

References

- Andrews J C, Furnas M J (1986) Subsurface intrusions of Coral Sea water into the central Great Barrier Reef. 1. Structure and shelf scale dynamics. *Cont Shelf Res* 6:491–514
- Babcock R C (1991) Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. *Ecol Monogr* 61:225–244
- Babcock R C, Bull G D, Harrison P L, Heyward A J, Oliver J K, Wallace C C, Willis B L (1986) Synchronous spawning of 105 scleractinian coral species on the Great Barrier Reef. *Mar Biol* 90:379–394
- Babcock R C, Heyward A J (1986) Larval development of certain gamete spawning scleractinians. *Coral Reefs* 5:111–116
- Birkeland C, Lucas J S (1990) *Acanthaster planci*: Major Management Problem of Coral Reefs. CRC, Boca Raton
- Black K P, Gay S L, Andrews J C (1990) Residence times of neutrally-buoyant matter such as larvae, sewage or nutrients on coral reefs. *Coral Reefs* 9:105–114
- Black K P, Moran P J (1991) Influence of hydrodynamics on the passive dispersal and initial recruitment of larvae of *Acanthaster planci* (Echinodermata: Asteroidea) on the Great Barrier Reef. *Mar Ecol Prog Ser* 69:55–65
- Black K P, Moran P J, Hammond L S (1991) Numerical models show coral reefs can be self-seeding. *Mar Ecol Prog Ser* 74:1–11
- Bradbury R H, van der Laan J D, MacDonald B (1990) Modelling the effects of predation and dispersal on the generation of waves of starfish outbreaks. *Mathl Comput Modelling* 13:61–67
- Bull G (1986) Distribution and abundance of coral plankton. *Coral Reefs* 4:197–200
- Cameron A N, Edean R, DeVantier L M (1991) Predation on massive corals: are devastating outbreaks of *Acanthaster planci* novel events? *Mar Ecol Prog Ser* 75:251–258
- Chapman A R O, Johnson C R (1990) Disturbance and organization of macroalgal assemblages in the northwest Atlantic. *Hydrobiologia* 192:77–121
- Colgan M W (1987) Coral reef recovery on Guam (Micronesia) after catastrophic predation by *Acanthaster planci*. *Ecology* 68:1592–1605
- Done T J (1985) Effects of two *Acanthaster* outbreaks on coral community structure—the meaning of devastation. *Proc 5th Int Coral Reef Symp* 5:315–320
- Done T J (1987) Simulation of the effects of *Acanthaster planci* on the population structure of massive corals in the genus *Porites*: evidence of population resilience? *Coral Reefs* 6:75–90
- Done T J (1988) Simulation of recovery of pre-disturbance size structure in populations of *Porites* spp. damaged by the crown of thorns starfish *Acanthaster planci*. *Mar Biol* 100:51–61
- Done T J, Osborne K, Navin K F (1988) Recovery of corals post-*Acanthaster*: progress and prospects. *Proc 6th Int Coral Reef Symp* 2:137–142
- Edean R, Cameron A M, DeVantier L M (1988) *Acanthaster planci* predation on massive corals: the myth of rapid recovery of devastated reefs. *Proc 6th Int Coral Reef Symp* 2:143–148
- Fisk, D A, Harriot V J (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: implications for dispersal hypotheses. *Mar Biol* 107:485–490
- Harriot V J, Fisk D A (1988) Recruitment patterns of scleractinian corals: a study of three reefs. *Aust J Mar Freshwater Res* 39:409–416
- Harrison P L, Wallace C C (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed.) *Coral Reefs. Ecosystems of the World* 25:133–207
- Hughes T P (1988) Long-term dynamics of coral populations: contrasting reproductive modes *Proc 6th Int Coral Reef Symp* 2:721–725
- James M K, Scandol J P (1992) Larval dispersal simulations: correlation with the crown-of-thorns starfish outbreaks database. *Aust J Mar Freshwater Res* 43:569–582.
- Jokiel P L (1990) Transport of reef corals into the Great Barrier Reef. *Nature* 347:665–667
- Johnson C R (ed) (1992a) Crown-of-thorns starfish on the Great Barrier Reef: reproduction, recruitment and hydrodynamics. CSIRO, Australia.
- Johnson C R (1992b) Settlement and recruitment of *Acanthaster planci*: questions of process and scale. *Aust J Mar Freshwater Res* 43:611–627
- Keesing J (1990) Feeding biology of the crown-of-thorns starfish *Acanthaster planci* (L.). PhD thesis, James Cook University of North Queensland 197pp
- Moran P J (1986) The *Acanthaster* phenomenon. *Oceanogr Mar Biol Ann Rev* 24:379–480
- Moran P J, Bradbury R H, Reichelt R E (1988) Distribution of recent outbreaks of the crown-of-thorns starfish (*Acanthaster planci*) along the Great Barrier Reef: 1985–1986. *Coral Reefs* 7:125–137
- Oliver J K, Willis B L (1987) Coral-spawn slicks in the Great Barrier Reef: preliminary observations. *Mar Biol* 94:521–529
- Pearson R G (1981) Recovery and recolonization of coral reefs. *Mar Ecol Prog Ser* 4:105–122
- Reichelt R E, Bradbury R H, Moran P J (1990) Distribution of *Acanthaster planci* outbreaks on the Great Barrier Reef between 1966 and 1989. *Coral Reefs* 9:97–103
- Sammarco P W (1980) *Diadema* and its relationship to coral spat mortality: Grazing, competition, and biological disturbance. *J Exp Mar Biol Ecol* 45:245–272
- Sammarco P W (1991) Geographically specific recruitment and post settlement mortality as influences on coral communities: The cross-continental shelf transplant experiment. *Limnol Oceanogr* 36:496–514
- Sammarco P W, Andrews J C (1988) Localized dispersal and recruitment in Great Barrier Reef corals: The Helix experiment. *Science* 239:1422–1424
- Sammarco P W, Andrews J C (1989) The Helix experiment: Differential localized dispersal and recruitment patterns in Great Barrier Reef Corals. *Limnol Oceanogr* 34:896–912
- Scandol J P, James M K (1992) Hydrodynamics and larval dispersal: a population model of *Acanthaster planci* on the Great Barrier Reef. *Aust J Mar Freshwater Res* 43:583–596
- van der Laan J D, Bradbury R H (1990) Futures for the Great Barrier Reef ecosystem. *Mathl Comput Modelling* 14:705–709

- Wallace C C, Watt A, Bull G D (1986). Recruitment of juvenile corals onto coral tables preyed upon by *Acanthaster planci*. Mar Ecol Prog Ser 32:299-306
- Williams D McB, Wolanski E, Andrews J C (1984) Transport mechanisms and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. Coral Reefs 3:229-236
- Wolanski E, Pickard G L (1985) Long term observations of currents on the central Great Barrier reef continental shelf. Coral Reefs 4:47-57
- Yamaguchi M (1986) *Acanthaster planci* infestations of reefs and coral assemblages in Japan: a retrospective analysis of control efforts. Coral Reefs 5:23-30.