Attachment 14

8 Modelling and Visualizing Interactions between Natural Disturbances and Eutrophication as Causes of Coral Reef Degradation

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INTRODUCTION

There is increasing concern globally that enhanced runoff from human land uses is leading to degradation of coral reefs. Land-clearing, deforestation, excess fertilization of agriculture, and sewage runoff have all been implicated in contributing to nutrient and sediment overload of coral reef waters, leading to so-called "phase shifts," in which areas formerly dominated by corals become overgrown by algae

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(e.g., Smith et al., 1981; Hatcher et al., 1989; Done, 1992; Edinger et al., 1998). These changes have serious ecological, environmental, and economic consequences. On the Great Barrier Reef (GBR) in particular (Figure 1), there is concern that abundant macroalgae on inshore fringing reefs indicate degradation due to anthropogenic increases in terrestrial inputs of sediments and nutrients (Bell & Elmetri, 1995; reviewed in McCook & Price, 1997a; McCook & Price, 1997b; Wachenfeld et al., 1998; Atkinson, 1999; Prideaux, 1999).

It is widely assumed that these phase shifts occur simply because increased nutrients or sediments lead to increased algal growth and consequent overgrowth of corals. However, there has been surprisingly little research to understand the mechanisms of these changes, and critical review of the available evidence suggests that the processes are likely to be more complex (Miller, 1998; McCook, 1999; McClanahan et al., 1999). Nutrients can only affect algal growth rates, not abundance, and changes in algal growth rates, are only expressed as changes in abundance and consequent overgrowth of corals, when reef herbivory is unusually low (McCook, 1996; McCook & Price, 1997a; Hughes et al., 1999; McCook, 1999; Aronson & Precht, 1999). In particular, it seems that a major impact of eutrophication may involve the failure to recover from natural events such as coral bleaching, storms (cyclones, hurricanes), or freshwater coral kills (Kinsey, 1988; Done et al., 1997).

The objective of this chapter is to demonstrate the application of mathematical simulations combined with computer visualisation techniques in formalising the ecological concepts involved, and providing clear, effective output which is accessible to an audience with a broad range of technical backgrounds. The scientific arguments and evidence on which the model is based are discussed in detail in a recent review and perspective on management applications for the GBR (McCook, 1999), and so are not reiterated here. The model used here focuses on the relative abundance of corals and algae, and is intended only as a simplification of their interactions, and not as a specific, quantitative, or predictive model of the processes involved.

MODEL DESIGN

ECOLOGICAL STRUCTURE

The model simplifies reef communities to include only competing corals and algae, as benthic space occupants, and herbivorous fish, which consume algae (Figures 1 and 2). External impacts include terrestrial runoff as sediments and nutrients, and natural disturbances, such as storms (cyclones, hurricanes), bleaching, crown-of-thorns starfish outbreaks, freshwater coral kills, etc., which are assumed to primarily affect corals. Sediment and nutrient loads may occur as chronic, long-term loads and as short-term pulses such as river flood plumes, related to storm events (e.g., Russ & McCook, 1999). Algae and corals compete for substrate space, which is limiting. Bare space may be colonised by either corals or algae, but colonisation by algae is much more rapid. Coral recruitment and percent cover of adult corals are modelled separately. As algal abundance may increase in both area and in biomass per unit area, total algal and coral abundance may exceed 100% cover, with the excess representing increased algal standing crop or biomass per unit area. Reef structure and the outcome of events are summarised by the trajectories through time of the relative abundances of coral and algae. Effects of sediment deposition and turbidity are not distinguished. Nutrients affect algal growth rates, but the accumulation of algal growth depends on the rate of consumption by herbivores.

The model also includes several indirect impacts of eutrophication, based on the discussion in McCook (1999): sediments inhibit fish grazing (S. Purcell, personal communication), algal growth (McClanahan & Obura, 1997; Umar et al., 1998), coral recruitment (Hodgson, 1990a), and coral survival (Hodgson, 1990b; Stafford-Smith, 1992; McClanahan & Obura, 1997). Disturbances are modelled as killing coral, which is then rapidly colonised, predominantly by algae. Algal overgrowth of dead corals is a general consequence of natural disturbances such as storm damage, severe mass bleaching of corals, or outbreak feeding of crown-of-thorns starfish (McCook et al., in press).

MATHEMATICAL STRUCTURE

The processes and interactions are modelled using Logistic/Lotka-Volterra-type equations based on Figure 2. The dependent variables are non-dimensionalised with respect to values representative of equilibrium in clean, oligotrophic waters (i.e., low nutrient and sediment levels) and the model calibrated for these conditions. Model parameters are set to result in an equilibrium coral cover of ~80% under those conditions, with algal cover at 20%. The non-dimensionalisation enables rates to be expressed as a change per generation of a coral polyp, which is 100 time units or iterations.

The equations are

$$
\begin{aligned}
F &= F_o/(1 + K_{sf}S) \\
dA/dt &= -K_{caa}C_a(1 - C_a/C_{ao})/(1 + K_{scaa}S) + K_{na}AN(1 - A)/(N_o(1 + K_{sa}N)) - K_{af}FA/F_o \\
dC_a/dt &= K_{caa}C_a(1 - C_a/C_{ao})/(1 + K_{scaa}S) - K_d\delta_1C_a(1 + S)(1 + A/(1 - C_{ao})) + 2K_{cjca}C_j/(1 + S) \\
dC_j/dt &= -K_{cjca}C_j + K_{cacj}C_aC_{jo}/(C_{ao}(1 + K_{scj}S))
\end{aligned}
$$

where

t = time
F = fish abundance
F_o = equilibrium F
S = fine sediment load ($S \geq 1$; $S = 1$ is the clean water value)
A = algal abundance
N = nutrient abundance
N_o = equilibrium N
C_a = adult coral abundance
C_{ao} = equilibrium C_a
C_j = juvenile coral abundance
C_{jo} = equilibrium C_j
$\delta_1 = C_a + A$

K_{sf} = proportional dependence of F on S
K_{caa} = at equilibrium, relative dominance of competitiveness for space of adult coral over algae
K_{scaa} = proportional dependence of K_{caa} on S
K_{d} = coral death rate at equilibrium
K_{cjca} = rate at which juvenile corals mature to adulthood
K_{cacj} = recruitment rate of coral juveniles
K_{scj} = proportional dependence of K_{cacj} on S
K_{na} = equilibrium growth rate of algae from nutrients
K_{sa} = proportional dependence of K_{na} on S
$\delta = A/(1 - C_a)$ = thickness of the algal mat

The external variables are (1) sediments (S), (2) nutrients (N), and (3) disturbances. Disturbances are modelling as a step decrease of cover of adult corals, providing empty space; in the model runs presented here, the disturbances removed 70% of previous coral cover (75% in Animation 6 discussed later). Empty space is rapidly colonised by algae:

$$A = (1 - C_a)\,H(-A - C_a + 1)$$

where H = the Heavyside function (1 for values of independent variable greater than 0, otherwise 0).

Because disturbances such as cyclones are often associated with nutrient pulses which lead to pulses in algal growth (e.g., Russ & McCook, 1999), the model allows for a pulse of algal growth at the time of disturbances. This is simulated by multiplying the increase in algal colonisation by a scaling factor. It should be emphasized that the model structure includes several indirect impacts of sediments or nutrients, and thus the outcomes of eutrophication are not those of the simple, direct-effects model criticised by McCook (1999). The model presented here is primarily intended as an initial demonstration of the effectiveness of the approach; explanations and refinements of the equations and structure will be discussed in more detail in a subsequent paper.

VISUALIZATIONS

The model output is displayed as the trajectories of coral and algal abundance through time (i.e., time series graphs). These trajectories are displayed as animated graphs, proportional views of the two reef scenes in Figure 1, and as glyphs (or bars). In the final animation, the glyphs are superimposed on a three-dimensional chart of the central GBR. Visualisation of the data and bathymetry was performed using OpenDX (formerly Data Explorer), an open source product available at http://www.opendx.org. The model data used in Animation 6 were *Tubed, Glyphed* as cylinders, and stacked on top of each other (algal abundance on top of coral). The bathymetry data were *RubberSheeted,* and coloured according to height (grey representing z-values above MSL). The z-scale (topographic height or depth) was manipulated in order to emphasize the coral reef lagoon area. Single frames were then written out and converted to AVI using VideoMach (http://www.gromada.com).

SIMULATED EFFECTS OF EUTROPHICATION AND NATURAL DISTURBANCES ON CORAL TO ALGAL PHASE SHIFT TRAJECTORIES

MODEL REEF TRAJECTORIES: EFFECTS OF STARTING CONDITION AND DISTURBANCES

The model trajectory equilibrates to the same final levels of coral and algal abundance, independent of starting points (Animations 1 and 2). Similarly, after a disturbance which kills corals, algal cover undergoes an immediate increase, but again equilibrates to the same final values, assuming sufficient time without further disturbances (Animation 3).

RESPONSES TO EUTROPHICATION

However, the specific levels of the equilibrium cover are dependent on the levels of sediments and nutrients in the model. Comparisons of the trajectories for moderately increased (Animation 4) and strongly increased sediment and nutrient conditions (Animation 5, "eutrophic"), with the trajectory in the "oligotrophic" conditions (Animation 1), show similar basic system behaviour, except that the trajectories equilibrate at lower coral cover for the more eutrophic conditions. Thus eutrophication results in a partial "phase shift" toward a state with higher algal abundance and less coral cover. (It should be emphasised that this shift occurs because the model structure assumes eutrophication affects corals and herbivory as well as algal growth.)

COMBINED EFFECTS OF NATURAL DISTURBANCE AND HUMAN IMPACTS

The impacts of chronic long-term stresses such as overfishing or eutrophication on established communities may be relatively small, but may be much more severe where those communities are also subjected to acute, short-term disturbances, whether natural or human in origin. Coral reef communities are naturally subject to frequent, major disturbances, such as cyclones, crown-of-thorns outbreaks, or bleaching, and may be able to recover rapidly from such events. However, the recovery process may be hampered by chronic human impacts (Kinsey, 1988), and, in particular, rapid macroalgal growth subsequent to a disturbance may prevent coral regrowth or recruitment and reef recovery (Connell et al., 1997; Hughes & Tanner, 2000).

This is well illustrated by the model results in Figure 3, which show a matrix of community trajectories for increasingly eutrophic conditions and increasing frequencies of acute coral damage. It can be clearly seen that the coral cover declines more severely when subjected to both eutrophic conditions and frequent disturbances than accounted for by either factor alone.

This observation has important implications in terms of attributing causality of the decline in coral cover. The immediate cause of the coral death may be natural, but the failure to recover, and consequent long-term decline in reef condition, may in fact be a direct consequence of the human-derived stresses (discussion in McCook, 1999). However, such causality would be very difficult to demonstrate in a field study, because the changes caused by the human impact are intrinsically confounded by the often much larger changes caused by the natural events.

LARGE-SCALE AND LONG-TERM CHANGES: INTEGRATION OF HUMAN IMPACTS AND NATURAL DISTURBANCE

The problem of attributing causality becomes even more significant when the potential large-scale and long-term nature of the changes is considered. Most natural disturbances occur in a patchy manner in time and space, and are difficult to predict. This may result in relatively small, localised, and intermittent impacts, which nonetheless accumulate over larger scales in time and space as a significant overall degradation. The human impact, via terrestrial runoff, may then be piecemeal, diffuse, and subtle, but with serious long-term consequences.

This problem is illustrated by the final animation, which simulates reef trajectories for a range of runoff and disturbance regimes (Animation 6, parameter details in Table 1). The animation portrays model output for a series of 30 "virtual reefs" along and across the continental shelf of the central GBR (Figure 4), and simulates gradual eutrophication of inshore and, to a lesser extent, midshelf water quality, combined with intermittent disturbances, and nutrient pulses resulting from flood plumes (further details in captions).

The model results indicate an overall, large-scale and long-term decline in inshore "reefs," which have an average final coral cover of 13% (range 31 to 0%) compared to 41% (62 to 23%) on midshelf reefs, and 60% (77 to 34%) on the pristine offshore reefs. As the disturbance regimes in the model are identical across the shelf, this inshore decline is unambiguously due to the eutrophic conditions on those (model) reefs. It is particularly significant that some inshore reefs were completely degraded, with essentially no coral left.

However, the animation also demonstrates how the short-term and smaller-scale dynamics, especially the disturbances, effectively obscure the overall pattern, even when viewed at relatively large scales. The overall marked decline in condition of inshore reefs would therefore be very difficult to detect and attribute, despite being unequivocally due to the eutrophication (in the model). The considerable temporal and spatial variability among model reefs, due to timing of disturbances and nutrient pulses, overshadows and confounds the sediment and nutrient effects, even though the disturbance effects are short-lived, whereas the eutrophication effects are long-term.

DISCUSSION

The model results demonstrate the *potential* for eutrophication to have significant long-term impacts on coral populations beyond any direct impacts, by reducing the ability of coral reefs to recover from disturbances. The combined consequences of natural disturbances and eutrophication were significantly greater than either factor alone, demonstrating the need to explicitly consider such interactions in contributing to phase shifts (Done, 1995). The results thus support the argument that eutrophication impacts are likely to be more complex than simply enhancing algal overgrowth of established corals (McCook, 1999). The interaction impacts may be further exacerbated if human activities also serve to increase the frequency or intensity of the otherwise "natural" disturbances (e.g., climate change: Hoegh-Guldberg, 1999; Lough, Chapter 17, this book).

TABLE 1
Design of Cross-shelf and Longshore Comparisons of Community Trajectories Used for Animation 6

Cross-Shelf:		Inshore			Midshelf			Outershelf		
Eutrophication:		S & N 1.5 to 2			S & N 1 to 1.5			S & N = 1		
North		Cyclone Period	N Pulse	Cyclone Start	Cyclone Period	N Pulse	Cyclone Start	Cyclone Period	N Pulse	Cyclone Start
	1	200	1	100	200	1	100	200	1	100
	2	100	1.1	180	100	1	180	100	1	180
	3	200	1.2	140	200	1.1	140	200	1	140
	4	100	1.3	120	100	1.1	120	100	1	120
	5	200	1.4	160	200	1.2	160	200	1	160
River	6	100	1.4	100	100	1.2	100	100	1	100
	7	200	1	180	200	1	180	200	1	180
	8	100	1	140	100	1	140	100	1	140
	9	200	1	120	200	1	120	200	1	120
	10	100	1	160	100	1	160	100	1	160
South										

Notes: Nutrient and disturbance conditions for the model runs shown in Animation 6. Nutrient and sediment conditions vary across the continental shelf. Outershelf reefs remain oligotrophic for the entire period. On mid-shelf reefs, sediment and nutrient conditions are oligotrophic for the first half of the time period (t = 1 to 500), and then linearly increase to moderately eutrophic for the remaining time. Sediments and nutrients on inshore reefs are initially moderately eutrophic (t = 1 to 500), then increase linearly to strongly eutrophic by the end of the time period. Disturbances (e.g., cyclones, coral bleaching) are uniform in timing and frequency across the continental sheif, but vary within cross-shelf regions in frequency (100 or 200 time units) and in timing. Finally, inshore and midshelf reefs vary longshore, with simulated flood plumes providing nutrient pulses simultaneous with the disturbances; the influence of this nutrient pulse extends northward from the river mouth, declining with distance longshore or offshore (Wolanski, 1994; see also King et al., Chapter 10, this book).

This "failure to recover" scenario has important implications in terms of attributing causality, since the immediate cause of the coral death may be natural, but the failure to recover and consequent long-term decline in reef condition may in fact be a direct consequence of the human-derived stresses (Done, 1995; discussion in McCook, 1999). Importantly, although the acute natural disturbances had the most severe short-term impacts, the system rapidly recovered, whereas the chronic human impact resulted in a long-term decline. However, as the model results illustrate, such causality may be very difficult to demonstrate because the changes caused by the human impact are intrinsically confounded by the often much larger changes caused by the natural events. In nature, this difficulty will be exacerbated by the stochasticity and variability inherent in many of the physical and ecological processes involved (e.g., storm timing and severity, recruitment, competition, succession/recovery: McCook, 1994; McCook & Chapman, 1997). The variability inherent in each of these processes means the outcomes will themselves be inherently stochastic and variable.

This is an important observation: even with a relatively simple model system in which we know there is a long-term decline due to the human impact, it is unlikely that a short-term impact assessment could detect differences between sites or times that would demonstrate anything except the inherent variability and changes in the community. It is difficult to imagine a feasible sampling design based on benthic cover which could satisfactorily demonstrate the eutrophication impact. Whilst the model not only illustrates this difficulty, however, it also potentially provides ecologists with a means to portray and illustrate this uncertainty and its implications in terms of risk assessment and management — to the public, to policymakers, and to each other.

Even the preliminary applications of the model in this chapter demonstrate the utility of this approach as an exploratory and explanatory tool for understanding coral reef phase shifts. It should be reiterated that the model provided here cannot realistically predict the behaviour of real reef communities, which are vastly more complex, nor has the model the capacity to predict the consequences of specific changes or events. However, the approach has a number of advantages, including:

1. The ability to simulate a wide range of concepts and interactions and their consequences, and to effectively portray them to a non-expert audience;
2. The increased rigour in understanding the concepts and processes involved, required in order to formulate their mathematical approximations;
3. The ability to explore (model) system behaviour under different conditions, assumptions, and disturbance regimes, including circumstances leading to degradation, and thereby:
4. The ability to identify and assess relative and potential risks under different circumstances;
5. The absence of large, vertebrate predators from the model, which increases researcher viability both inshore and offshore.

This exploratory potential, effectively allowing "virtual reef experiments," with few limitations on spatial and temporal scales, can provide a valuable means to explore potential outcomes and identify significant factors and interactions. Thus, although the approach cannot serve as a substitute for careful field experiments, it may serve to direct experimental effort more effectively by identifying processes and factors likely to have most impact. The ability to illustrate and communicate the significance of different processes, such as the interactions between eutrophication and natural disturbance regimes shown here, has application to scientific debates, management applications, and public education. It may also provide policymakers with a means to demonstrate risks which are otherwise difficult to prove.

The results presented here illustrate that eutrophication impacts are unlikely to be limited to a simple, direct process. In particular, eutrophication may inhibit the recovery from natural disturbances, an impact which may be diffuse and variable, and consequently difficult to detect at short time scales.

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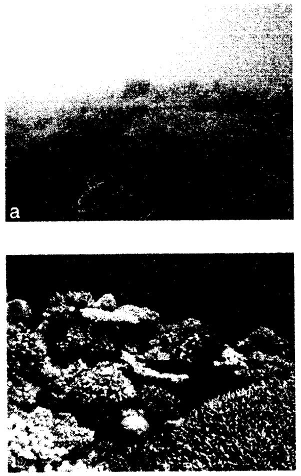


FIGURE 1 Photographs of inshore and offshore reefs of the GBR, showing differences in both area and amount of algae, and algal overgrowth of corals. (a) Inshore reef, dominated by fleshy brown algae, with high biomass per unit area, apparently overgrowing corals. These reefs have relatively high nutrient and sediment inputs, indicated by the turbidity in this photograph, and low abundances of herbivorous fish. (b) Offshore reef with lower inputs of terrestrial nutrients and sediments (low turbidity), and higher abundance of herbivorous fishes. Although filamentous turf algae, coralline algae and larger macroalgae are common in this scene, the biomass is much lower than on the inshore reef.

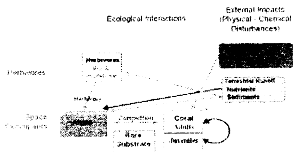


FIGURE 2 Diagram showing ecological processes influencing the relative abundance of corals and algae on coral reefs, as modelled in this chapter. Red arrows indicate negative effects (inhibition), black arrows positive effects (enhancement).

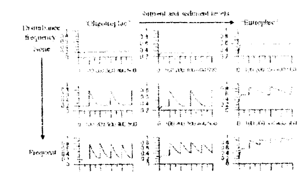


FIGURE 3 Combined effects of eutrophication and disturbances on coral and algal trajectories. Matrix of community trajectories for combinations of circumstances from oligotrophic to eutrophic (left to right), and from no disturbances to frequent disturbances (top to bottom). It can be seen that overall coral cover (blue line) is reduced more when frequent disturbances occur in eutrophic conditions (bottom right), compared to either frequent disturbances alone (bottom left) or eutrophic conditions alone (top right).

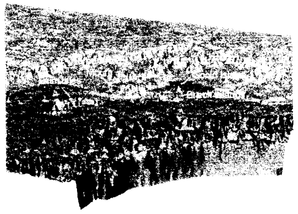
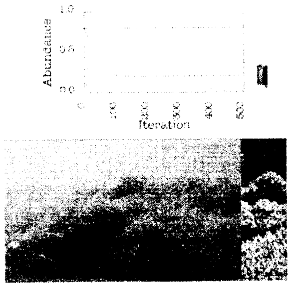
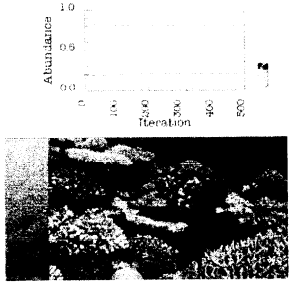


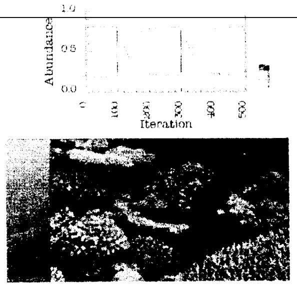
FIGURE 4 Bathymetric chart of central GBR area used in Animation 6. The area shown is north of Townsville, and includes the Palm Islands, Hinchinbrook Island, and Goold and Brook Islands. The view is vertically distorted in order to emphasize the coral reef lagoon area. The mouth of the Herbert River is in the middle of this area, and flood plumes have been shown to extend as far out as the midshelf, and to move north from the river mouth (Wolanski, 1994; see also King et al., Chapter 10, this book).



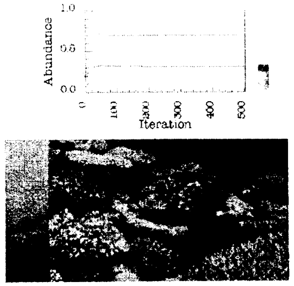
ANIMATION 1 Trajectories of algal and coral abundance through time on an oligotrophic model "reef" with low levels of sediments and nutrients. The graph at the top shows the time course of algal and coral abundance; the glyph (bar) to the right of the graph shows the relative abundances of coral (blue) and algae (brown), synchronised with the moving indicator on the graph. The changes between algal and coral dominance are portrayed by the varying proportion of the two scenes at the bottom. Initial conditions were set to be low in coral (20%) and high in algae (80%), but rapidly equilibrate to the final conditions (~80% coral and 20% algal cover).



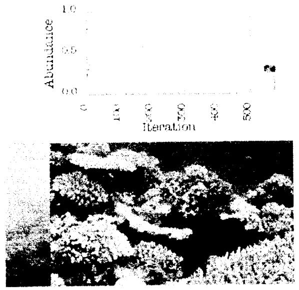
ANIMATION 2 Trajectories of coral and algal abundance with the same (oligotrophic) model parameters as Animation 1, except that initial coral and algal abundance are reversed, and little change occurs. Comparison with Animation 1 shows that the system equilibrates to the same levels independent of starting conditions.



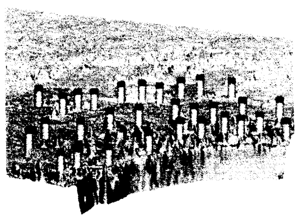
ANIMATION 3 Same as Animation 2 (oligotrophic), except that two disturbances kill 30% of coral cover (at t = 100 and 300), resulting in an immediate rapid dominance by algae (indicated by the sudden increases in algae). However, the trajectories after each disturbance return to the same equilibrium levels, with high coral cover, provided there is sufficient recovery time after each disturbance.



ANIMATION 4 Effects of moderately enhanced sediments and nutrients on coral and algal trajectories; otherwise, starting conditions and parameters as for Animation 2.



ANIMATION 5 Effects of eutrophic conditions (strongly enhanced sediments and nutrients) on coral and algal trajectories; otherwise, starting conditions and parameters as for Animation 2. The effect of the sediments and nutrients is to shift the equilibrium state to a lower coral cover and higher cover of algae: i.e., a partial phase shift. Note that the model dynamics underlying this shift simulate effects of eutrophication on corals and herbivory, not simply effects on algal growth.



ANIMATION 6 Large-scale and long-term interactions between terrestrial runoff and disturbances. Model community trajectories for a range of reefs across and along the continental shelf (as shown in Figure 4). The trajectories shown are based on a change in water conditions halfway through the time periods (see Table 1), representing the changes in terrestrial runoff over the last 100 years (Pulseford, 1991; Moss et al., 1993; Brodie, 1995). Offshore conditions remain oligotrophic, whereas inshore conditions become progressively more eutrophic; midshelf conditions are intermediate. Disturbance frequencies and timing vary within cross-shelf regions (details in Table 1), but are uniform across the shelf. The effect of the flood plumes are simulated by brief "nutrient pulses" of decreasing strength to the north of the mouth of the Herbert River, simultaneous with disturbances. The relative heights of the glyphs or bars indicate the relative abundance of corals (blue) and algae (brown; sudden shifts indicate disturbance changes). The simulations run for twice as long as those in animations 1 to 5; all "reefs" have high initial coral cover (80%). It can be seen that even in this relatively simple system with a known structure (i.e., the model, plus Table 1), the background variation overshadows the effects of eutrophication, despite a definite, gradual decline of inshore reefs. Note that, by the end of the simulations, several inshore reefs are completely dominated by algae, to the exclusion or near exclusion of corals.