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A model of the effects of land-based, human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia

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Abstract

A model is proposed to explain coral and algal abundance on coastal coral reefs as a function of spike-like natural disturbances from tropical cyclones and turbid river floods, followed by long recovery periods where the rate of reef recovery depends on ambient water and substratum quality. The model includes competition for space between corals and algae, coral recruitment and reef connectivity. The model is applied to a 400-km stretch of Australia's Great Barrier Reef and to the 200-m-long reef tract at Fouha Bay, in Guam, Micronesia. For these two sites and at these two scales, the model appears successful at reproducing the observed distribution of algae and coral. For both sites, it is suggested that the reefs have been degraded by human activities on land and that they will recover provided remedial measures are implemented on land to restore the water and substrate conditions. We suggest ways to improve the model and to use the model to guide future ecological research and management efforts on coastal coral reefs.

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1. Introduction

Coral reefs are marine ecosystems that possess the highest diversity of any marine and most terrestrial ecosystems (Veron, 1995; Birkeland, 1997). They are also being destroyed at an alarming rate throughout

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the world (Wilkinson, 1999). While coral reefs are relatively robust and have survived millions of years of natural disturbances, anthropogenic influences are a major concern for the sustainability of these important ecosystems (Done, 1992a; Richmond, 1993, 1994; Wolanski, 2001).

Until recently, the major strategy for coastal reef management is to rely on marine protected areas. Managers draw a line around coral reefs on a map, inside of which extractive and destructive activities are prohibited or regulated. This management practice

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derives in part from limited ability to influence land management practices in adjacent catchments, outside the jurisdiction of the marine management agencies, and from the assumption that coral reefs were resilient and would recover from occasional human impacts from land runoff. This management practice has proven insufficient where coral reefs are found near land and where human activities within adjacent watersheds contribute to the decline of water and substratum quality (Birkeland, 1997; Done, 1992a; Fabricius and Wolanski, 2000; Jameson et al., 2002; Fabricius et al., 2003; McCook, 1999; McCook et al., 2001a, b; Richmond, 1993, 1994; Rogers, 1990; Tomascik and Sander, 1987a,b; Wilkinson, 1999; Wolanski, 2001; Wolanski and Duke, 2002; Wolanski et al., 2003a). It is now recognized that coastal coral reefs adjacent to population centres often do not recover from disturbances, in contrast to remote reefs in relatively pristine environments, because chronic human influences have degraded water and substratum quality, thereby inhibiting recovery (McCook, 1999). Indeed, field observations revealed that corals were prevented from recovering or re-establishing themselves on surfaces covered by mud, cyanobacteria or fleshy algae. Filamentous and fleshy algae can be very abundant. Indeed, replacement of corals by filamentous or fleshy algae is the most common symptom of coral reef degradation.

There is a need for models of the interactions between natural ecological processes and human impacts from land runoff on coastal coral reefs. Based on a number of observations of reefs following an acute disturbance (Diaz-Pulido and McCook, 2002; McCook et al., 2001b), McCook et al. (2001a) proposed such a conceptual model for isolated reefs subject to occasional, acute, natural disturbances. The empty space was assumed to be rapidly colonized by algae, as is almost universally the case in coastal coral reefs (e.g., Diaz-Pulido and McCook, 2002). Corals later recovered and the rate of recovery depended on water and substratum quality. If successive disturbances occurred within periods smaller than the recovery time scale, the reef was unable to recover and the degraded state persisted in the long term.

In this study, we expand on this model and apply it to two field sites for which ecological, meteorological and oceanographic data are available. The two sites are a 400-km-long section of the Great Barrier Reef of Australia, and the 200-m-long Fouha Bay, in Guam, Micronesia. We used historical data on natural disturbances, oceanographic conditions, and the natural evolution of reefs to extract the various model parameters. The model appears successful at reproducing the spatial distribution of coral and algae cover. The model is then used to quantify the likely impact of land-based human activities on the health of coral reefs, and the effectiveness of various remedial measures. We suggest that, both in the Great Barrier Reef and in Fouha Bay, human-induced changes in quality and quantity of terrestrial runoff have lead to reef degradation by generating "phase shifts"—the process by which areas formerly dominated by corals are overgrown by algae, without recovery. We also suggest that, with land-based remedial measures, the reef is capable of recovering its biodiversity.

2. Study sites

Australia's Great Barrier Reef stretches along 2600 km of the east coast of Australia from 25°S to 10°S. The study area (i.e., the model domain) is in the central region, comprising 261 reefs in a 400-km-long stretch of the Great Barrier Reef, and extending from Lizard Island in the North to the Whitsunday Islands in the South (Fig. 1). Mean water depth between reefs is about 10-40 m, and most reefs are emergent at spring low tides. The surrounding waters receive runoff from rivers spread along the coast; river discharges are dominated by short-lived flood events during a short wet season, during which time the river plumes impact on the reefs. The effects vary both spatially and temporally (Wolanski, 1994, 2001). In addition, there are also a number of tropical cyclones, typically 1-4 per year, impacting the reefs. Their effects vary spatially according to the cyclone strength and trajectory; which are different for every cyclone. The geographic extent of the model domain was chosen to cover a region believed to be the most susceptible to anthropogenic impacts from land runoff. Of these 261 reefs, 20 (see location map in Fig. 1) are surveyed annually for their assemblages of reef fishes and communities of benthic organisms in the upper North East reef slope (Sweatman et al., 1998). These reefs were chosen from three shelf positions (inshore, mid-shelf, and outer shelf). Coastal reefs are the most impacted by runoff

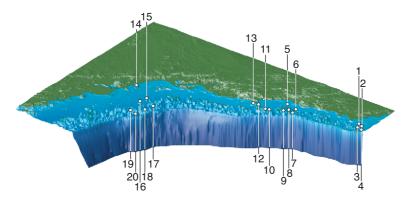


Fig. 1. Map of the central region of the Great Barrier Reef, Australia, showing the 400-km-long model domain and the location of the coral reefs that have been for monitored for A and C_a since 1992. 1 = Martin Reef, 2 = Lizard Island, 3 = North Direction Island, 4 = No Name, 5 = Low Isles, 6 = Mackay Reef, 7 = Agincourt No. 1, 8 = St. Crispin Reef, 9 = Opal Reef, 10 = Hastings Reef, 11 = Michaelmas Cay, 12 = Green Island, 13 = Fitzroy Island, 14 = Havannah Island, 15 = Rib Reef, 16 = John Brewer Reef, 17 = Myrmidon Reef, 18 = Dip Reef, 19 = Chicken Reef, 20 = Davies Reef.

but are not monitored because of poor visibility and the presence of crocodiles.

Reef-fringed Fouha Bay, Guam (143°39′ E, 13°17′ N; Fig. 2), is funnel-shaped, about 200 m long, with a depth varying between 6 m at the base of the reef flat to about 11 m at the mouth of the bay. The adjoining La Sa Fua River catchment area is 5 km² and

much of it is composed of volcanic, steeply sloping, highly erodible lateritic soil. Erosion is intense and the fine sediment discharge from the watershed is estimated to be about 480–1200 t km⁻² year⁻¹ (DeMeo, 1995; Scheman et al., 2002; Wolanski et al., 2003b). This sediment is imported into Fouha Bay by pulse-like river floods; there are typically 10 floods per year.

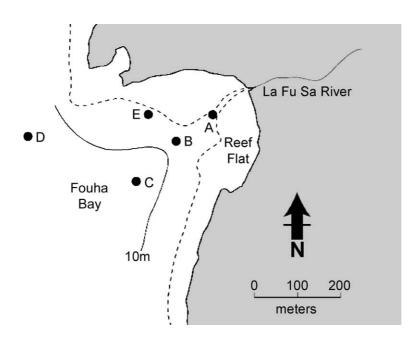


Fig. 2. Map of reef-fringed Fouha Bay, Guam, Micronesia, with depth in m. Point A is the river mouth.

About 75% of this fine sediment settles in Fouha Bay. It is resuspended and exported under storm-driven swell; this occurs typically 2–5 times a year (Wolanski et al., 2003b).

3. Model description

The HOME model combines those of McCook et al. (2001a) and Wolanski et al. (2003a). Reefs are modelled as discrete ecosystems. Each reef has its own coral-algae-herbivorous fish ecology. Algae and corals compete for limited substrate space (McCook et al., 2001b). When corals are killed or damaged, the population can be re-established by regrowth from remaining fragments, or through the import and subsequent recruitment of coral larvae from healthy (or less impacted) reefs. Coral and fish larvae can also be imported from healthier reefs; import of coral and fish larvae is controlled by oceanography. Algal cover is used as a proxy measure of reef health. The ecological components of the model include hard corals in two age groups, juvenile and adult, together with algae and herbivorous fish. Herbivorous fish consume algae. The reefs are disturbed by acute, natural disturbances following rain-generated river plumes and tropical cyclones. These events kill coral, thereby providing free space that is rapidly colonized by fleshy and/or filamentous algae (Diaz-Pulido and McCook, 2002). Corals can recover from fragments, or through recruitment of larvae from less impacted reefs (Harrison and Wallace, 1990; Heyward and Babcock, 1986; Richmond, 1988, 1990, 1996). The recovery rate depends on substratum quality and quantity as affected by turbidity, nutrient concentration, and numbers of herbivorous fish. Nutrients affect algal growth rates. The thickness of the algal mat depends on the rate of consumption by herbivorous fish. The model includes chronic effects from human activities on land through resulting increased turbidity.

The model does not include controls on the abundance of herbivorous fish because in the Great Barrier Reef, where fishermen do not target herbivorous reefs, there is a strong linear relationship between herbivorous fish abundance and water visibility (Fig. 3). This may reflect reduced recruitment of reef fishes on reefs with less suitable conditions (Williams, 1991). It is thus sufficient for the model to set the prevailing visibility conditions during the coral recovery period from field observations for which data are available in the Great Barrier Reef (Wolanski and Spagnol, 2000) and in Fouha Bay (Wolanski et al., 2003b).

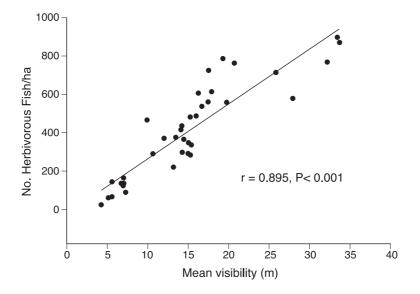


Fig. 3. Scatter plot (dots) and suggested mean relationship (line) between mean visibility (in m), and mean abundance of herbivorous fish (number ha⁻¹) in the Great Barrier Reef. These data were averaged for 10 years of surveys at 48 reefs scattered along a 400-km stretch of the continental shelf.

The ecosystem dynamics equations are: adult coral (C_a)

$$\begin{split} \mathrm{d}C_{\rm a}/\mathrm{d}t &= K_{\rm caa}C_{\rm a}(1-C_{\rm a}/C_{\rm ao})\gamma/(1+K_{\rm scaa}S) \\ &- K_{\rm d}C_{\rm a}(1+K_{\rm sd}S)(1+A/(1-C_{\rm ao})) \\ &+ 2K_{\rm cjca}C_{\rm j}/(1+S) \end{split} \tag{1}$$

Juvenile coral (C_i)

$$dC_{j}/dt = -K_{cjca}C_{j} + K_{cacj}C_{a}C_{jo}/(C_{ao}(1 + K_{scj}S))R$$
(2)

Algae (A)

$$dA/dt = -K_{caa}C_{a}(1 - C_{a}/C_{ao})\gamma(1 + K_{scaa}S) + \delta_{1} - \delta_{2}$$
(3)

Herbivorous fish (F)

$$F = F_o/(1 + K_{\rm sf}S) \tag{4}$$

where t=time, and the other symbols are defined in Table 1.

Eq. (4) expresses the empirical relationship shown in Fig. 3. The values of the non-dimensionalised parameters were taken to be the same as those used by McCook et al. (2001a) and are shown in Table 2. The model time step, dt = 0.01 year.

In the model, the reefs are disturbed by pulse-like, natural disturbances from river plumes and tropical cyclones. Their impacts are modelled as a step decrease in cover of adult corals, providing empty space. Algae are assumed to instantaneously colonise the empty space, because algal growth is very rapid (McCook et al., 2001b; Diaz-Pulido and McCook, 2002). Therefore,

$$C_{\text{a(post-event)}} = \alpha C_{\text{a(pre-event)}}$$
 (5)

$$A_{\text{(post-event)}} = \beta - C_{\text{a(post-event)}}$$
 (6)

where α is the event transfer coefficient for coral ($\alpha < 1$) and β is the event transfer coefficient for algae ($\beta > 1$).

For the case of a tropical cyclone impact, parameters α and β are determined by the strength of the cyclone affecting a particular reef. Cyclones were classified by their strength and only reefs within a distance of twice the radius of maximum wind area were considered impacted, and from these data the

Table 1
Definition of the parameters in the ecology sub-model

$\mathrm{d}t$	time step	
F	herbivorous fish abundance	
F_{o}	equilibrium F	
S	log(suspended sediment concentration/reference	
	suspended sediment concentration)	
A	algal abundance on the reef substrate $(A < 1)$	
N	non-dimensional nutrient concentration	
$N_{\rm o}$	equilibrium N	
$C_{\rm a}$	adult coral abundance on the reef substrate	
	$(C_a < 1)$	
C_{ao}	equilibrium C_a	
$C_{\rm i}$	juvenile coral abundance on the reef substrate	
,	$(C_i < 1)$	
$C_{\rm jo}$	equilibrium C_{i}	
δ_1	$C_{\rm a} + A$	
$K_{\rm sf}$	a constant expressing the dependence of F on S	
K_{caa}	a parameter quantifying the relative dominance of	
	competitiveness for space of adult coral over algae	
K_{scaa}	a parameter expressing the dependence of K_{caa}	
	on S	
$K_{\rm d}$	coral death rate at equilibrium	
K_{sd}	a parameter expressing the dependence of K_d on S	
$K_{\rm cjca}$	rate at which juvenile coral mature to adulthood	
K_{cacj}	recruitment rate of juvenile coral	
K_{scj}	proportional dependence of K_{caci} on S	
K_{na}	equilibrium growth rate of algae from nutrients	
K_{sa}	proportional dependence of K_{na} on S	
$\delta (=A/(1-C_{\rm a}))$	thickness of the algal mat	
γ	coral growth potential rate= $(C_i/C_a)/(C_{io}/C_{ao})$ if	
	$\gamma < 1, \ \gamma = 1$ otherwise	
δ_1	$K_{\text{na}}AN(1-A)/(N_{\text{o}}(1+K_{\text{sa}}S))$	
R	coral recruitment after mass spawning= $(S_s + C_n)M$	
M	coral larvae mortality	
$S_{\rm s}$	recruitment by self-seeding	
$C_{\rm n}$	recruitment by oceanographic import of larvae	
	from other coral reefs in the GBR	

values of α and β were calculated (e.g., Cheal et al., 2002; Done, 1992b; Done et al., 1986; Van Woesik et al., 1991). The adopted values are shown in Table 3.

For the case of river floods, α and β are determined by two parameters characterising the river plume, namely the minimum salinity ($T_{\rm flood}$, and the duration ($T_{\rm flood}$, in h) of the river plume over the reef. The values were chosen to follow the observations of Steven (1994) and Done (personal communication), so that α decreases linearly with decreasing $S_{\rm min}$ and with increasing $T_{\rm flood}$, to reach a minimum value of 0.2 for $T_{\rm flood}$ = 2000 h and $S_{\rm min}$ = 10, with starting threshold values for $T_{\rm flood}$ and $S_{\rm min}$ of, respectively, 50

Table 2
Parameters used in the model for the Great Barrier Reef and Fouha
Bay to calculate reef recovery

Parameter	Value
$\overline{F_{o}}$	10
$N_{\rm o}$	1
C_{ao}	0.9
$C_{ m jo}$	0.05
$K_{ m sf}$	1
$K_{\rm caa}$	10
$K_{ m scaa}$	0.5
$K_{ m d}$	0.15
$K_{ m sd}$	1
$K_{ m cjca}$	1.4
$K_{ m cacj}$	0.5
$K_{ m scj}$	1
K_{na}	10
K_{sa}	0.1

h and 32. The values of α and β were calculated for every reef and for every river flood since 1969, from the output of a three-dimensional river plume model predicting the salinity over the model domain for every river flood that occurred during that period.

The river plume model follows the hydrodynamic model equations (King et al., 2001)

$$\frac{\partial u}{\partial x} + \frac{\partial v}{\partial y} + \frac{\partial w}{\partial z} = 0 \tag{7}$$

$$\frac{\partial u}{\partial t} + \frac{\partial (uu)}{\partial x} + \frac{\partial (vu)}{\partial y} + \frac{\partial (wu)}{\partial z} - fv$$

$$= -\frac{1}{\rho_0} \frac{\partial p}{\partial x} + \frac{\partial}{\partial z} \left(A \frac{\partial u}{\partial z} \right) \tag{8}$$

$$\frac{\partial v}{\partial t} + \frac{\partial (uv)}{\partial x} + \frac{\partial (vv)}{\partial y} + \frac{\partial (wv)}{\partial z} + fu$$

$$= -\frac{1}{\rho_0} \frac{\partial p}{\partial y} + \frac{\partial}{\partial z} \left(A \frac{\partial v}{\partial z} \right) \tag{9}$$

$$\frac{\partial p}{\partial z} = -\rho g \tag{10}$$

where A is the eddy viscosity. Density ρ is mainly dependent on salinity. The salinity conservation equation is:

$$\frac{\partial S}{\partial t} + \frac{\partial (uS)}{\partial x} + \frac{\partial (vS)}{\partial y} + \frac{\partial (wS)}{\partial z} = \frac{\partial}{\partial z} \left(K \frac{\partial S}{\partial Z} \right)$$
(11)

where *K* denotes the eddy diffusivity. The eddy viscosity and diffusivity are obtained from a turbulence closure model (see King et al., 2001). The model mesh size was 2 km and there were 5 layers in the vertical plane.

The model requires daily river discharges, as well as wind speed and direction data. These historical data were available, and were used by the model to calculate the river flood plumes' movement for every flood event from 1969 onwards in the GBR in the model domain. The hydrodynamic model was calibrated using an extensive data set collected during the 1981 flood (King et al., 2001).

Eq. (2) requires knowledge of coral recruitment. Corals spawn yearly early in the summer at night, on a date set by the moon phase. In the model, the spawn material is carried by the water currents for 10 days; during which time, the larvae drifting at sea are assumed to suffer mortality at a rate of $M=0.2 \text{ day}^{-1}$ a value reported from laboratory experiments (A. Heyward, unpublished data). The currents are affected by the tides, the forcing by the Coral Sea, and the wind. This creates connectivity among reefs, and recruitment rates were calculated for every spawning year since 1969. The annual coral spawning date for each year from 1969 onwards was calculated from the lunar phase. Historical wind data during the spawning events were obtained from the Commonwealth Bureau of Meteorology (before 1980) and from the AIMS weather database (after 1980). The oceanographic model was used to calculate the water circulation during and just after mass coral spawning using these historical wind data, for every year individually.

Table 3
Parameters used in the model to calculate the impact of tropical cyclones

α	0.9, 0.8, 0.7, and 0.6 for tropical cyclone
	force 1, 2, 3, and 4, respectively
β	1, 1.1. 1.15, and 1.2 for tropical cyclone
	force 1, 2, 3, and 4, respectively

The transport of coral spawn material was modelled by the two-dimensional, depth-averaged equation

$$\frac{\partial (hc)}{\partial t} = \frac{\partial}{\partial x} \left(kh \frac{\partial c}{\partial x} - uhc \right) + \frac{\partial}{\partial y} \left(kh \frac{\partial c}{\partial y} - vhc \right)$$
(12)

where c(t,x,y) denotes the concentration of the material under study, while k (>0), h and (u,v) represent the horizontal diffusivity, the depth of the water column and the depth-averaged horizontal velocity vector along the (x,y) axes, respectively. A Lagrangian approach was adopted. At time $t_n = n\Delta t$ (n = 0, 1, 2, ...), where Δt is a suitable time increment, the position (X_n, Y_n) of a particle of coral spawn material is updated by means of the Lagrangian algorithm

$$(X_{n+1}, Y_{n+1}) = (X_n, Y_n) + (U, V)\Delta t + \sqrt{\frac{2k\Delta t}{r}}(R_{x,n}, R_{y,n})$$
(13)

where $R_{x,n}$ and $R_{y,n}$ are zero-mean random numbers with a variance equal to r. The velocity components U and V were defined to be

$$(U,V) = (u,v) + \frac{1}{h} \left[\frac{\partial (kh)}{\partial x}, \frac{\partial (kh)}{\partial y} \right]$$
 (14)

In Eq. (14), the correction velocity $(1/h)[\partial(kh)/\partial x, \partial(kh)/\partial y]$ is necessary to prevent the spurious accumulation of particles in regions where the water depth or the diffusivity is smallest (Spagnol et al., 2002).

A two-dimensional barotropic oceanographic submodel was used to obtain the velocity vector (u,v). It is based on the 2-D barotropic equations of motion and it includes the influence of the tides, the wind, and the large-scale circulation in the Coral Sea (Wolanski, 1994; Brinkman et al., 2002): The velocity field was calculated from the momentum and mass conservation equations, following

$$\frac{\partial uH}{\partial t} + \frac{\partial u^2H}{\partial x} + \frac{\partial uvH}{\partial y} - fvH + gH \frac{\partial (\bar{\eta} + \eta')}{\partial x} + \frac{gu |\mathbf{u}|}{C^2} - \frac{\tau_{sx}}{\rho} - \beta \nabla^2 (vH) = 0$$
(15)

$$\frac{\partial vH}{\partial t} + \frac{\partial vuH}{\partial x} + \frac{\partial v^2H}{\partial y} + fvH + gH \frac{\partial (\bar{\eta} + \eta')}{\partial y} + \frac{gv |\mathbf{u}|}{C^2} - \frac{\tau_{sy}}{\rho} - \beta \nabla^2 (vH) = 0$$
(16)

$$\frac{\partial \eta'}{\partial t} + \frac{\partial uH}{\partial x} + \frac{\partial vH}{\partial y} = 0 \tag{17}$$

where $\bar{\eta}$ is the mean sea surface elevation determined by the large-scale circulation in the Western Coral Sea; η' is a time-varying fluctuation about $\bar{\eta}$; h is water depth below mean sea level; H is total water depth $(h+\eta)$, f is the Coriolis parameter; g is acceleration due to gravity; C is the Chezy coefficient, $C=H^{1/6}/n$, where n is the Manning coefficient; $\tau_{\rm sx}$ and $\tau_{\rm sy}$ are wind stress components in the x and y directions, respectively; ρ is the fluid density; β is the horizontal eddy viscosity; and ∇^2 is the Laplacian operator $\nabla^2=(\partial^2/\partial x^2+\partial^2/\partial y^2)$. The model mesh was 2000 m.

For Fouha Bay, the salinity impact was not considered because the river plume is shallow (<1 m) and floats over the corals (Wolanski et al., 2003b). Therefore, the runoff impact in Eqs. (1)–(3) was calculated as due only to sedimentation. High water turbidity was assumed to occur in 15 events/year; 10 of these correspond to pulse-like river floods when 75% of the riverine mud settles in the bay. The remaining 5 events/year are assumed to be due to oceanic swell resuspending this settled mud. Following field observations (Wolanski et al., 2003b), $S \propto x^{-2}$ in the model, where x is the distance from the river mouth. Since the water currents can distribute larvae throughout Fouha Bay in a few hours, coral recruitment was assumed spatially uniform.

4. Results

For the Great Barrier Reef, the predicted values of C_a compare favourably with observations (Fig. 4). A similar good fit is found for A (not shown) The outlier points all correspond to situations where the observed value of C_a is smaller than the predicted value; all these reefs had been infested by crown-of-thorns starfish. This suggests that the model adequately tracks reef response to river floods and cyclones.

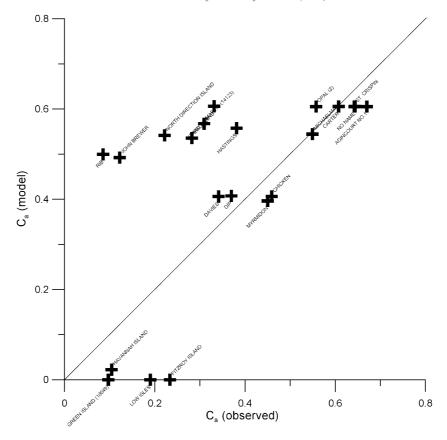


Fig. 4. Scatter plot between observed and predicted C_a at monitored reefs in the Great Barrier Reef. See the location map in Fig. 1. The outlier points are reefs impacted by coral-eating, crown-of-thorns starfish *Acanthaster planci*.

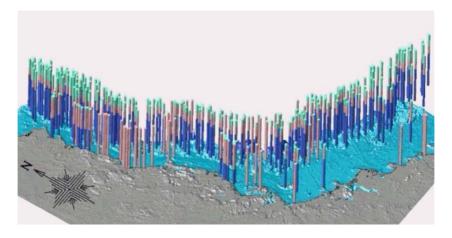


Fig. 5. Predicted mean distribution of C_a and A for present water quality conditions in the Great Barrier Reef. Each glyph comprises two glyphs stacked one on top of the other, the top glyph represents A and the bottom glyph represents C_a . The cover is relative to 100% cover, which is the total length of the glyph (for colour see online version).

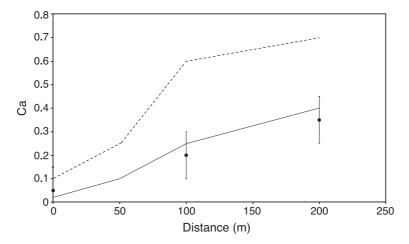


Fig. 6. Predicted distribution of C_a in Fouha Bay as a function of distance x from the river mouth, for (-) present and (--) historical water quality. The circles show estimated values of C_a (V. Bonito, personal communication). x=0 at point A in Fig. 2.

The predicted mean distribution of A and C_a is shown in Fig. 5. It reveals both cross-shelf and along-shelf gradients in A and C_a . The cross-shelf gradients are largely due to the impacts of land-runoff and turbidity. The differences in along-shelf gradients are mainly due to the uneven distribution of cyclones, differences in flood plume frequency and intensity between catchments, as well as to the mean water circulation patterns that favour coral recruitment in mid-shelf reefs in the south and the far north of the model domain.

For Fouha Bay, herbivorous fish abundance was assumed to follow the same dependence on visibility as in the Great Barrier Reef. This validity of this assumption may be poor because the fishing pressure on herbivorous fishes in Fouha Bay is intense. There are however no data on abundance of herbivorous fish that would enable us to remove this assumption. The predicted values of $C_{\rm a}$ (Fig. 6) compare favourably with observations, although there is a tendency for over-prediction.

5. Discussion

The same model and the same values of the parameters were used for both the Great Barrier Reef and Fouha Bay. The fact that the model performs qualitatively well in both situations suggests that the underlying model is fairly robust and is applicable to

situations where the reef is occasionally disturbed by cyclones and river floods, and that it can recover during the in-between periods.

The model could be further useful in helping to attribute causality between natural and human influences and their relative effects on declines in coral cover. The model can help determine the extent to which anthropogenic effects, via land-runoff, may be responsible for the failure of reefs to recover after disturbance, with a consequent long-term decline in reef health. Eqs. (1) and (2) are used to calculate the effect of changing turbidity as a result of changing land use practices (increased agriculture and land clearing) which change the nutrient supply, sediment load and turbidity; this affects the time scale for damaged reefs to recover. For the Great Barrier Reef, there is evidence (Fig. 7; see also Wolanski and Spagnol, 2000) that, as a result of human, land-based activities, the mean visibility has apparently halved hence S has doubled in the recovery periods-since 1927 in the Low Isles area (site 5 in Fig. 1). Using, as illustration, the simple assumption that turbidity has doubled uniformly throughout the model domain, and also (this is a conservative assumption) that there have been no changes in nutrient concentration, the model can be used to estimate the vulnerability of different reefs to such changes. Fig. 8 shows the distribution of predicted Ca decrease based on the assumption that turbidity has uniformly doubled. Under that scenario, the model suggests that increases in sediments from

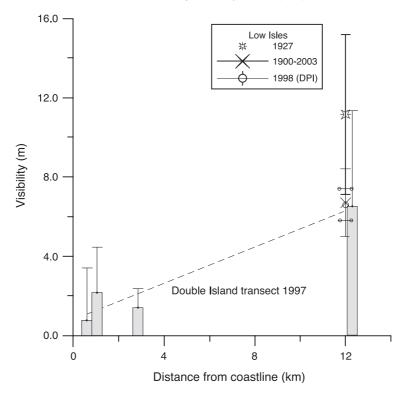


Fig. 7. This graph shows the increase of visibility (mean and deviation) with increasing distance from the coast off Double Island in 1997 and the changes in visibility between 1927 and 2003 in waters near Low Isles (for location map, see site 5 in Fig. 1; Wolanski and Spagnol, 2000). The 1998 DPI data were provided by L. McKenzie. The 1990–2003 data were provided by H. Sweatman, G. Coleman and A. Thompson.

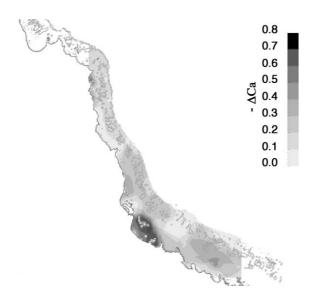


Fig. 8. Distribution of the predicted decrease of C_a in the Great Barrier Reef as a result of a uniform doubling of turbidity.

human activities will lead to reef degradation of most reefs of the Great Barrier Reef, but that the degradation would not be uniform. By combining the model in this way with emerging estimates of anthropogenic changes in sediment and nutrient supply from different catchments (Devlin et al., 2001), it will be possible to estimate hindcast changes in coral cover which reflect actual changes in water quality. The model also suggests that, in the long term, A and C_a can return to original values characteristic of pristine conditions in the Great Barrier Reef if, through land-based remedial activities, the original water visibility conditions can be recovered.

For Fouha Bay, there are no visibility data before the land in the catchment was cleared. Hearsay evidence from fishermen suggests that the waters were much clearer in the 1960s and the coral reef was healthy. Coral outcrops at the river mouth provide evidence for declines; algae now cover the dead coral skeletons. Assuming that water visibility has been halved following land clearing, the predicted historical values of C_a were significantly larger than at present (see Fig. 6). This suggests that land erosion in the catchment has significantly impacted the health of coral reefs. The model does suggest that the most logical approach to coral reef restoration is through remedial measures on land in order to restore water and substrate quality to a level that allows corals and other reef organisms to successfully reproduce and recruit. The discrepancy between observed and predicted values of Ca suggests that protecting herbivorous fish may also help improve C_a . The HOME model appears able to forecast a key indicator of coastal reef health, C_a , under various management strategies for land-use and reef fisheries.

Such predictions are inherently uncertain. Indeed, the model is simple and neglects important processes such as warm water events that can result in bleaching (Hoegh-Guldberg, 1999), crown-of-thorns starfish infestations (Moran, 1988), and the variability introduced by the diversity of taxa and growth forms of corals and algae. These ecological processes should be added to the model. They would improve its relevance; they would also add complexity and generate the need to obtain additional data on these parameters for understanding feedback mechanisms for which field data are largely unavailable (Kinzig et al., 2002; May, 1973; Starfield and Bleloch, 1991). Based on the experience of developing and applying fishery models (Schnute and Richards, 2001), the improved model may still have inherent limitations that make its predictions inherently uncertain. By testing its limitations, the improved model could be used as a tool to identify the physical and biological processes in coastal reef ecology that are most important in controlling reef health and that need additional detailed field studies.

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