

Coral Reef Ecosystem Stability in Response to Climate Change

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Introduction

Coral reefs are unique habitats that host an enormous diversity of species and play an important role in the marine ecosystem [1]. In recent years, rising sea temperatures have caused widespread coral bleaching events that result in high coral mortality. As a result, coral reefs are also one of the most vulnerable habitats on the planet, with more than one-third of reef-building species at elevated risk of extinction [2]. Thus, being able to predict coral reef ecosystem collapse is critical to preserving this crucial habitat. We constructed a three-species predator-prey model using the Lotka-Volterra predator-prey models. We chose for the intermediate species (referred to as the consumer) to have an attack rate with a saturating functional response given by Holling's disk equation [3].

System of Equations

We constructed a three-species predator-prey model using the Lotka-Volterra predator-prey models. We chose for the intermediate species (the parrotfish) to have an attack rate with a saturating functional response given by Holling's disk equation (Holling 1959). Let R be the abundance of coral colonies, let N be the abundance of parrotfish, which feeds on coral, and let P be the abundance of a piscivore, which feeds on parrotfish.

$$\begin{aligned}\frac{dR}{dt} &= r(t)(1 - \frac{R}{K}) - \frac{aRN}{1 + ahR} \\ \frac{dN}{dt} &= \frac{abRN}{1 + ahR} - dN - \alpha NP \\ \frac{dP}{dt} &= \alpha \beta NP - \delta P\end{aligned}$$

where $r(t)$ is the coral growth rate, K is the coral carrying capacity, a is the feeding rate of parrotfish on coral, h is the amount of time it takes for a parrotfish to consume one coral colony when coral are abundant, b is the coral to parrotfish conversion rate, d is the death rate of parrotfish, α is the attack rate of the predator on parrotfish, β is the parrotfish to predator conversion rate, and δ is the predator death rate. To maintain biological feasibility we restrict the system to $P, N, R \geq 0$.

Let the initial conditions of the system be given by:

$$P(0) = P_0, N(0) = N_0, R(0) = R_0$$

Parameters

We considered a 10km^2 reef and assumed the average coral colony size was 1m^2 . The maximum coral carrying capacity of the reef occurs at 100% coral cover, which is equivalent to 10^8 coral colonies. Coral extension rates are estimated to be between 0.003 m/yr and 0.0004 m/yr [4]. We chose the upper estimate of 0.003 m/yr [5]. For a coral colony 1m^2 in diameter, 0.003 m/yr of outward growth from its perimeter is $0.012\text{ m}^2/\text{yr}$ or 0.012 individuals/yr. So, r_0 was estimated as 0.012 individuals/yr.

To determine $r(t)$, we assumed that $r(T) = 0$ when $T = T_{crit}$ where T is temperature. We used a coral bleaching threshold of 1°C sea surface temperature anomaly (SSTA) was used [6]. We then assumed that coral attains its maximum growth rate for SSTA less than or equal to 0.75°C . Our estimate for $r(T)$ was then:

$$r = \begin{cases} r_0 & T \leq 0.75 \\ r_0 - 16r_0(T - 0.75)^2 & T > 0.75 \end{cases}$$

We used SSTA data from Nino Region 4, located in the equatorial Western Pacific Ocean, a hotspot for coral reefs. SSTA were calculated using the Extended Reconstructed Sea Surface Temperature version 4 [7] and accessed from the National Oceanic and Atmospheric Administration (NOAA) website [8].

We estimated the trend in temperature anomaly over time and averaged the maximum values of SST anomalies during El Nino events to get a sinusoidal function with period 4 year [9]. The final result was:

$$T(t) = 0.0918 + (4.42 \times 10^{-4})t + 1.0051 \sin \frac{\pi}{2}t$$

Parrotfish are important to the maintenance of reef ecosystems, contributing substantially to coral bioerosion and helping to regulate levels of algae [10,11]. The per capita consumption of coral by certain species parrotfish has been estimated to be as high as $1017.7\text{ kg yr}^{-1}\text{ individual}^{-1}$ [10]. The average coral colony size (1 m^2) was multiplied by the density of calcium carbonate (2710 kg m^{-3}) to get colony mass. The consumption rate of coral by parrotfish (a) was estimated to be 0.3755 individuals yr^{-1} . The remaining parameters were selected either based on plausible natural values or in order to make the model comparable to natural systems. The values are:

$$b = 1, d = 0.5, \beta = 0.1, \alpha = 0.1, \delta = 1, h = \frac{1}{d} - \frac{2}{\alpha K}$$

Equilibria

First, we nondimensionalized the system of equations using the following dimensionless variables:

$$x = \frac{P}{P_0}, y = \frac{N}{N_0}, z = \frac{R}{R_0}, \tau = \frac{K}{r_0}t$$

The nondimensionalized equations were:

$$\begin{aligned}x' &= (\alpha \beta N_0 xy - \delta x)t_c \\ y' &= \left(\frac{abR_0 yz}{1 + ahR_0 z} - d y - \alpha P_0 xy \right)t_c \\ z' &= \left(r(t)z \left(1 - \frac{R_0}{K}z\right) - \frac{azN_0 yz}{1 + ahR_0 z} \right)t_c\end{aligned}$$

with initial conditions $x(0) = 1, y(0) = 1, z(0) = 1$.

At stable points, $x' = y' = z' = 0$, which lead to the following conditions:

$$\begin{aligned}x(\alpha \beta N_0 y - \delta) = 0 &\rightarrow x^* = 0 \text{ or } y^* = \frac{\delta}{\alpha \beta N_0} \\ y(abR_0 z - d - \alpha P_0 x) = 0 &\rightarrow y^* = 0 \text{ or } \frac{abR_0 z^*}{1 + ahR_0 z^*} = d + \alpha P_0 x^* \\ z(r(t)(1 - \frac{R_0}{K}z) - aN_0 y) = 0 &\rightarrow z^* = 0 \text{ or } r(t)(1 - \frac{R_0}{K}z^*) = \frac{aN_0 y^*}{1 + ahR_0 z^*}\end{aligned}$$

Then, we consider the following cases:

If we choose the first choice of every condition,

$$x^* = y^* = z^* = 0 \text{ (case 1)}$$

This equilibrium represents ecosystem collapse. If we choose the second choice of the third condition,

$$x^* = y^* = 0, z^* = \frac{K}{R_0} \text{ (case 2)}$$

At this equilibrium, coral colonies survive, but don't support high trophic levels.

If we choose the second choice of the second condition, we can't let $z^* = 0$, since x^* would be negative by the second condition. Then, we choose the second choice of the third condition.

$$x^* = 0, y^* = r(t) \frac{b}{a(b - dh)N_0}, z^* = \frac{d}{a(b - dh)R_0} \text{ (case 3)}$$

At this equilibrium, the reef is only able to support one trophic level.

Finally, if we choose the second choice of the first condition, we are forced to choose the second choice of the second condition, and for similar reason as above, we can't let $z^* = 0$. Then, the only remaining equilibrium is:

$$x^* = \frac{1}{\alpha P_0} \left(\frac{abK}{1 + ahK} - d \right), y^* = \frac{\delta}{\alpha \beta N_0}, z^* = \frac{K}{R_0} \text{ (case 4)}$$

This is the case where the coral reef supports the complete food chain.

Then, the Jacobian matrix looks as follows:

$$A = t_c \begin{bmatrix} \alpha \beta N_0 y - \delta & \alpha \beta N_0 x & 0 \\ \alpha P_0 y & \frac{abR_0 z}{1 + ahR_0 z} - d - \alpha P_0 x & -\frac{abR_0 y^2}{(1 + ahR_0 y)^2} \\ 0 & -\frac{aN_0 z}{1 + ahR_0 z} & r(t)(1 - \frac{2R_0}{K}z) + \frac{aN_0 y^2}{(1 + ahR_0 y)^2} \end{bmatrix}$$

For cases 1 and 2, stability analysis is possible by solving $\det(A - \lambda I) = 0$.

In case 1,

$$\lambda_1 = -d, \lambda_2 = -\delta, \lambda_3 = r(t)$$

Thus, equilibrium 1 is a global attractor when $r(t) < 0$, and a saddle node otherwise.

In case 2,

$$\lambda_1 = -\delta, \lambda_2 = \frac{abK}{1 + ahK} - d > 0, \lambda_3 = -r(t)$$

Thus, equilibrium 2 is a saddle node, no matter the growth rate. However, note that an eigenvector corresponding to λ_3 is

$$\begin{bmatrix} 0 \\ 0 \\ 1 \end{bmatrix}$$

Thus, equilibrium 2 is stable on the z -axis when $r(t) > 0$.

Stability

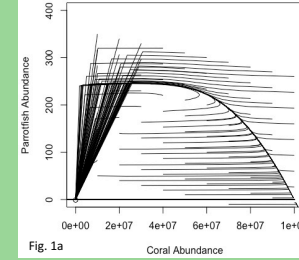


Fig. 1a

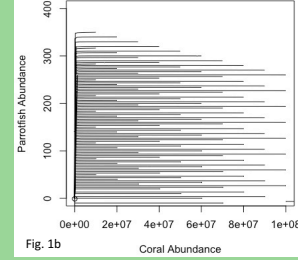


Fig. 1b

For case 3, the system was numerically analyzed for $t = 0$ to $t = 2 \times 10^8$ assuming $r(t) = r_0$ (Fig. 1a). The system moved slower than is biologically plausible. The system is unstable. When $r(t)$ varies, the system collapses on the scale of $t = 0$ to $t = 2 \times 10^4$ (Fig. 1b). The system moves faster than in the unforced case, but the timescale remains biologically implausible.

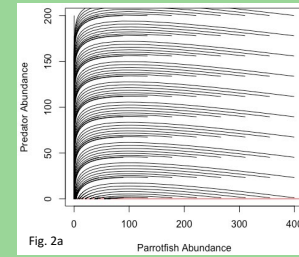


Fig. 2a

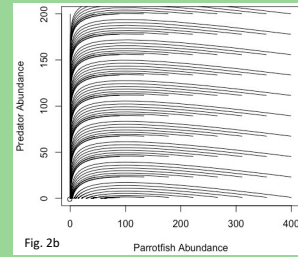


Fig. 2b

For case 4, the system was numerically analyzed for $t = 0$ to $t = 20$ both with and without the forcing term (Fig. 2a, 2b). P and N move quickly relative to R , so the dynamics of R are negligible. Adding forcing changes nothing.

Conclusion

The model does not match biological expectations. Either more sophisticated parameter estimates or models are needed. The slow timescale at which the coral dynamics occur is likely due to the combination of small r_0 and large K . Because the choice of K was influenced by the magnitude of r_0 , higher values of r_0 will likely result in a more realistic model. There is reason to believe that our estimate of r_0 is too low. Estimates of coral extension rate are likely insufficient to model coral growth. More sophisticated, simulation-based models use a mixture of coral extension rate and coral recruitment rates in order to model coral populations, which results in a larger r_0 than extension rate alone [12]. This added complexity is likely necessary to generate biologically meaningful results.

References

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