

MODELING FISH BIOMASS STRUCTURE AT NEAR PRISTINE CORAL REEFS AND DEGRADATION BY FISHING

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Inverted biomass pyramids (IBPs) seem to be extremely rare in natural communities. Until recently, the only examples have been in freshwater and marine planktonic communities. In 2002 and 2008, investigators documented inverted biomass pyramids for nearly pristine coral reef ecosystems within the NW Hawaiian islands and the Line Islands, where apex predator abundance comprises up to 85% of the fish biomass. Large predator:prey biomass ratio seems to be a signature of nearly pristine coral reefs. While the mechanism responsible for the IBP for homogeneously mixed planktonic communities seems to be well understood, this mechanism is not strictly applicable to nearly pristine coral reefs where much of the prey use coral as refuge and are inaccessible to the predators. We construct a mathematical model with an explicit refuge to illustrate a new biologically plausible mechanism that can explain stable IBPs in nearly pristine coral reefs. New modeling components include a refuge of explicit size, a refuge size dependent functional response, and refuge size dependent prey growth rate. Utilizing

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realistic life history parameters of coral reef fishes, our model exhibits a stable inverted biomass pyramid. We prove that all fishing decreases the biomass ratio and sufficiently strong fishing transforms the inverted biomass pyramid to be bottom heavy. Finally we use our model to test the conjecture that pristine coral reefs will rebound faster from environmental shocks and find that it is not always true.

Keywords: Refuge; Fishing; Coral; Functional Response; Recovery.

1. Introduction

An inverted biomass pyramid has increasing biomass along trophic levels.¹ Inverted biomass pyramids in ecology are highly counterintuitive as energy pyramids are always non-inverted. Inverted biomass pyramids appear to be exceedingly rare and until recently, have only been observed in aquatic planktonic communities.^{1–5} Odum¹ hypothesized that the high turn-over rate and the metabolism of phytoplankton can produce inverted biomass pyramids. Other hypotheses include the low turn-over rate of predators^{3,6} and the influx of organic matter which act as food for heterotrophic predators.³ Well known community ecology models which incorporate these hypotheses along with homogeneous mixing between predators and prey lead to stable IBPs.

Recently, inverted biomass pyramids have also been observed at coral reefs where up to 85% of the fish biomass was composed of apex predators.^{7,8} The coral cover at these pristine reefs is far more extensive and healthier than at conventional reefs, and these reefs seem to be either resistant or resilient to ocean warming and rising acidity.^{8,9} The high predator biomass at these “nearly pristine” reefs is in sharp contrast to conventional reefs, where the prey biomass substantially dominates the total fish biomass.⁸ A large predator:prey biomass ratio seems to be a signature of nearly pristine coral reefs. Historical observations suggest that this high abundance of predators was common^{8,10} and such reefs can be considered “nearly pristine”,⁹ and thus provide a baseline for studying natural reefs.

Investigators have found that much of the prey use coral holes as refuge from the predators at nearly pristine coral reefs. Previous experimental and theoretical studies of prey refuges have demonstrated how refuges increase the abundance of prey and add stability to the system.¹¹ Few studies have analyzed the impact of refuges on predator abundances (see Ref. 12 for an analysis of how refuges impact predator growth), and none have addressed how refuges affect predator to prey biomass ratios.

Since much of the prey use coral holes as refuge from the predators, predators and prey are far from being homogeneously mixed. Therefore, classical predator–prey models with Holling type functional responses that exhibit stable IBPs,¹³ including models for planktonic communities, assume that predators and prey are homogeneously mixed, e.g., all prey are accessible to the predators, are poorly suited to pristine coral reefs. Based on observations from field studies, we construct a new

mathematical model with an explicit refuge to illustrate a biologically plausible mechanism that can explain stable IBPs in nearly pristine coral reefs. New modeling components include a refuge of explicit size, a refuge size dependent predator feeding response, and refuge size dependent prey growth rate (see Sec. 2.1). Field study investigators found that the larger nearly pristine reef had higher biomass ratio and our model yields this fact. Although our model is conceptual, and nearly impossible to validate, capturing this phenomenon provides additional confidence in the model. In the appendix, we perform a classical sensitivity analysis of the parameters of the model.

Fishing is conversely considered to be deleterious to coral reefs, although the mechanisms are not clearly understood.⁹ We use our model to study the effect of fishing on a nearly pristine coral reef and we prove that all fishing decreases the biomass ratio. We also show that sufficiently strong fishing transforms the inverted biomass pyramid to be bottom heavy.

Finally we use our model to test the conjecture that pristine coral reefs will rebound faster from environmental shocks and find that it is not always true. In particular, we use our model to simulate the sudden removal of half of predator biomass, e.g., the kill off by a rogue fishing fleet of half of predator biomass and study the recovery time. Surprisingly, it follows from our model that larger reefs take longer to recover.

2. Derivation of the Model

Guided by field observations at pristine coral reefs, we derive a model for the biomass of coral reef fishes using a pair of differential equations. Following the field study Sandin *et al.*,⁸ we classify reef fishes as prey or predators. As the field study recorded the fish biomass, we choose to model the fish biomass directly in our models rather than through a proxy of fish population. We include prey when they are large enough to be seen by the divers on the survey and are a possible source of food for the apex predators (i.e., past the high mortality experienced during recruitment). We include herbivores and planktivores within our prey categories, and the top predators form our predator category. We currently have not incorporated the carnivores (i.e., small predators) into the model as they consume mainly small invertebrates (Sandin *et al.*, 2008) and thus have minimal direct impact on the abundance of prey fishes.

Prey fish eat plankton and algae, hide from predators in coral holes and few prey fish were observed to be roaming freely at Kingman and Palmyra.^{8,14-16} The presence of coral holes drives prey biomass dynamics in two separate ways. First, coral holes decrease fish mortality by providing a safe sanctuary for juvenile fish during settlement before they become adults and are hunted by predators. Therefore, we assume that prey biomass grows logistically and the per capita prey productivity depends on the coral refuge size (details in Sec. 2.1). Second, coral holes prevent the predators from consuming the adult prey fish, therefore the (per capita

predator) predation rate depends on prey biomass and availability of coral holes to hide. Predators grow by eating prey fish and die a natural death at pristine reefs. Prey fish find “refuge” in coral holes and rarely venture out of the holes at Kingman.¹⁴ Therefore, the availability of hiding space for prey in coral holes is a major determinant of the predator functional response. We define the “refuge size” as the maximum prey biomass which can sustainably hide in coral holes, i.e., the coral-specific prey carrying capacity in presence of predators.¹⁷ We distinguish the refuge size from the prey carrying capacity in absence of predators (K); the prey will not be forced to stay inside the holes when the predators are absent and the reef can support a much greater prey biomass. We assume that the refuge size is an increasing function of coral cover at pristine reefs. The equations describing such a community are

$$\frac{dx}{dt} = a(r)x\left(1 - \frac{x}{K}\right) - bf(x, r)y, \quad (2.1)$$

$$\frac{dy}{dt} = cbf(x, r)y - dy. \quad (2.2)$$

x : Prey biomass density (kg/m²),

y : Predator biomass density (kg/m²),

$a(r)$: Prey growth rate (/day),

b : Maximum predation rate: maximum prey biomass,
hunted per kg of predator biomass (/day),

K : Prey carrying capacity in absence of predators (kg/m²),

r : Refuge size (kg/m²),

$f(x, r)$: Predation response,

c : Biomass conversion efficiency,

d : Predator death rate (/day).

The estimated annual mortality rates of small reef fish can be as high as 5–6/year,^{18,19} suggesting that in the absence of predation, prey fish can double in 2–3 months. Therefore for our model, prey growth rate varies between 0.003 and 0.007, which is equivalent to prey doubling every 7 and 3 months, respectively. Predator death rate ($d = 0.0005/\text{day}$) was estimated using the equation: $d = -\ln(0.01)/\text{longevity}$,²⁰ with the estimated longevity for grey reef shark of 25 years.²¹ We set prey carrying capacity at $K = 2\text{ kg/m}^2$, roughly seven times the maximum prey biomass measured at Kingman reef.²² We set the biomass conversion efficiency (c) to 0.15, a reasonable estimate given that conversion efficiencies are higher in marine versus terrestrial environments.²³ Predation rates of 12% predator body weight per day have been documented for smaller sedentary predators,²⁴ suggesting that rates for active predators would be higher. We therefore set the maximum predation, $b = 0.24/\text{day}$.

2.1. Influence of refuge on the predator functional response

The predator functional response $f(x, r)$ at nearly pristine coral reefs should have the following properties. It should be an explicit decreasing function of the refuge size since coral holes prevent the predators from consuming the adult prey fish. It should be a monotonically increasing function of prey biomass. When the prey biomass is less than the refuge size, it should be small. When prey biomass approaches refuge size, it should rapidly increase and as prey biomass greatly exceeds the refuge size, the predators become satiated and the response function approaches a constant; thus forming an S shaped curve.

In Ref. 13 we use mathematical models to explore different ways in which refuge can influence the functional response. We use the function

$$f(x, r) = \frac{1}{1 + e^{-10(x-r)}}. \quad (2.3)$$

Figure 1 is a plot of $f(x, r)$ for fixed refuge size of 2 kg/m^2 .

We are not aware of any empirical study either for coral reefs or even in laboratory communities quantifying this function in an explicit way. Although the effect of refuges on the predator functional response has been modeled before, we introduce a few new features: Unlike the responses functions considered by McNair,²⁵ we do not assume that refuge protects only a fixed number of prey. Neither do we assume that the refuge protects a fixed percentage of prey. Our functional response models more complex and realistic situations where the amount of protected prey biomass is a non-linear function of the total prey biomass and the available refuge size. The shape of our functional response, although similar to the Holling Type III, differs from it in one crucial way: we introduce the refuge size as a parameter explicitly in our model; unlike the Holling Type III that only considers it implicitly. This enables us to compare the fish population dynamics at reefs with different refuge sizes. Our results are qualitatively robust to changes in the exact mathematical form of $f(x, r)$

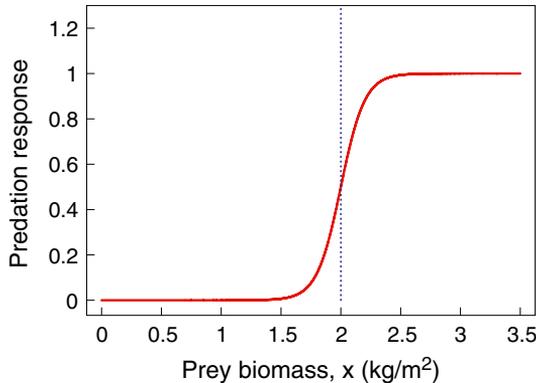


Fig. 1. Predation function $f(x, r)$ versus biomass of prey for fixed refuge size $r = 2 \text{ kg/m}^2$.

as long as the function retains its key features such as explicit refuge dependence and sigmoid shape.

2.2. Influence of refuge on prey productivity

Empirical studies of refuges have not analyzed the quantitative dependence of prey productivity and prey growth rate on refuge size. Research shows that an increase in the refuge size can increase the survival rate of juveniles^{26,27} and may increase the prey growth rate. It has been suggested that juvenile fish mortality during and directly after settlement can create a population bottleneck.²⁸ Since we have defined prey abundance as the number of prey that have survived to a size where they are visually detectable and viable food for the top predators, increasing the shelter available to recruits will increase the number of fish that become available prey. This idea is similar to the idea of recruitment within fisheries science where fish are considered recruits when they have reached a size where they can be captured by the fishery. For this reason, we include in our model a variable prey growth rate dependent on the refuge size, i.e., $a(r)$. We model $a(r)$ as a sigmoid curve where at low refuge cover, there is low survival of recruits, with survival increasing to some upper level where saturation of refuges for recruits results in an asymptote. Our results are qualitatively robust to changes in the exact mathematical form of $a(r)$ as long as the function retains its key features such as explicit sigmoidal dependence on refuge size. We use the function

$$a(r) = 0.003 + \left(\frac{0.004r^{12}}{0.1 + r^{12}} \right). \quad (2.4)$$

We plot the refuge-dependent prey growth rate $a(r)$ in Fig. 2.

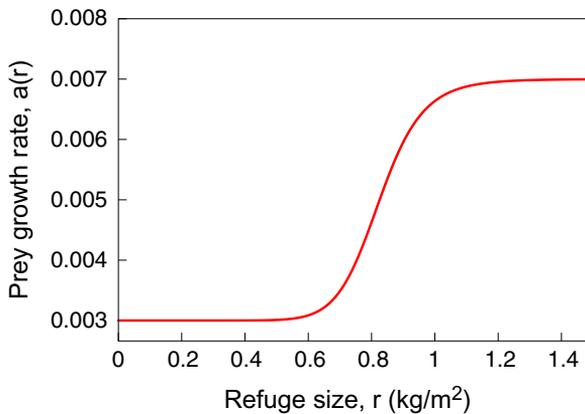


Fig. 2. Prey growth rate, $a(r)$ is a function of the refuge size.

The following equations describe the complete model:

$$\frac{dx}{dt} = \left(0.003 + \frac{0.004r^{12}}{0.1 + r^{12}}\right) x \left(1 - \frac{x}{K}\right) - \frac{by}{1 + e^{-10(x-r)}}, \quad (2.5)$$

$$\frac{dy}{dt} = c \frac{by}{1 + e^{-10(x-r)}} - dy. \quad (2.6)$$

3. Results

The system of differential equations has three equilibrium points. The unstable equilibrium point, $x = 0$, $y = 0$ corresponds to a reef with no fish. The equilibrium point $x = K$, $y = 0$ corresponds to the absence of predators and is rarely seen in reefs. The third and the most interesting equilibrium point, which we call the interior equilibrium point is

$$x^*(r) = r - \frac{1}{10} \ln\left(\frac{bc}{d} - 1\right), \quad (3.1)$$

$$y^*(r) = \frac{a(r)c}{d} x^* \left(1 - \frac{x^*}{K}\right). \quad (3.2)$$

This equilibrium point is locally attractive for the refuge size between 0.65–0.9 kg/m². The predator–prey biomass ratio at the third equilibrium point is

$$\frac{y^*(r)}{x^*(r)} = \frac{a(r)c}{d} \left(1 + \frac{1}{10K} \ln\left(\frac{bc}{d} - 1\right) - \frac{r}{K}\right). \quad (3.3)$$

Figure 3 illustrates the dependence of the predator–prey biomass ratio on the refuge size. The predator–prey biomass ratio is now an increasing function of refuge size, a prediction supported by data from Kingman and Palmyra. The coral cover

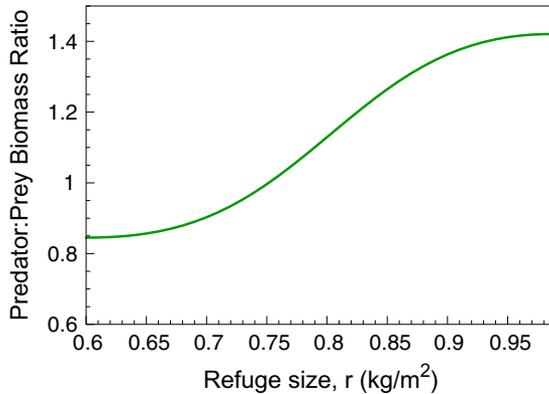


Fig. 3. The biomass pyramid is inverted and the predator:prey biomass ratio is an increasing function of refuge size.

at Kingman is more extensive than Palmyra: Predators constitute 85% of the fish biomass at Kingman while they constitute only 66% of the fish biomass at Palmyra.⁸

4. Effects of Fishing

Fishing is considered to be deleterious to coral reefs; the fish biomass pyramid becomes bottom heavy at reefs with fishing.^{8,29} We add fishing to our model and show that sufficiently high fishing pressure will destroy the inverted pyramid. Destruction of the inverted pyramid in the presence of predator fishing is direct, but we show that prey fishing alone will also destroy the inverted biomass pyramid.

As an illustrative example, we assume that predator fishing rate is proportional to the predator biomass and prey fishing is similar to predator hunting. We understand that this is not the only form of prey fishing and thus we further show that our results are qualitatively robust to changes in forms of prey fishing. The model equations incorporating fishing are

$$\frac{dx}{dt} = a(r)x\left(1 - \frac{x}{K}\right) - b\frac{y}{1 + e^{-10(x-r)}} - b\frac{m}{1 + e^{-10(x-r)}} \quad (4.1)$$

$$\frac{dy}{dt} = cb\frac{y}{1 + e^{-10(x-r)}} - dy - ly, \quad (4.2)$$

m : Prey fishing effort (/day),

$$l : \text{Predator fishing effort (/day)}. \quad (4.3)$$

The prey and predator biomass at the interior equilibrium point are

$$\tilde{x}(r, l) = r - \frac{1}{10} \ln\left(\frac{bc}{(d+l)} - 1\right), \quad (4.4)$$

$$\tilde{y}(r, l) = \frac{a(r)c}{(d+l)} \tilde{x}(r, l) \left(1 - \frac{\tilde{x}(r, l)}{K}\right) - m. \quad (4.5)$$

The new predator–prey biomass ratio at the interior equilibrium point is

$$\frac{\tilde{y}(r, l)}{\tilde{x}(r, l)} = \frac{a(r)c}{d+l} \left(1 - \frac{\tilde{x}(r, l)}{K}\right) - \frac{m}{\tilde{x}(r, l)}, \quad (4.6)$$

$$\text{with } \tilde{x}(r, l) = r - \frac{1}{10} \ln\left(\frac{bc}{(d+l)} - 1\right). \quad (4.7)$$

We plot the predator–prey biomass ratio for various refuge sizes and fishing rates in Fig. 4.

We now deduce the effect of fishing on the predator–prey biomass ratio by inspecting Fig. 4 and comparing Eq. (4.6) with Eq. (3.3): *the predator–prey biomass ratio is a decreasing function of fishing pressure and the biomass pyramid becomes bottom heavy (ratio less than unity) at conventional coral reefs that experience high*

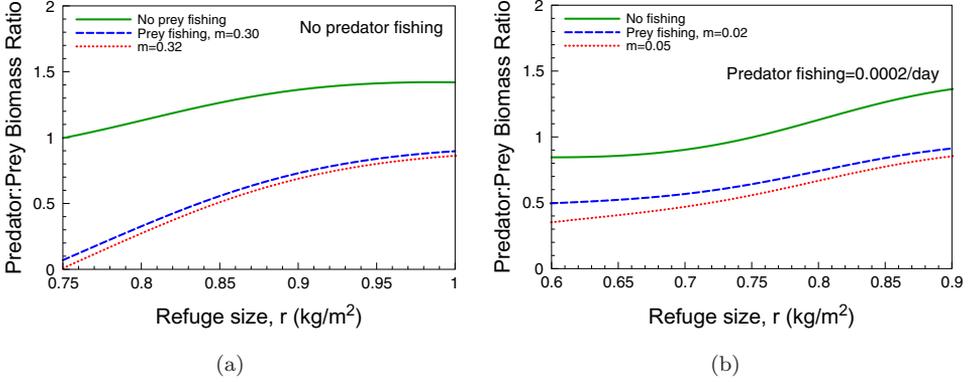


Fig. 4. Predator–prey biomass ratio as a function of refuge size with different prey fishing effort(e). Parameters: $K = 2.0$, $b = 0.24$, $d = 0.0005$, predator fishing rate: (a) $l = 0$; (b) $l = 0.0002$.

fishing pressure. Figure 4(a) shows that the biomass ratio decreases even with prey fishing only and this makes the pyramid bottom heavy.

Our results are independent of the form of prey fishing. Let $p(x)$ be the general prey fishing rate. The modified equations are

$$\frac{dx}{dt} = a(r)x \left(1 - \frac{x}{K}\right) - b \frac{y}{1 + e^{-10(x-r)}} - p(x) \quad (4.8)$$

$$\frac{dy}{dt} = cb \frac{y}{1 + e^{-10(x-r)}} - dy - ly. \quad (4.9)$$

The predator–prey biomass ratio at the interior equilibrium point is

$$\frac{\tilde{y}(r, l)}{\tilde{x}(r, l)} = \frac{a(r)c}{d+l} \left(1 + \frac{1}{10K} \ln\left(\frac{bc}{d} - 1\right) - \frac{r}{K}\right) - \frac{c}{d+l} \frac{p(\tilde{x})}{\tilde{x}}, \quad (4.10)$$

the biomass ratio at the fished reef ($\tilde{y}(r, l)/\tilde{x}(r, l)$) is lesser than the biomass ratio at a reef without fishing ($y^*(r)/x^*(r)$)

$$\frac{\tilde{y}(r, l)}{\tilde{x}(r, l)} \leq \frac{a(r)c}{d} \left(1 + \frac{1}{10K} \ln\left(\frac{bc}{d} - 1\right) - \frac{r}{K}\right) = \frac{y^*(r)}{x^*(r)}. \quad (4.11)$$

As a result of fishing, the predator–prey biomass ratio is less than the biomass ratio at reefs without fishing. This result is robust under different forms of prey fishing.

As another example of prey fishing, if the prey fishing rate is proportional to prey biomass, $p(x) = vx$, the predator–prey biomass ratio

$$\frac{\tilde{y}(r, l)}{\tilde{x}(r, l)} = \frac{a(r)c}{d+l} \left(1 + \frac{1}{10K} \ln\left(\frac{bc}{d} - 1\right) - \frac{r}{K}\right) - \frac{c}{d+l} v. \quad (4.12)$$

This is less than the biomass ratio for the model without fishing in Eq. (3.3) and high fishing pressure will destroy the inverted biomass pyramid.

5. Recovery Time After Population Shock

Some experts believe that pristine reefs are more resilient and recover faster from population shocks such as extreme fishing.⁹ We test this hypothesis in our model and find that it may not be true.

More precisely, we perturb the biomass equilibrium by instantaneously removing predator biomass and tracking the time taken by reefs of different sizes in recovering to equilibrium. Figure 5 shows the recovery time for a spectrum of reefs which have lost 50% of their predator biomass. We defined the recovery time as the interval between the perturbation and time when the biomass reaches 99.9% of the initial equilibrium biomass. Overall, we find that larger reefs take a longer time to recover as compared to smaller reefs, but the recovery time is not a strictly increasing function of reef cover.

We checked the validity of our results by perturbing the equilibria in different ways, our results did not change when the reefs lost 66% of the fish biomass and we achieved the same result when all the reefs lost the same amount of fish biomass. The recovery time depends on two quantities: the total biomass gained and lost by the predators and prey(recovery) and the speed of biomass recovery.

Figure 6 compares the recovery of two reefs of different sizes: 0.7 kg/m^2 and 0.99 kg/m^2 . The y -axis plots the “biomass distance” i.e., the length of the biomass trajectory as a function of time. We make two broad inferences from this figure: The larger reef recovers with a much faster speed (the slope of the larger reef is much steeper than the small reef) but the larger reef has a much longer trajectory than the smaller reef. In this case, the longer distance is the dominating factor and thus the larger reef takes much longer to recover to equilibrium.

However, Fig. 5 showed that the recovery time is not a monotonic function of the reef size. Figure 7 shows the case of two reefs of similar but slightly different

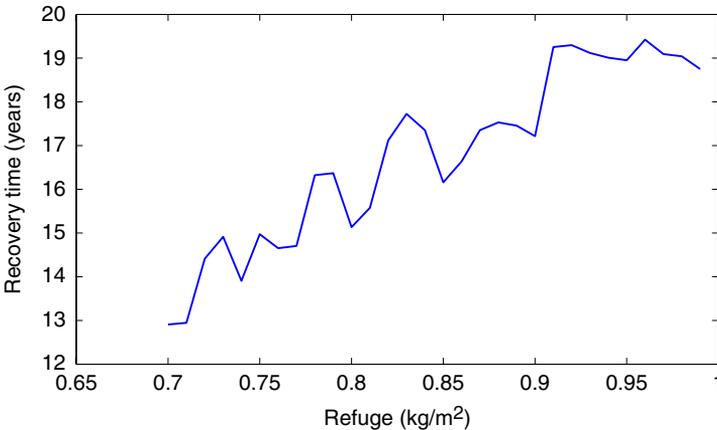


Fig. 5. Time taken to recover to equilibrium in reefs which have lost 50% of predator biomass.

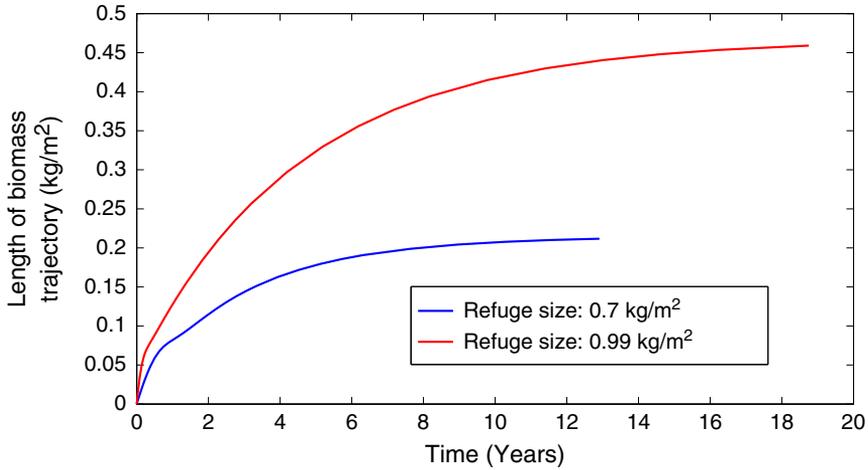


Fig. 6. Comparing speed of biomass recovery in two reefs of very different sizes: 0.7 kg/m² versus 0.99 kg/m².

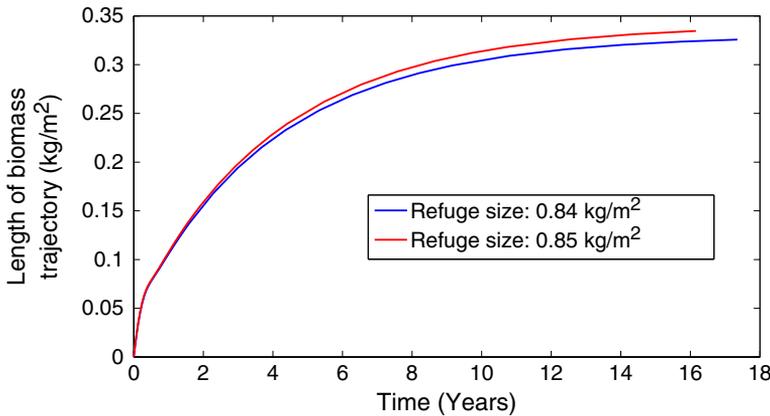


Fig. 7. Comparing speed of biomass recovery in two reefs of slightly different sizes: 0.84 kg/m² versus 0.85 kg/m².

sizes (0.84 kg/m² versus 0.85 kg/m²), where the speed of recovery is the determining factor even though larger reef covers a slightly longer distance.

There is an arms race between the recovery distance and recovery speed, both are increasing as the reef size increases from 0.7 to 1 kg/m². In the long run, the recovery distance dominates and therefore, the time to recovery broadly increases as a function of reef size; occasionally, the recovery speed can outgun the recovery distance which leads to the occasional dips in recovery time as seen in Fig. 5.

6. Discussion

In this manuscript, we construct a mathematical model with an explicit refuge to illustrate a new biologically plausible mechanism that can explain stable IBPs in nearly pristine coral reefs. We show how the presence of refuge can influence the inverted biomass pyramid through the modification of prey growth rate and predator response function. Our model confirms previous suggestions that high prey growth rate and low predator growth rate leads to inverted biomass pyramids.^{1,3,6} Both conditions are satisfied at “nearly pristine” reefs where apex predators such as sharks can live up to 20 years and reproduce rarely³⁰ and smaller prey fish can reproduce at least three times a year.³¹ In addition, we show that sufficiently high fishing pressure will destroy the inverted biomass pyramid.

By incorporating realistic parameter values, we show that inverted biomass pyramids on reefs are possible. Coral holes are essential to our model as prey fish at pristine reefs take “refuge” in coral holes from predators and were rarely observed to leave the holes.⁸ Prey fish also practice “hot-bunking”, i.e., if one prey fish left a coral hole, another immediately occupied that hole.¹⁴ Our model assumes that the refuge size influences prey growth rate. The protection provided to juveniles by the coral cover ends up boosting the overall supply of prey fish by increasing prey growth rate $a(r)$. If we assume that prey survival to adult size is dependent on the cover of coral reef, we find that the predator–prey biomass ratio is an increasing function of refuge size. This relationship is supported by data from⁸ comparing Palmyra and Kingman.

The predator and prey life-history estimates utilized for this paper are at the extremes of those measured in the field. For example, the prey growth rate variation from 0.003 to 0.007 applies to small planktivorous fish. Larger herbivores (i.e., parrotfish) have much lower growth rate estimates (0.0013/day; Fishbase). However, all available parameter estimates are from the highly impacted reefs with low predator abundances. No estimates exist for life history parameters of coral reef fish at any of the locations with the inverted biomass structure.

When the fishing pressure is sufficiently strong, the inverted biomass pyramid disappears (see Fig. 4). This is consistent with field observations where reefs with fishing exhibit a non-inverted bottom heavy pyramid.⁸ Our model shows that the biomass ratio decreases when either predator or prey fishing or a combination of both takes place. Further computations, which we do not present, show that prey fishing alone can have the same effect.

Some experts believe that pristine reefs are more resistant and recover faster from population shocks such as extreme fishing. We use our model to test this assumption. We perturb the biomass equilibrium by instantaneously removing predator biomass and track the time taken by reefs to recover to 99.9% of equilibrium biomass. Surprisingly, we find that fish recovery is not faster at larger reefs as hypothesised and overall larger reefs take longer to recover to equilibrium fish biomass.

Appendix A.

A.1. Local stability of equilibrium points

The equations governing the dynamics of predator and prey biomass are described by

$$\begin{aligned}\frac{dx}{dt} &= a(r)x\left(1 - \frac{x}{K}\right) - bf(x,r)y, \\ \frac{dy}{dt} &= cbf(x,r)y - dy.\end{aligned}$$

The equilibrium points are $(0, 0)$, $(K, 0)$ and (x^*, y^*) .

$$x^* = r - \frac{1}{10} \ln\left(\frac{bc}{d} - 1\right), \quad (\text{A.1})$$

$$y^* = \frac{a(r)c}{d} x^* \left(1 - \frac{x^*}{K}\right). \quad (\text{A.2})$$

We determine the local stability of the equilibrium points by computing the Jacobian at the equilibrium points. The Jacobian

$$J = \begin{bmatrix} a(r) - 2a(r)\frac{x}{K} - 10by\frac{(e^{-10(x-r)})}{(1+e^{-10(x-r)})^2} & -\frac{b}{1+e^{-10(x-r)}} \\ 4bc\frac{y(e^{-10(x-r)})}{(1+e^{-10(x-r)})^2} & \frac{bc}{1+e^{-10(x-r)}} - d \end{bmatrix}.$$

At $(0,0)$

$$J(0,0) = \begin{bmatrix} a(r) & -\frac{b}{1+e^{10r}} \\ 0 & \frac{bc}{1+e^{10r}} - d \end{bmatrix}.$$

The eigenvalues of the Jacobian are $a(r)$ and $(bc/(1+e^{10r}) - d)$. As $a(r) \geq 0$, $(0,0)$ is an unstable equilibrium point.³²

At $(K,0)$,

$$J(K,0) = \begin{bmatrix} -a(r) & -\frac{b}{1+e^{-10(K-r)}} \\ 0 & \frac{bc}{1+e^{-10(K-r)}} - d \end{bmatrix}$$

$$\text{and } \det(J(K,0)) = -a(r) \left(\frac{bc}{1+e^{-10(K-r)}} - d \right) < 0.$$

As $1 + e^{-10(K-r)} \leq 2$ and $bc > 2d$, $\det(J(K,0)) < 0$. Therefore, $(K, 0)$ is a saddle equilibrium point.³²

At (x^*, y^*) ,

$$x^*(r) = r - \frac{1}{10} \ln\left(\frac{bc}{d} - 1\right),$$

$$y^*(r) = \frac{a(r)c}{d} x^* \left(1 - \frac{x^*}{K}\right),$$

$$J(x^*, y^*) = \begin{bmatrix} a(r) - 2a(r)\frac{x^*}{K} - 10by^* \frac{e^{-10(x^*-r)}}{(1+e^{-10(x^*-r)})^2} & \frac{-b}{1+e^{-10(x^*-r)}} \\ 10bc \frac{y^* e^{-10(x^*-r)}}{(1+e^{-10(x^*-r)})^2} & 0 \end{bmatrix},$$

$$\det J(x^*, y^*) = \frac{10a(r)cx^*(1-x^*/K) \left(\frac{c}{d} - 1\right)}{b \left(\frac{c}{d}\right)^2},$$

$$\text{Tr}(x^*, y^*) = a(r) - 2a(r)\frac{x^*}{K} - 10by^* \frac{e^{-10(x^*-r)}}{(1+e^{-10(x^*-r)})^2}.$$

The determinant and the trace of the Jacobian are complicated functions of the parameters and equilibrium predator and prey biomass. Computer assisted analysis shows that $\det J(x^*, y^*) \geq 0$ and $\text{tr} J(x^*, y^*) \leq 0$ when $0.60 \leq r \leq 0.99$. Therefore, (x^*, y^*) is an attractive equilibrium point when $0.60 \leq r \leq 0.99$.

A.2. Sensitivity analysis

We determine the sensitivity of the predator:prey biomass ratio to variation in the parameters of the Eqs. (2.1), (2.2) and (3.3) by means of a sensitivity index. The normalized forward sensitivity index of a variable to a parameter is the ratio of the relative change in the variable to the relative change in the parameter.³³ As an example, the sensitivity of the biomass ratio to variation in maximum predation rate (b) is given by

$$\gamma_b^{\text{ratio}} = \frac{\partial_{\text{ratio}}}{\partial b} \cdot \frac{b}{\text{ratio}} = \left(\frac{a(r)c}{10Kd}\right) \left(\frac{1}{(bc/d) - 1}\right) \frac{c}{d} \frac{b}{\text{ratio}}.$$

The absolute value and the sign of the sensitivity index both contain useful information. The absolute value measures the sensitivity of the variable to variation in the parameter: A low absolute value denotes robustness in the value of the variable to variation in the parameter and vice versa. A positive sensitive index for a parameter shows that the variable is an increasing function of the parameter. Table 1 shows the sensitivity index for each parameter and organizes them in decreasing order of influence on the biomass ratio.

The predator:prey biomass ratio is most sensitive to variation in the refuge size (r) and least sensitive to variation in the predation response (b). The signs of

Table 1. Sensitivity indices for parameters in Eqs. (2.1), (2.2) and (3.3). Baseline value for parameters: ($b = 0.24, c = 0.15, d = 0.0005, K = 2.0, r = 0.8$, biomass ratio = 1.1).

Parameter	Sensitivity Index
r	2.0
c	0.8
d	-0.8
K	0.2
b	0.06

the sensitivity indices tell us that the predator:prey biomass ratio is an increasing function of r (per unit area coral reef refuge size), b (maximum predation rate), c (biomass conversion efficiency) and K (prey carrying capacity) and a decreasing function of d (predator death rate).

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