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Coral Reefs

Model of a Coral Reef Ecosystem

III. Resource Limitation, Community Regulation, Fisheries Yield and Resource Management

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Abstract. The results of modelling of a coral reef ecosystem at French Frigate Shoals and independent field measures of benthic primary productivity indicate relatively good agreement between food required by consumer trophic levels and organic carbon produced by primary producers. Based upon the high internal predation necessary for the model to match primary production estimates, we reason that the ecosystem is primarily regulated from the top down by forces of predation and that primary production appears to be controlled by nutrients, rate limits, and the distribution of space and habitat. In spite of relatively high primary productivity, potential yield at the top of the food chain is low because of high internal predation and high trophic complexity (6 trophic levels). Fishery yield might be maximized by harvesting low on the food chain particularly if top carnivores can be cropped to release predator pressure on selected prey. Agreement between field measures of metabolism and model (ECOPATH) results provides reasonable confidence that the model can be used as one tool for resource management.

Introduction

One of the most important problems facing coral reef biology today is the question of what factor(s) control the production of organic carbon at all levels within the ecosystem. Are coral reefs truly nutrient limited ecosystems? Does primary production depend on the supply of nutrients (concentration or flux) across the reef? Or is primary, secondary and higher level production simply regulated by predators operating downward from the top of the food chain? And, given nutrient limitation or predator regulation or some combination of the two, what is the quantitative effect of space (available sustratum) and habitat on primary or secondary levels of benthic production? In the sense of Hairston et al. (1960) is the reef green or is it brown? That is, is production of organic matter limited by "nutrients" (Nitrate, $NH_3 \cdot PO_4^{=}$ and sunlight) from below, or by predation by grazing herbivores from above? At higher levels in the ecosystem, is production limited by the flow of nutrients up the chain or is the system controlled (regulated?) by various forces of mortality? The results of this research at French Frigate Shoals, Hawaii, the first attempt to analyze the trophic energetics of an entire atoll ecosystem, may shed some light on this major problem in coral reef biology. The approach has been to dissect a reef ecosystem or foodweb simultaneously from the bottom up and the top down. The analysis is intended to produce an understanding of the dynamics of a coral reef ecosystem out of which certain management options might logically follow.

Results of Part I and Part II

Before addressing these questions directly, it is useful to reconsider the major conclusions presented in Parts I and II of this paper (Polovina 1984; Aktinson and Grigg 1984). These are briefly restated below.

Part I

1. The average rate of net primary production for the reef ecosystem at French Frigate Shoals (adjusted to 700 km^2) predicted by the ECOPATH model is 4.3×10^6 kg/km^2/year (wet weight).
2. Net primary productivity by the plankton over the reef is about 1/10 the benthic net primary productivity.
3. The ECOPATH model estimate of net community benthic production is 2.2×10^5 kg/km^2/year.
4. The model predicts that only about 5% of the net benthic primary productivity is passed up the food chain to non-benthic reef consumers.
5. The model analysis suggests that the reef ecosystem at French Frigate Shoals consists of six trophic levels. The average ecological efficiency of all trophic levels is 0.17.
6. High internal predation exists within the heterotrophic benthos and reef fish compartments of the ecosystem.

Part II

1. Rates of metabolism and calcification of reef ecosystems (reef flats, coral knolls and lagoons) at French Frigate Shoals are similar to rates for corresponding coral reef ecosystems elsewhere in the world.

2. The average rate of net primary productivity for the reef ecosystem at French Frigate Shoals based on field measures and literature *P/R* ratios averaged over a year is 6.1×10^6 kg/km^2/year. The field estimate for net community production was 9.4×10^5 kg/km^2/year.

3. The *P/R* ratio for the entire benthic ecosystem at French Frigate Shoals was 1.10. Field results indicate that about 10% of the net primary production (6% of the gross primary production) might be permanently lost to the atoll ecosystem by burial or offshore transport.

4. The close agreement between the field and model estimates of net benthic primary productivity is interpreted as conceptual support for the ecosystem model and suggests that it can be used as a tool for resource management.

Field Validation of the Model

The model estimate of net benthic primary productivity is only slightly lower than the estimate based primarily on field measures (4.3×10^6 kg/km^2/year versus 6.1×10^6 kg/km^2/year). Given the errors associated with the calculation of each of these estimates, their agreement is closer than expected. The difference might have been even smaller were it not for high values of lagoon net productivity. The average value of net productivity for the whole system may therefore be slightly less than that calculated.

Looking at the other side of the comparison, the model estimates of net primary productivity could be too low if for example the biomass of major top carnivores at French Frigate Shoals had been initially underestimated. Also the model estimate of net primary productivity would be too low if more trophic complexity actually exists than that built into the model. On these two points, however, it is believed that neither biomass or trophic complexity were mis-approximated. Another consideration is the amount or organic carbon that might be lost to the system. Since the model estimate is based on only carbon (wet weight) flowing through the system, it cannot take into account any losses even if they exist. In Part II of this paper, it was estimated that approximately 10% of the net benthic primary productivity might be permanently lost to the system. Therefore the model estimate of NPP could be low by approximately this amount.

Returning to the field estimate, if the value of net benthic primary production is increased or lowered by 50% (the error of estimate associated with all field measures), the revised field estimate for the average net primary production of the atoll would be about 3.0 -9.0×10^6 kg/km^2/year. Given either change the field estimate of net benthic primary production is still within a factor of about 2.0 of the model estimate. Hence the degree of agreement observed between these two independent estimates of net benthic primary productivity appears to be good. Similarly the field estimate of net benthic community productivity is in reasonable close agreement with the model estimate (9.4×20.5 kg/km^2/year versus 2.2×10^5 kg/km^2/year).

Coral Reef Ecosystem Dynamics

Having reviewed the results of Parts I and II of this paper and reconsidered the degrees of agreement between field and model estimates of net benthic primary productivity, it is now possible to deal with the question of community function. Are coral reef ecosystems nutrient limited or predator controlled? The results of this research as discussed below suggest that nutrient limitation is of less significance than formerly believed and that predation mortality is the most important factor controlling secondary and higher production. The balance of this section is given to a consideration of the evidence for this conclusion both from this research and the literature.

The role of predation in the ecosystem can be examined by considering ecotrophic efficiency. Ecotrophic efficiency is the fraction of a species' annual production which is consumed by predation (Ricker 1969). Based on the model's estimate of trophic efficiency of 0.17, annual production at the top level of 462 kg/km^2/year, and six trophic levels, the net benthic primary production required to support the ecosystem can be calculated as a function of ecotrophic efficiency (see Part I). For an ecotrophic efficiency of 0.95 which implies that 95% of the production of each species group is consumed by predators, the net benthic primary production required by the ecosystem is 4.2×10^6 kg/km^2/year (Table 5, Part I). The net benthic primary production estimated as a function of ecotrophic efficiency increases as ecotrophic efficiency decreases (Table 5, Part I). If as discussed earlier, our confidence interval for the net benthic primary production is from 3.0×10^6 kg/km^2/year to 9.0×10^6 kg/km^2/year, then based on Table 5, Part I, the average ecotrophic efficiency for the ecosystem at French Frigate Shoals would be contained in the interval of 0.85–1.0 which indicates that at least 85% of the production of each species group is consumed by predators. Ricker's estimates for ecotrophic efficiency for marine communities in general are somewhat lower with an estimate of 0.66 for primary consumers and 0.75 for all higher consumers (Ricker 1969). Based on the simulation presented in Table 5, Part I, and our confidence in the field estimate of net benthic primary production, it appears very likely that on the average, ecotrophic efficicency for the coral ecosystem at French Frigate Shoals exceeds 0.85. It most certainly exceeds 0.50. For example, if the ecotrophic efficiency were 0.50, the net benthic primary production required to support the ecosystem would be 104.1×10^6 kg/km^2/year or about 25 times the estimated field value (Table 5, Part I). Hence, it appears that a high level of predation mortality exists within the coral reef ecosystem at French Frigate Shoals suggesting that predation mortality is the major driving force regulating higher trophic production of the ecosystem. This model result is supported by the quantitative fit between the model and field measures of net primary and community benthic productivity.

It is now useful to distinguish between regulation of production vis-a-vis production per se. Production per se is the process of producing new organic carbon while regulation is the process that determines how much of that carbon reaches various trophic levels. Given all of the above, it is now possible to re-examine the basic question, to what extent do nutrients limit the productivity of coral reef ecosystems.

The only true test of the nutrient limitation hypothesis for a coral reef community that has been done to date, is the work of Kinsey and Domm (1974) at One Tree Island on the Great Barrier Reef where they conducted fertilization experiments over an eight month period using a lagoon patch reef system. Levels of phosphorus and nitrogen were increased by 10 and 40 fold respectively during 3 h incubations. The result showed that the rate of community primary production increased by about 50% over the previous year (Kinsey and Davies 1979). Since levels of nutrient enrichment used in the experiment were higher than those that would be expected to occur naturally in the world's oceans, this increase in primary production should represent a maximum response of a coral reef ecosystem to natural nutrient enrichment. Kinsey (1979) has determined that metabolite rates of coral ecosystems at One Tree Island are representative of coral ecosystems in general therefore their response to nutrient enrichment might also be considered representative. If so, the most by which the productivity of a coral reef ecosystem might be expected to increase as a function of natural nutrient enrichment would be by about a factor of 1.5. Hence, while the nutrient limitation hypothesis must be considered valid because it is unquestionable that the photosynthetic process requires light and nutrients, it appears that natural nutrient enrichment can at best produce relatively small (50%) increases in production. This conclusion puts into perspective the dogma that coral reefs owe their high productivity to the highly efficient recycling of nutrients by endosymbiotic zooxanthellae (Muscatine and Porter (1977). While coral reefs do exist in nutrient poor water in terms of concentration, the *flux* of nutrients under normal conditions appears sufficient to maintain high biomass and high areal primary production. Perhaps rather than viewing coral reefs as nutrient limited systems, a more accurate interpretation may be that coral reefs are operating near their upper limit set by metabolic rates associated with the photosynthetic process rather than nutrient concentration per se. Of course within environments such as confined embayments, estuaries, etc., where nutrients may be drawn down to limiting levels, nutrients can limit productivity and benthic biomass (Smith and Jokiel 1978). This condition, however, would not apply to coral reefs which exist in unconfined environments.

If nutrients under normal conditions do not exert strong control over primary production of most coral reefs in unconfined environments, then what does? Recent work by S. V. Smith (1981) has shown that very high rates of reef calcification (11.7 kg $CaCO_3/m^2$/year) and gross primary productivity (17 g $C/m^2/d$) exist at the Houtman Abrolhos Islands (29° south latitude). These rates can be compared to average rates for reefs in general which according to Kinsey (1979) are about 5 kg $CaCO_3/m^2$/year for calcification and 7 g $C/m^2/d$ for gross primary productivity. Smith (1981) attributes the very high values at the Abrolhos Islands in spite of seasonally low temperature (20°C) and light intensity (300 Langleys/d), to the three dimensional structure of shallow thickets of *Acropora* corals which occur there. In describing the Abrolhos transects Smith states that "virtually the entire surface of the coral transect is not only covered but stacked with photosynthetically active organisms." This result clearly shows the effect of space which may serve to double or even triple gross primary production. The same result is evident in Table 1, Part II of this paper which clearly demonstrates how differences in habitat (which in turn alters space) produce differences in primary production. Space and habitat then may be of equal or greater importance than nutrients in controlling primary production on coral reefs.

The argument that space (photosynthetically active area) is a limiting factor for coral reef primary productivity can also be interpreted as a biomass (photosynthetic) limitation argument. The more the space, the more the biomass, the more the production. The relation of space to reef productivity is also evident if one considers the bio-fouling that occurs when artificial structures (wrecks, pilings, artificial reefs, etc.) are placed on reefs. In general, such structures are quickley covered by a rich epiflora and epifauna that otherwise would not exist. Extensive bio-fouling on artificial structures on coral reefs appears to be a ubiquitous phenomenon. Clearly, in such instances nutrients in the water are not limiting and often a much greater reef biomass can be supported than that which naturally exists.

So much for the production of new organic carbon. Let us now reconsider production at higher levels in the ecosystem. We have seen from the ECOPATH model that only about 5% of the net primary production at French Frigate Shoals is passed up the food chain to higher non-benthic trophic levels. We have also seen that very high internal predation exists within the heterotrophic benthos and the reef fishes. The *P*/*R* radio of many whole reef systems is not much higher than 1.0 (Kinsey 1979) underlining the point that most of the carbon produced is respired (via predation) within the system. On occasion, however, there can also be a substantial loss of organic carbon probably in the form of offshore transport (Qasim and Sankaranarayanan 1970). Given all of these sources of loss, it is not surprising that production at the top of the food chain is so low (462 kg/km^2/year, see Part I). Thus in spite of high productivity relative to other marine and terrestrial ecosystems, coral reefs may not be very efficient in terms of producing biomass yield. The ratio of fish yield to phytoplankton primary production of those reefs for which estimates of each are available ranges between 0.0001 and 0.0008 with a mean of 0.0004 (this paper and Martin and Polovina 1982). Most of the losses described above have to do with predation (respiration is a by-product of predation). That predation is the major force regulating secondary and higher production of coral reef ecosystems is also indicated by the high level of ecotrophic efficiency estimated from the results of the ECOPATH model.

In conclusion, the answer to the question "are coral reefs nutrient limited or predation controlled" is that both processes are important, but for primary productivity, photosynthetic rate limits, space and how it is used (habitat), may be even more important than nutrients per se. For secondary and higher production, predation is clearly the major controlling factor.

Several examples from the literature illustrate the controlling effects of predation on aquatic or coral reef ecosystems. Dramatic examples include explosions in fish herbivores as a consequence of heavy exploitation of the carnivores in the Gulf of Thailand and Lake Victoria (Pauley 1979). Lower down on the foodchain, herbivores are often in close balance with plant production. Experiments using exclusion cages to protect algae from grazing often lead to rapid colonization by fleshy algae (Wanders 1977). Also the abundance of fleshy algae in most turbulent sectors of the reef is often attributed to exclusion of fish from grazing in such areas (Conner and Adey 1977). Conversely the scarcity of fleshy algae in more exposed areas of the reef is thought to be a result of grazing (Hawkins and Lewis 1982). Another effect illustrating the control of herbivory on coral reef macroalgae are the "halos" (areas of heavily grazed algae) that exist around patch reefs in so many parts of the world (Randall 1963).

The apparent balance between herbivores and algal production on coral reefs may explain why in some instances of eutrophication large increases in benthic algae have occurred. In Hawaii for example, during the late 1960's when about 4 million gallons of sewage were discharged into Kaneohe Bay daily, large mats of the benthic algae *Dictyospheria cavernosa* rapidly developed throughout portions of the bay (Banner and Bailey 1970). Herbivory, in quantity and kind, was possible unable to provide sufficient grazing pressure to control plant growth. In other polluted systems reports of algal population explosions (Benayahu and Loya 1977) may owe their existence to a similar imbalance. Given enough time these situations could possibly attain a new balance at higher rates of primary production.

In conclusion, the results of this research presented in Parts I and II and other numerous examples in the literature, suggest that in general coral reef ecosystems are regulated from the top down by forces of predation. Trophic regulation is similar to many terrestrial ecosystems particularly near the top of the food chain where carnivores control herbivore populations. On land herbivores in general are regulated by carnivores and do not keep pace with plant production explaining why the world is green (Hairston et al. 1960). On the French Frigate Shoals reef, predator control appears to generally extend all the way down the food chain. This explains why fleshy algae are so inconspicuous or rare on coral reefs. Compared to land, the reef is brown.

The conclusion that coral reef ecosystems are limited by a combination of nutrients, photosynthetic rate limits and space (habitat), and regulated by predator control is a departure from the traditional view that coral reefs are simply nutrient limited. This new hypothesis, call it the rate-space-predation hypothesis, does not refute "nutrient limitation" but rather puts it into a larger perspective in which the significance of other factors acting in combination are accounted for.

Finally, from the equilibrium or long term average perspective that we view the coral reef ecosystem, larval recruitment would not appear to be a limiting factor. While variation in larval recruitment produces variation in year class strength and is very important in the short term variation in the ecosystem, this variation averages out in the long term perspective. Further, even short term recruitment variation is probably primarily due to predation and environmental factors which affect the survival of the larvae and juveniles rather than variation in larvae production (Sale 1982; Bohnsack 1983).

Management Implications

The holistic perspective gained by attempting to analyze a coral reef ecosystem simultaneously from the top down and the bottom up, suggests several rather obvious but important principles for purposes of resource management.

1. To maximize efficiency, harvest at levels of sustained yield as low on the food chain as possible (Pauley 1979). Cropping of predators would increase potential yield. Reef invertebrates and algae present many opportunities for this strategy. In some coral reef environments this approach has been taken inadvertently (Smith and Stimson 1979). The large variation in fishery yield for coral reefs around the world (Acala and Lucharez 1982) may primarily be due to harvest at different trophic levels rather than intrinsic differences in primary production.
2. Fisheries targeted as top carnivores will serve to ease or release predation pressure on prey species. At French Frigate Shoals a tiger shark fishery could possibly help restore population levels of the endangered monk seal (*Monachus schauinslandi*) and the threatened Hawaiian green turtle (*Chelonia mydas*).
3. Reef ecosystems may be easily overfished because annual production is lower than rates suggested by levels of gross primary production and because natural mortality is high and cannot support heavy fishing mortality. It has been suggested that due to high predation, prey

stocks are already optimally exploited by predators so that even limited fishing pressure on the prey stocks can cause rapid stock decline (Pauley 1979; Ursin 1982).

4. At the level of primary and benthic secondary production, the most efficient means of stimulating production might be a combination of increased space (artificial reefs or substratum) and slight nutrient enrichment. Rapid and large scale nutrient enrichment such as that brought about by artificial upwelling, could result in choking the system by turning it green. It would be of theoretical and practical interest to gradually increase nutrients on a large scale to see if the ecosystem could slowly adapt. This might be attempted in combination with increased harvesting levels on primary producers or carnivores feeding on herbivores. The latter condition should result in higher standing crops of herbivores and corresponding higher grazing rates. Discovering the proper balance between these offsetting effects is an important problem for future research.

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