

Model of a Coral Reef Ecosystem

I. The ECOPATH Model and Its Application to French Frigate Shoals

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Abstract. A simple model termed ECOPATH is presented which estimates mean annual biomass, production, and consumption for components of an ecosystem. To use the model, the ecosystem must be partitioned into groups of similar species and provide for these species groups, estimates of production to biomass, diet, and food consumption. The ECOPATH model is applied to an ecosystem at French Frigate Shoals in the Northwestern Hawaiian Islands. Extensive field work provides both estimates of the input parameters as well as estimates of mean annual biomass and production. Biomass and production estimates for some of the species groups modeled are used to validate the estimates generated by the model.

Introduction

In general, coral reefs have very high rates of gross primary production compared with other marine ecosystems (Odum and Odum 1955; Gordon and Kelly 1962; Ryther 1969; Lewis 1977). This characteristic is often considered to be a paradox since most coral reefs in the world occur at ocean latitudes characterized by nutrient poor waters (Muscatine and Porter 1977). Atolls in fact have been likened to oases in the desert. In answer to this apparent paradox, many workers have associated the high productivity found on coral reefs with a highly efficient mechanism that recycles nutrients within the system (Muscatine and Porter 1977). These considerations have led some biologists to conclude that reef ecosystems are in general nutrient limited.

Another widespread view about coral reefs is that because of their high productivity, they are potentially capable of supporting relatively high sustainable fishery yields (Marten and Polovina 1982). If the latter contention is true, this raises a question of why so many coral reef fisheries in the world are in serious decline (Johannes 1978). Irrespective of the cause, the common depletion of coral reef resources underlines the need to develop a bet-

ter understanding of the structure and function of coral reef ecosystems and the development of better tools for their management.

In this paper these questions and problems are re-examined in detail. The approach has been to construct a mathematical ecosystem model, ECOPATH, for an entire coral reef ecosystem and then use the model to estimate its standing stock and production budget. The ECOPATH model operates from the top of the food chain down, using field estimates of the biomass of top carnivores as a starting point. One of the outputs of the model is the net primary production of the entire system necessary to support the biomass of major species complexes known to be present. A major strength of this approach is that the ecosystem model can be tested by providing an independent measure of primary productivity. This was done using standard methods for analyzing reef metabolic performance (Smith and Marsh 1973; Smith and Kinsey 1978; Kinsey 1979). The results and discussion of this work are reported in Parts II and III (Atkinson and Grigg 1984b; Grigg et al. 1984).

The island selected for study is French Frigate Shoals (FFS) in the Hawaiian Archipelago. It is situated at lat. 24° N and long. 166° W, approximately midway in the archipelago. This island was chosen for the modeling study because of the large number of research projects conducted there as a result of the Northwestern Hawaiian Islands (NWHI) fisheries investigations, a large-scale multidisciplinary 5-year study of resources in the Hawaiian Archipelago (Grigg and Pfund 1980; Grigg and Tanoue 1984).

The study is divided into three parts. In Part I (this paper), the ECOPATH model is described in general and then applied specifically to the marine ecosystem at FFS. The results of this work produce estimates of mean annual biomass and annual production for all the components of the ecosystem and in particular, the minimum net primary productivity needed to support the ecosystem. In Part II of the paper, actual measures of gross and net primary productivity for the entire reef ecosystem at

FFS are presented and compared with data for reef ecosystems elsewhere in the world. In Part III of the paper, net values of measured primary productivity are contrasted to those predicted by the model, and possible causes of the difference are discussed. In Part III, interrelationships of the results of Part I and Part II are described, particular regarding factors limiting primary production and the effects of predation and nonpredation mortality on community regulation. Potential and actual fishery yields and implications regarding various management options that might maximize production are also discussed.

Portions of this study (Part I) appear in a proceedings volume of a symposium on the Northwestern Hawaiian Islands held in Honolulu, Hawaii on May 25–27, 1983 (Grigg and Tanoue 1984). Those sections of this manuscript which appear in Grigg and Tanoue (1984) are so indicated by a footnote. The proceedings volume is a technical report of the University of Hawaii with a limited distribution. Hence those sections which are necessary to fully describe the model and the parameter estimates, are included here for completeness and the convenience of the reader.

The ECOPATH Model¹

There are a number of published examples of ecosystem models developed with the goal of simulating the dynamics of an exploited marine ecosystem (Parrish 1975; Andersen and Ursin 1977; Laevastu and Larkins 1981). Most of these models, however, require a level of understanding of the static and dynamic elements of an ecosystem which have not yet been achieved for tropical systems. In a review of the Bering Sea model developed by Laevastu and the North Sea model developed by Andersen and Ursin, Larkin and Gazey (1981) conclude:

“As in the case of the Bering Sea simulation it seems reasonable to conclude that the North Sea model has little utility for multispecies fisheries management in tropical water. To even construct a model at a comparable level of detail for tropical fish communities is at present impractical. Even if the data were available for estimating the several thousand parameters involved, it would take many years of observation and experimentation to verify the utility of the model. It is also difficult to visualize what kind of experimental management might be adopted to test the validity of such a model.”

However, in many situations the construction of a biomass budget box model of an ecosystem is relatively simple and can provide important information about the ecosystem standing stock and energy flow (Walsh 1981; Pauly 1982). The goal of the mathematical modeling work at FFS was to estimate annual production and mean annual biomass for the major components of the coral reef ecosystem for a static situation under general

equilibrium conditions. The mathematical model developed to construct the biomass box model for the ecosystem is termed “ECOPATH”.

The ECOPATH model partitions the ecosystem into species groups and, given a set of parameter estimates as inputs, produces estimates of mean annual biomass, annual biomass production, and annual biomass consumption for each of the species groups. A species group is an aggregation of species having common physical habitat, similar diet, and similar life history characteristics.

Equilibrium conditions exist when the mean annual biomass for each species group does not change from year to year. This condition results in a system of biomass budget equations which, for species group i , can be expressed as:

Production of biomass for species i – all predation on species i – nonpredatory biomass mortality for species $i=0$ for all i . (1)

The ECOPATH model expresses each term in the budget equation as a linear function of the unknown mean annual biomasses (B_i 's) so the resulting biomass budget equations become a system of simultaneous equations linear in the B_i 's. The formulation of each term of the biomass budget equation is presented in detail below.

Biomass Production

Production (P) for a cohort of animals over 1 year is defined as:

$$P = \int_0^1 N_t \frac{d}{dt}(w_t) dt$$

and mean annual biomass (B) for the cohort is defined as:

$$B = \int_0^1 N_t w_t dt,$$

where N_t is the number of animals and w_t the mean individual weight at time t .

Allen (1971) has investigated the production to biomass (P/B) ratio for a cohort of fish over a range of mortality and growth functions. For a number of growth and mortality functions, including negative exponential mortality and von Bertalanffy growth, the ratio of annual production to mean biomass for a cohort is the annual instantaneous total mortality (Z_i). For a species group which consists of n cohorts or species and instantaneous annual total mortality (Z_i) for cohort or species i , where mortality is determined by a negative exponential function and growth by a von Bertalanffy growth function, the total species group production (P) is the sum of the cohort production (P_i) and can be expressed as:

$$P = \sum_{i=1}^n P_i = \sum_{i=1}^n Z_i B_i. \quad (2)$$

Under the assumption that the Z_i 's are all equal to Z , then total species group production can be expressed as:

$$P = ZB$$

where B is the mean annual species group biomass.

¹ Portions of this section also appear in Grigg and Tanoue (1984)

lonia mydas (Linnaeus), various species of seabirds, and the Hawaiian monk seal, *Monachus schauinslandi* (Matschie).

The ecosystem of interest is the reef and nearshore community from shoreline to a depth of 365 m (200 fathoms). This habitat describes a circular area with a radius of approximately 20 km and a total area of approximately 1,200 km². The reef habitat in this region is defined as the area from shoreline to 55 m (0–30 fathoms) and is approximately 700 km².

Fifteen species groups were identified as the major components of the ecosystem within the region down to 365 m (200 fathoms) around FFS. These species groups described in detail below, are tiger sharks, monk seals, seabirds, reef sharks, sea turtles, small pelagics, jacks, reef fishes, lobsters and crabs, bottom fishes, nearshore scombrids, benthic algae, heterotrophic benthos, zooplankton, and phytoplankton.

The parameters which are required as inputs to the ECOPATH model are (for each species group): the *P/B* ratio C_i (usually M_i), the energetic parameters a_i and b_i , the diet vector DC_{ij} , and the nonpredation mortality parameter d_i . In addition, as discussed earlier, it is necessary to enter an estimate of at least one of the species group biomass values to have a nonzero solution to the biomass equations. The observed apex predator at FFS which drives the system is the tiger shark, *Galeocerdo cuvieri*. However, in addition to the tiger shark biomass as a fixed input, biomass estimates for birds and monk seals were treated as fixed inputs since these estimates are based on visual censuses and are considered reliable.

Many of the estimates for input parameters are determined from field data collected at FFS. For some groups, however, data to estimate parameters were not available from FFS, or anywhere in the NWHI, so parameter estimates from the literature were used. This was almost exclusively true for the estimate of the nonpredatory mortality d_i . The d_i exclusive of fishery mortality used in a Gulf of Alaska simulator ranged from 0.019 to 0.029 per year (Livingston 1977)² so a mean value of $d_i = 0.024$ was used in ECOPATH in the absence of any other information.

Typically the value C_i was estimated as annual instantaneous natural mortality (M_i) in the absence of fishing mortality. In some instances only von Bertalanffy growth parameters were estimated from field work and then M_i was estimated from a regression equation proposed by Pauly (1980):

$$\log_{10} M_i = 0.0066 - 0.279 \log_{10} L_i + 0.6543 \log_{10} K_i + 0.4634 \log_{10} T_i$$

where L_i is the asymptotic maximum length (cm) of the stock, K_i the von Bertalanffy annual growth coefficient,

² Livingston P (1977) Numerical evaluation of marine biomasses in Gulf of Alaska (Evaluation of minimum sustainable biomasses of fisheries resources in the Gulf of Alaska using the Laevastu-Favorite bulk biomass model). Northwest and Alaska Fisheries Center, Natl Mar Fish Serv, NOAA, Seattle, WA 98112. Processed Report, 61 pp

and T_i the mean environmental temperature (°C) for the stock.

Little research has been done on trophic energetics of tropical stocks. Estimated food uptake for a temperate North Sea stock of cod, based on a study of stomach contents, suggests that the stock consumes an average of 0.75% of its body weight per day (Daan 1973). For faster growing fishes such as salmon, food consumption may be as high as 2.0% of its body weight per day (Laevastu and Larkins 1981). Consumption relative to net production, or ecological efficiency, has been examined for a number of stocks and found to range from 10 to 25% (Crisp 1975). Ecological efficiencies for three size groups of a Bermuda reef fish, *Epinephelus guttatus*, ranged from 15 to 25% (Menzel 1960).

In the absence of any energetics input to estimate a_i and b_i , the value of b_i used was 2.0 from Laevastu and Larkins (1981). Since the amount of food needed for the maintenance of a species group i is $b_i B_i$, $b_i = 2.0$ implies that the species group must annually consume twice its biomass for maintenance. The food required to support production (P_i) is $a_i P_i$. In the absence of any food requirement information, a value of $a_i = 5$ was used, which typically results in ecological efficiencies in the range of 10–25% for the model's *P/B* values.

Species Groups

Tiger Shark. The tiger shark is the predominant apex predator at FFS. The stomach contents of 27 tiger sharks indicate a diet vector consisting of 0.30 seabird, 0.01 tiger shark, 0.28 reef fish, 0.01 turtle, 0.08 monk seal, 0.14 lobster, 0.05 jack, 0.08 small pelagics, 0.03 reef shark, and 0.02 nearshore scombrids (DeCrosta 1981). Respirometry studies suggest that on the average tiger sharks consume about 4.5 times their weight per year (DeCrosta 1981). The tiger shark population at FFS is estimated at 504 individuals; the mean individual weight is 100 kg (DeCrosta 1981). These values result in a density of 42 kg/km² for tiger shark biomass over the 1,200 km² area at FFS.

Monk Seal. Another apex species is the Hawaiian monk seal. The diet of the monk seal is estimated to be 0.85 reef fish and 0.15 lobster and crab, and it is estimated that the monk seal must consume, on the average, 45 times their weight in food per year to support growth and maintenance (WG Gilmartin, personal communication 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812). The estimate of biomass for the seal population in the 1,200 km² region around FFS is 75,500 kg obtained from a visual census, which results in a density of 63 kg/km² (WG Gilmartin, personal communication).

Seabirds. Studies by the U.S. and Wildlife Service indicate that the following seabirds are abundant at FFS: sooty tern, *Sterna fuscata*; black noddy, *Anous tenuirostris*; brown noddy, *A. stolidus*; great frigatebird, *Fregata*

minor; red-footed booby, *Sula sula*; masked booby, *S. dactylatra*; wedgetailed shearwater, *Puffinus pacificus*; Laysan albatross, *Diomedea immutabilis*; and black-footed albatross, *D. niaripes*. An estimated peak population of 320,000 birds and a mean residence time of 6 months produce a mean annual seabird population estimated at 160,000 birds. Of this population, 25–50% of the birds (mean individual weight of 0.31 kg) feed in the 1,200 km² area around FFS (Harrison et al. 1983). Thus, the estimated mean density for seabirds is 15.4 kg/km². Their diet composition vector is 0.68 small pelagics, 0.15 reef fish, 0.10 jack, 0.02 nearshore scombrids, and 0.05 zooplankton, and they consume an average of 80 times their biomass annually (Harrison et al. 1983).

Reef Sharks. This is a group of nearshore warm water sharks other than the tiger shark. Based on observations and catches at FFS, this group includes the gray reef shark, *Carcharhinus amblyrhynchos*, the Galapagos shark, *C. galapagensis*, the small blacktip shark, *C. limbatus*, the sandbar shark, *C. milberti*, the dusky shark, *C. obscurus*, and the whitetip reef shark, *Triaenodon obesus*. They occur in greatest numbers in the deeper waters outside of the reef, but are also in the shallow waters of the inner reef. These sharks prey primarily on the smaller reef fishes, but their diet also includes pelagic fishes, bottom-dwelling fishes, stingrays, crustaceans, squids, and octopuses. Based on an analysis of stomach contents (DeCrosta 1981), we estimate their diet as: 0.90 reef fish, 0.05 lobster, and 0.05 jack. Mortality estimates are not available for reef sharks in the NWHI. However, Holden (1977) presents estimates of annual instantaneous natural mortality for a number of shark species. These estimates generate a range of annual natural mortality from 0.1 to 0.25. The midpoint of this range 0.175 was used as an estimate of reef shark natural mortality and as the estimate of the P/B ratio.

Sea Turtle. This species group consists of the green turtle. The diet of the green turtle is estimated at 0.90 benthic algae and 0.10 zooplankton (G. H. Balazs, personal communication 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812). The annual instantaneous mortality is estimated at 0.15 and the annual food requirement for growth and maintenance is estimated at 22 times the mean annual biomass (G. H. Balazs personal communication).

Small Pelagics. This group consists of small surface pelagic fishes and squid including flyingfish, Exocoetidae, opelu, *Decapterus* spp., akule, *Selar crumenophthalmus*, needlefish, Belonidae, and halfbeaks, Hemiramphidae. The bulk of the biomass for the group consists of akule, opelu, squid, and flyingfish. Based on a von Bertalanffy growth parameter of $L_{\infty} = 27$ cm and $k = 0.215$ for akule in Hawaii (Kawamoto 1973), $M = 0.65$ was es-

timated. The growth parameters for opelu in Hawaii are estimated at $L_{\infty} = 35$ cm and $k = 0.82$ (Yamaguchi 1953) resulting in an estimate of $M = 1.50$. An average value of $M = 1.1$ is used at the P/B ratio. The flyingfish, squid, akule, and opelu feed almost exclusively on zooplankton.

Jacks (Carangids and Large Carnivores). This is a group of active, fast-swimming carnivores including the white ulua, *Caranx ignobilis*; omilu, *C. melampygus*; ulua, *Carangoides ferdau*; and barracuda, *Sphyrna barracuda*. This group is found both within the reef and nearshore regions. Based on an analysis of stomach contents (Sudekum 1983), it is estimated that their diet is 0.80 reef fish, 0.12 lobster and crab, and 0.08 small pelagics. Based on estimated growth parameter for *Caranx melampygus* of $L_{\infty} = 91.7$ cm, $k = 0.22$ (Sudekum 1983), M is estimated as 0.47 and this is used as the P/B estimate.

Reef Fishes (Reef Fishes and Octopuses). This group consists primarily of the coral reef fishes, excluding the snappers, groupers, and carangids. Their habitat ranges from the surge zone down to depths of 55 m (30 fathoms).

Based on analysis of stomach contents from reef fishes collected at FFS, the diet is estimated at 0.17 zooplankton, 0.248 benthic algae, 0.459 heterotrophic benthos, and 0.123 reef fish (J. D. Parrish, personal communication 1981. Hawaii Cooperative Fishery Research Unit, University of Hawaii, Honolulu, HI 96822). Typically, members of this group have a relatively high natural mortality. For the kumu, *Parupeneus porphyreus*, the growth parameters are estimated at $L_{\infty} = 49$ cm and $k = 0.54$ (Moffitt 1979) which yields an estimate of $M = 1.0$. The butterflyfish, *Chaetodon miliaria* has growth parameters $L_{\infty} = 12.7$ cm and $k = 1.13$ (Ralston 1976) which yields an estimate of $M = 2.3$. Natural mortality estimates for six reef fish species from the Families Mugilidae, Mullidae, Blennidae, and Balistidae range from 0.31 to 2.60 (Pauly 1980). The value of $M = 1.5$ is taken as a mean for the reef fishes group and is used as the P/B estimate.

Lobsters and Crabs. This group includes the spiny lobsters, *Panulirus marginatus* and *P. penicillatus*, the slipper lobster, *Scyllarides squammosus*, and various crabs including the kona crab, *Ranina ranina*. The M for *P. marginatus* at FFS has been estimated from tagging studies as 0.32 for males and 0.71 for females (MacDonald 1984). An average value of $M = 0.52$ is taken as the P/B estimate for this group. The diet of this group is 0.98 heterotrophic benthos and 0.02 zooplankton. Production and consumption rates were estimated for the spiny lobster, *P. homarus*, on a reef off South Africa (Berry and Smale 1980). They estimated the P/B ratio as 0.42, the production to consumption ratio as 0.45, and the consumption to biomass ratio as 9.5. To approximate these consumption and efficiency rates, the values of $a = 2$ and $b = 12$ were used in the food requirement equation.

Bottom Fishes. This is a commercially important group of food fishes including opakapaka, *Pristipomoides fila-*

Table 1. Diet of species groups at French Frigate Shoals as a percentage of total diet

<i>Birds</i>		<i>Monk seals</i>	
Small pelagics	68	Reef fishes	85
Jacks	10	Lobsters and crabs	15
Reef fishes	15	<i>Reef sharks</i>	
Nearshore scombrids	2	Small pelagics	5
Zooplankton	5	Reef fishes	90
<i>Tiger sharks</i>		Lobsters and crabs	5
Birds	30	<i>Turtles</i>	
Monk seals	8	Zooplankton	10
Tiger shark	1	Benthic algae	90
Reef sharks	3	<i>Jacks</i>	
Turtles	1	Small pelagics	8
Small pelagics	8	Reef fishes	80
Jacks	5	Lobsters and crabs	12
Reef fishes	28	<i>Lobsters and crabs</i>	
Lobsters and crabs	14	Heterotrophic benthos	98
Nearshore scombrids	2	Zooplankton	2
<i>Small pelagics</i>		<i>Nearshore scombrids</i>	
Small pelagics	6	Small pelagics	48
Zooplankton	94	Reef fishes	8
<i>Reef fishes</i>		Bottom fishes	8
Reef fishes	12.3	Zooplankton	36
Zooplankton	17	<i>Heterotrophic benthos</i>	
Heterotrophic benthos	45.9	Heterotrophic benthos	15
Benthic algae	24.8	Benthic algae	85
<i>Bottom fishes</i>		<i>Zooplankton</i>	
Small pelagics	12.5	Phytoplankton	91
Reef fishes	46.9	Benthic algae	9
Lobsters and crabs	1.8		
Bottom fishes	2.6		
Zooplankton	10.4		
Heterotrophic benthos	25.8		

mentosus; kalekale, *P. sieboldii*; gindai, *P. zonatus*; onaga, *Etelis coruscans*; ehu, *E. carbunculus*; uku, *Aprion virescens*; hapuupuu, *Epinephelus quernus*; kahala, *S. dumerili*; and butaguchi, *Pseudocaranx dentex*. Fishermen report that these bottom fishes are caught predominantly between 75 and 220 m (40 and 120 fathoms). They are all active, carnivorous fishes which prey on small fish, shrimp, and other crustaceans, and macrozooplankton.

Stomach contents have been examined for the predominant species in this multispecies complex, and mean diet vectors for this group are estimated to be 0.125 small pelagics, 0.469 reef fish, 0.018 lobster and crab, 0.026 bottom fish, 0.104 zooplankton, and 0.258 heterotrophic benthos (S. Ralston, personal communication January 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812).

A detailed analysis of growth and mortality for the opakapaka provided an estimate of $M=0.32$ (Ralston 1981) which is used for the bottom fish species group P/B estimate.

Nearshore Scombrids (Nearshore Scombrids and Other Carnivores). This is a group of commercially important tunas and tunalike fishes, including skipjack tuna, *Katsuwonus pelamis*; kawakawa, *Euthynnus affinis*; yellowfin tuna, *Thunnus albacares*; wahoo, *Acanthocybium solandri*; dolphin, *Coryphaena hippurus*; and the rainbow runner, *Elagatis bipinnulata*. The members of this group are all pelagic or nearshore pelagic species which largely occupy the surface waters. The kawakawa is an inshore pelagic fish and has been observed foraging over the reefs in shallow water at FFS. These fishes are all active, fast-swimming carnivores, and are opportunistic feeders. Their diets have been observed to consist predominantly of small fish, juvenile fish (tunas, snappers, carangids), squid, stomatopods, and megalops (Yoshida 1979). Trolling from the RV *Townsend Cromwell* around FFS produced 277 scombrids in 366 line-hours. The relative biomass catch vector for the 277 scombrids was 0.58 kawakawa, 0.27 wahoo, 0.12 yellowfin tuna, and 0.03 skipjack tuna. The diet for each of these fishes caught around Oahu, based on analysis of stomach contents, is presented in Tester and Nakamura (1957). An average diet vector weight by the relative biomass of each of these fishes yields species group diet vectors of 0.91 for small pelagics and 0.09 for zooplankton.

Preliminary estimated growth parameters for kawakawa are $L_{\infty}=118$ cm and $k=0.42$ (J. H. Uchiyama, personal communication August 1982. Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96812). The estimated $M=0.66$ from these growth estimates served the estimate of the P/B ratio.

Zooplankton. This group includes fish larvae. The P/B ratio for zooplankton is size specific ranging from 18 to 91 (Crisp 1975). The geometric mean for this range is 40 and is the value taken for the P/B ratio. The zooplankton diet in 0.91 phytoplankton and 0.01 benthic algae.

Phytoplankton. Because the model is predator driven, the only parameter needed for phytoplankton is the P/B ratio which is estimated at 70 (Parsons and Takahashi 1973; Crisp 1975).

Heterotrophic Benthos. This group consists of all the benthic invertebrates. The P/B ratio for this species group is estimated at 3.0. The diet vector is 0.15 heterotrophic benthos and 0.85 benthic algae (Crisp 1975).

Benthic Algae. This group consists of fleshy algae, turf algae, and corals. The only parameter required for this species group is the P/B ratio which is estimated at 12.5 (Odum and Odum 1955).

A summary of all the input parameter estimates is provided in Tables 1 and 2.

Table 2. Input parameters for the tropical ecosystem biomass budget model

Species group	Production/ biomass (C_i)	Food for production biomass (a_i)	Food for maintenance biomass (b_i)	Nonpredatory mortality (d_i)	Biomass for apex species (B_i)
Tiger shark	0.25	10	2	—	42.0
Birds	5.4	15	2	—	15.0
Monk seals	3.0	15	2	—	63.0
Reef sharks	0.18	10	2	0.024	—
Turtles	0.15	10	2	0.024	—
Small pelagics	1.10	5	2	0.024	—
Jacks	0.47	5	2	0.024	—
Reef fishes	1.5	5	2	0.024	—
Lobsters and crabs	0.52	12	2	0.024	—
Bottom fishes	0.32	5	2	0.024	—
Nearshore scombrids	0.66	5	2	0.024	—
Zooplankton	40	7	2	0.024	—
Phytoplankton	70	—	—	0.024	—
Heterotrophic benthos	3.0	5	2	0.024	—
Benthic algae	12.5	—	—	0.024	—

Table 3. Mean annual biomass and annual production estimate from tropical ecosystem biomass budget model

Species group	Biomass per habitat area (kg/km^2)	Annual production per habitat area (kg/km^2)	Habitat area (km^2)	Ecological efficiency (production/ consumption)	Consumption/ biomass
Tiger shark	42	11	1,200.00	0.06	4.5
Monk seals	63	189	1,200.00	0.06	47.0
Birds	15	81	1,200.00	0.07	83.0
Reef sharks	38	7	1,200.00	0.05	3.8
Turtles	15	2	1,200.00	0.04	3.5
Small pelagics	1,836	2,020	1,200.00	0.15	7.5
Jacks	411	144	1,200.00	0.09	3.8
Reef fishes	23,941	35,912	700.00	0.16	9.5
Lobsters and crabs	2,311	1,202	700.00	0.06	8.2
Bottom fishes	377	121	300.00	0.09	3.6
Nearshore fishes	60	40	900.00	0.12	5.3
Zooplankton	899	35,944	1,200.00	0.14	282.0
Phytoplankton	3,295	230,679	1,200.00	0.00	0.0
Heterotrophic benthos	289,181	867,543	700.00	0.19	17.0
Benthic algae	342,598	4,282,471	700.00	0.00	0.0
Total biomass (kg/km^2)	390,604				
Total production (kg/km^2)		3,294,960			

Results³

The estimates of mean annual biomass and annual production for the species groups at FFS generated by the ECOPATH model are provided in Table 3, a food web based on the diet vector is given in Table 4, and a simplified ecosystem food web is schematically presented in Fig. 1. As might be expected, the reef fishes represent the largest biomass after the primary producers and heterotrophic benthos. The estimated mean reef fish biomass was 15,000 kg/km^2 over 700 km^2 area of reef fish habitat at FFS (Okamoto and Kanenaka 1983) which compares

with the model estimate of 23,941 kg/km^2 (Table 3). Production of reef fishes from a reef in Bermuda was estimated at 22,000 $\text{kg}/\text{km}^2/\text{year}$ (Bardach 1959) compared with the model's estimate of 35,912 $\text{kg}/\text{km}^2/\text{year}$ (Table 3).

Although we do not have any estimates of density for deep bottom fishes to check the model value, an estimate for maximum sustainable yield (MSY) of bottom fishes at Penguin Bank in the Hawaiian Archipelago has been obtained based on the Schaefer surplus production model. The estimated MSY, which is a lower bound because it does not take into account a recreational fishery, is 272 $\text{kg}/\text{nautical mile}$ (nmi) of 183-m (100-fathom) isobath

³ Portions of this section also appear in Grigg and Tanoue (1984)

Table 4. Predator consumption vector (kg/km²) based on a habitat area 1,200 km²

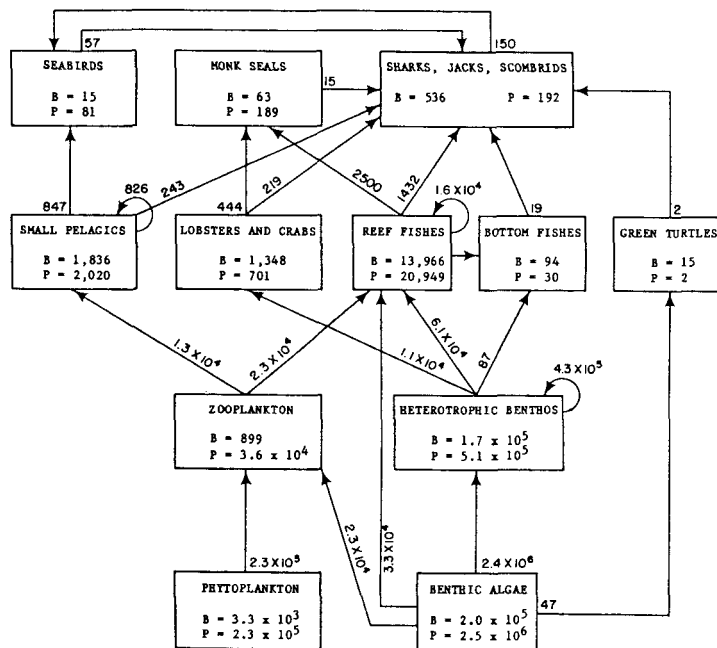
<i>Birds</i>		<i>Monk seals</i>	
Small pelagic	847	Reef fishes	2,517
Jacks	125	Lobsters and crabs	444
Reef fishes	187	<i>Reef sharks</i>	
Nearshore scombrids	25	Pelagics	7
Zooplankton	62	Reef fishes	127
<i>Tiger sharks</i>		Lobsters and crabs	7
Birds	57	<i>Turtles</i>	
Monk seals	15	Zooplankton	5
Tiger shark	2	Benthic algae	47
Reef sharks	6	<i>Jacks</i>	
Turtles	2	Small pelagics	123
Small pelagics	15	Reef fishes	1,233
Jacks	10	Lobsters and crabs	185
Reef fishes	53	<i>Lobster and crabs</i>	
Lobsters and crabs	27	Heterotrophic benthos	10,875
Nearshore scombrids	4	Zooplankton	233
<i>Small pelagics</i>		<i>Nearshore scombrids</i>	
Small pelagics	826	Small pelagics	115
Zooplankton	12,943	Reef fishes	19
<i>Reef fishes</i>		Bottom fishes	19
Reef fishes	16,319	Zooplankton	86
Zooplankton	22,555	<i>Heterotrophic benthos</i>	
Heterotrophic benthos	60,899	Heterotrophic benthos	4.3×10^5
Benthic algae	32,904	Benthic algae	2.4×10^6
<i>Bottom fishes</i>		<i>Zooplankton</i>	
Small pelagics	43	Zooplankton	
Reef fishes	160	Phytoplankton	2.3×10^5
Lobsters and crabs	6	Benthic algae	2.3×10^4
Bottom fishes	9		
Zooplankton	36		
Heterotrophic benthos	87		

(Ralston and Polovina 1982). Using Gulland's formula $MSY = 1/2 M B_0$, with the value $M = 0.32$ used in the model and the estimate of $B_0 = 387 \text{ kg/km}^2$ produced by the model, an estimated MSY of 62 kg/km^2 is obtained. Since the bottom fish habitat is approximately 300 km^2 and the length of the 183-m (100-fathom) contour at FFS is 65 nmi, the estimated MSY of 62 kg/km^2 can be converted to an MSY of 286 kg/nmi of 183-m (100-fathom) isobath which is in close agreement with the Penguin Bank value.

An estimate of the biomass of reef shark populations at FFS can be determined from population and mean weight estimates from DeCrosta (1981). The results of intensive fishing at FFS provide an estimate of the Galapagos shark population at 703 individuals and the gray reef shark population at 826 individuals. With these population estimates and estimated mean weight for the Galapagos shark of 60, and 20 kg for gray reef shark, the estimated biomass for the reef shark population is 48 kg/km^2 . This compares with the model estimate of 38 kg/km^2 .

Hirota et al. (1980) estimated the primary production in the nearshore region of the NWHI at 900 metric tons (MT) biomass/km²/year. The model estimates that $234 \text{ MT/km}^2/\text{year}$ of phytoplankton production is needed to support the reef and nearshore ecosystem.

Net benthic primary production over a 700 km^2 habitat at FFS has been estimated to be $4.1 \times 10^6 \text{ kg/km}^2/\text{year}$ (see Atkinson and Grigg 1984a). The ECOPATH model estimates the net benthic algal and coral primary production necessary to support the ecosystem at $4.3 \times 10^6 \text{ kg/km}^2/\text{year}$ (Table 3).

**Fig. 1.** Biomass budget schematic for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of kg/km^2 based on a habitat area of $1,200 \text{ km}^2$

The biomass of prey consumed by each predator is presented in Table 4. It can be determined from Fig. 1 and Table 4 that monk seals, for example, consume most of the lobster and crab production but that lobsters and crabs still constitute a small portion of the monk seal diet compared with their consumption of reef fishes.

Discussion

A schematic of the major prey-predator pathways for the ecosystem at FFS together with the model's estimate of mean annual biomass and annual production is presented in Fig. 1. The estimates of mean annual biomass and annual production in Fig. 1 are all normalized over a total habitat of 1,200 km² to facilitate estimation of trophic efficiencies. Hence in Table 3 net benthic primary production, for example, is 4.3×10^6 kg/km²/year over its habitat of 700 km² while when this value is adjusted or normalized to the total 1,200 km² habitat for Fig. 1 it becomes 2.5×10^6 kg/km²/year. From Fig. 1 the ratio of production from the zooplankton and heterotrophic benthos to primary production is 0.20. The ratio of production from the third level in Fig. 1, to zooplankton and heterotrophic benthos is 0.04. The ratio of production from the top level to that from the third level of Fig. 1 is 0.02. At first glance it would appear that these last two ratios do not conform to the usual range of ecological efficiencies which are in the order of 0.1 to 0.25 for these organisms (Steele 1974; Crisp 1975). However, the reason the values computed from Fig. 1 are low is that the levels in Fig. 1 do not represent single trophic levels as indicated by the arrows originating and ending in the same box for the small pelagics, reef fishes, and heterotrophic benthos species. If only the net production leaving one level and going to the level above is used as the denominator to compute the previous ratios, then the ratio of production at the second level to primary production is still 0.20, whereas the ratio of production from the third level to net production from the second level becomes 0.20, and the ratio of production from the top level to the net production from the second level becomes 0.08.

The high internal predation in the reef fishes group and the heterotrophic benthos group which is required by the diet composition inputs suggests that each of these groups probably represents two trophic levels. Under the assumption of two trophic levels within the reef fishes and heterotrophic benthos groups, the schematic food web in Fig. 1 indicates an ecosystem composed of six trophic levels. To go from the estimate of net annual primary production of 2.73×10^6 kg/km² to the estimated annual production for the top predator of 462 kg/km² with six trophic levels requires a mean ecological efficiency of 17.6%.

Figure 1 reveals that only 19% of the reef fishes production and only 22% of the heterotrophic benthic production are consumed by predators outside these groups. This high proportion of internal predation is one reason fishery yields for the coral reef ecosystem are typically

Table 5. Net benthic primary production as a function of ecotrophic efficiency

Ecotrophic efficiency	Net benthic primary production ($\times 10^6$ kg/km ² /year)
1.00	3.3
0.95	4.2
0.90	5.5
0.85	7.3
0.80	9.9
0.75	13.7
0.70	19.4
0.65	28.0
0.60	41.8
0.55	64.7
0.50	104.1

low relative to the high rate of primary production. It is also one reason there can be substantial variations in fishery yields due to the harvest strategy. For example, if harvests were limited to tunas, sharks, and jacks, the yield would not exceed 0.2 MT/km²/year. However, if all the top predators are removed, a sustainable yield from the next lower level of about 6 MT/km²/year which was going to the top predators can be harvested. Most of this yield comes from the reef habitat of 700 km² rather than the entire 1,200 km² habitat so the yield is actually about 11 MT/km²/year. Although it is not known how much of this yield could actually be harvested with fishing gear, it is evident that, in theory at least, even this yield is not the MSY yield from this ecosystem since it could be exceeded if a harvesting strategy were employed to fish down the piscivorous reef fishes to reduce the internal predation in the reef fishes group. Sustainable yields have been reported for coral reef fisheries covering the range 0.1–18 MT/km²/year (Marten and Polovina 1982).

Ecotrophic efficiency is defined by Ricker (1969) as the fraction of a prey species' annual production that is consumed by predators. A range of 0.66 to 0.75 is suggested as a range of the average ecotrophic efficiency in the marine ecosystems (Ricker 1969). Given our coral reef ecosystem which is estimated to consist of six trophic levels and an ecological efficiency of 0.17 and annual production at the top level of 462 kg/km²/year, the level of net benthic primary production necessary to sustain the production at the top level can be estimated as a function of ecotrophic efficiency (ee) as follows:

$$\text{Net benthic primary production} = 462 / [(0.17)(ee)]^5.$$

The net benthic primary production computed as a function of ecotrophic efficiency is given in Table 5. The net benthic primary production produced from the ECO-PATH model of 4.3×10^6 kg/km²/year corresponds to an ecosystem with an ecotrophic efficiency of 0.95 which suggests a very high level of predation mortality in the FFS ecosystem. If, for example, the ecotrophic efficiency for the ecosystem at FFS were only 0.5, then the net benthic primary production needed to drive the system would be 104×10^6 kg/km²/year which is 25 times greater

than actual field measures (see Table 5 and Parts II and III of this paper).

Simple sensitivity analysis was performed on the input parameters (Polovina 1984). The estimate of mean annual biomass and total ecosystem biomass is relatively insensitive to changes in the energetics input parameters a and b , the nonpredation parameter d , and the apex B 's. For example, on the average, an increase in a , the energetics parameter for growth, by 25% for a single species group only results in a 1.8% change in the average mean annual biomass for that species group and a 2.8% change in total biomass. However, the mean annual biomass is quite sensitive to changes in the P/B value. A 25% increase in the P/B value for a specific species group results in an average of almost a 22% change in the average mean annual biomass for that species group, and a 25% decrease in the P/B value for a specific species group results in an average of almost a 40% change in the average mean annual biomass for that species group. Fortunately, the sensitivity of the biomass estimate to changes in the P/B ratio is restricted only to the species group for which the parameter is being perturbed. The mean change in total ecosystem biomass is usually less than 8% for up to a 25% increase or decrease in the P/B parameter.

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