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ECOPATH - AN ECOSYSTEM MODEL APPLIED TO FRENCH FRIGATE SHOALS

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ABSTRACT

A simple model to estimate mean annual biomass, production, and consumption for components of an ecosystem is presented. The approach partitions the ecosystem into groups of similar species and requires estimates for these species groups of production to biomass, diet, and food consumption.

The approach was applied to an ecosystem at French Frigate Shoals in the Northwestern Hawaiian Islands where field work provided estimates of some of the input parameters as well as estimates of mean annual biomass and production, for some of the species groups modeled, to validate the estimates generated by the model. Simplified, the model depicts an ecosystem composed of four major trophic levels. The primary pro duction consists of benthic algae and phytoplankton, the second level is composed of zooplankton and heterotrophic benthos, the third level consists of reef fishes, lobsters, crabs, bottomfishes, and small pelagic species including squid, flyingfish, akule, and opelu, and the top trophic level is composed of sharks, jacks, tunas, seabirds, and monk seals.

Simple sensitivity analysis was performed to measure the sensitivity of the estimates of the model to errors or uncertainties in the input parameters.

biomass
ecosystem model
French Frigate Shoals
Northwestern Hawaiian Islands
tropical marine ecosystem

INTRODUCTION

The investigation of the resources of the Northwestern Hawaiian Islands (NWHI) is a multidisciplinary program with researchers from the National Marine Fisheries Service (NMFS), University of Hawaii Sea Grant College Program, U.S. Fish and Wildlife Service (FWS), and Hawaii Division of Aquatic Resources (Shomura, 1980) conducting studies on specific species which are important components of the marine ecosystem in the area. An ecosystem modeling project evolved out of a desire of many of the researchers to bring together common elements from the various research projects to form a quantitative picture of the entire marine ecosystem. Initially several existing ecosystem models were considered for application to the NWHI ecosystem, particularly the Prognostic Bulk Biomass (PROBUB) model (Laevastu and Larkins, 1981) developed for the Bering Sea and the Andersen and Ursin (1977) North Sea model. However, the models require a level of understanding which has not yet been achieved for a tropical ecosystem. Similar sentiments are expressed by Larkin and Gazey (1981):

> 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 waters. 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 experiment 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.
>
> The moral, it seems, is to simplify....

Although neither the PROBUB model nor the Andersen and Ursin model seemed appropriate for modeling the NWHI ecosystem, given the current level of knowledge, much of the philosophy and approach, particularly in the PROBUB model, was applicable to the NWHI ecosystem. Hence, a simple ecosystem model, termed the ECOPATH model was developed.

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 with similar diet and life history characteristics and which has a common physical habitat. Computationally and conceptually the model is very simple. The mean annual biomass estimates are obtained from the solution of a system of simultaneous linear equations.

THE ECOPATH MODEL

The objective of the ECOPATH model is to estimate the mean annual biomass for each species group and produce a biomass budget for the ecosystem, all under the assumption of equilibrium conditions. Such conditions are defined to 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 a period of 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) investigated the production to biomass (P:B) ratio for a cohort over a range of mortality and growth functions. For a number of mortality and growth 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 with 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:

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

Under the assumption that the Z_i's are all equal to say Z, then total species group production can be expressed as P = ZB, where B is the mean annual species group biomass.

Allen (1971) also showed that when growth in weight is linear for a range of mortality functions, the P:B ratio is equal to the reciprocal of the mean age. For a number of other growth and mortality functions the ratio of cohort P:B can be the reciprocal of the mean lifespan. Thus, for a range of growth and mortality functions, total species group production can be expressed as P = CB, where B is the mean annual species group biomass and C is a parameter. In the subsequent application of the ECOPATH model to an ecosystem where there is very little fishing mortality, the P:B ratio for fishes and crustaceans is taken as the annual instantaneous natural mortality (M), whereas the P:B ratio for primary and secondary producers whose growth is more likely to be linear rather than the von Bertalanffy is estimated as the reciprocal of the mean age.

Predation Mortality

Predation mortality is the fraction of the biomass of a species group which is consumed by all predators. The ECOPATH model computes this mortality in the same fashion as the PROBUB model. Two types of information are needed. First, the food web or predator-prey relationships must be defined. A diet composition matrix DC_{ij} must be specified where an entry DC_{ij} from this matrix refers to the proportion (by weight) of prey j in the diet of predator i. The primary source of this information is the analysis of stomach contents. The second type of information needed to ascertain predation mortality is the food requirements of the predator. The PROBUB model expresses the total food required (R_i) by a species group (i) as:

$$R_i = b_i B_i + a_i P_i$$

where

B_i is the annual mean species biomass, P_i is the annual production of species group i, and a_i and b_i are parameters to be estimated from energetics studies. The component b_i B_i is the food required to maintain the biomass B_i, and the component a_i P_i is the food required to support the biomass production P_i (Laevastu and Larkins, 1981).

In the ECOPATH model the production of species group i is $P_i = C_i B_i$, so the food required for species group B_i is

$$R_i = b_i B_i + a_i P_i$$

$$= b_i B_i + a_i C_i B_i$$

$$= (b_i + a_i C_i)\ B_i\ .$$

Thus the amount of species group j consumed by predator species group i is given as:

$$R_i DC_{ij} = (b_i + a_i C_i)\ B_i DC_{ij}\ .$$

Nonpredation Mortality

All mortality attributable to causes other than predation such as fishing mortality, spawning mortality, and disease is considered together under the category of nonpredation mortality. In the ECOPATH model this is determined as a fraction (d_i) of the mean annual biomass B_i.

For n species groups the biomass budget equation (1) becomes a system of n simultaneous equations as follows:

$$C_1 B_1 - \sum_{k=1}^{n} (b_k + a_k C_k)\ B_k DC_{k1} - d_1 B_1 = 0$$

$$\vdots \qquad \vdots \qquad \vdots \qquad \vdots$$

$$C_i B_i - \sum_{k=1}^{n} (b_k + a_k C_k)\ B_k DC_{ki} - d_i B_i = 0$$

$$\vdots \qquad \vdots \qquad \vdots \qquad \vdots$$

$$C_n B_n - \sum_{k=1}^{n} (b_k + a_k C_k)\ B_k DC_{kn} - d_n B_n = 0\ .$$

With input estimates for parameters C_i (usually M_i), b_i, a_i, DC_{ij}, and d for all i and j, this system of equations is a system of n simultaneous equations linear in the unknown B_i's. This system of equations can be expressed in matrix form as AB = 0, where A is an n x n matrix of coefficient, B is an n-dimensional vector of mean annual species group biomass, and 0 is the null vector. Typically the matrix A will be of full rank and will only have a trivial solution:

$B_i = 0$ for all i .

It is therefore necessary to provide an estimate of at least one of the species group biomass B_i before there exists a unique nontrivial set of B_i's which solves the biomass budget system.

The following is an application of the ECOPATH model to obtain estimates of biomass and production for the component of the marine ecosystem at French Frigate Shoals (FFS) in the NWHI.

FRENCH FRIGATE SHOALS

French Frigate Shoals is located at lat. 24°50'N, long. 166° 10'W, approximately midway along the chain of islands and banks comprising the NWHI. It is described by Bakus (1979) as a "crescent-shaped reef on a circular submerged platform about 18 mi in diameter (almost an atoll). The shoals form a large lagoon, bordered on one side by 12 sand islets (total area 56 acres) with a small rock pinnacle (La Perouse Pinnacle, ca. 1 acre) near the center of the platform. The highest elevation is generally 5 ft above sea level except for La Perouse Pinnacle (135 ft high)." The area is an important nesting ground for the green turtle, Chelonia mydas, various species of seabirds, and the Hawaiian monk seal, Monachus schauinslandi.

The ecosystem of interest to the model 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 km^2. The reef habitat in this region defined as the area from shoreline to 55 m (0 to 30 fathoms), consists of approximately 700 km^2.

Fifteen species groups have been identified as the major component of the ecosystem within the region down to the 365 m depth around FFS. These species groups which will subsequently be described in detail are seabirds, monk seals, tiger sharks, reef sharks, sea turtles, small pelagics, jacks, reef fishes, lobsters and crabs, bottomfishes, 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 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 logical apex predator to drive the system is the tiger shark, Galeocerdo cuviere. However, in addition to the tiger shark biomass as a fixed input, biomass estimates for birds and monk seals will be treated as fixed inputs since they are based on visual censuses and are considered reliable.

Many of the estimates for input parameters are determined from field data collected at FFS. In some cases, however, data to estimate parameters were not available from FFS, or anywhere in the NWHI, so estimates from the literature were used. This was almost exclusively the case 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 (Livingston, 1977); thus a mean value of $d_i = 0.024$ was used in the ECOPATH model 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) as:

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

where

L_i is the asymptotic maximum length (cm) of the stock, K_i the von Bertalanffy annual growth coefficient, and T_i the mean environmental temperature (°C) for the stock.

There is a shortage of energetics work on 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 percent of its body weight per day (Daan, 1973). For faster-growing fishes such as salmon, food consumption may be as high as 2.0 percent 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 percent (Crisp, 1975). Ecological efficiencies for three size groups of a Bermuda reef fish, *Epinephelus guttatus*, ranged from 15 to 25 percent (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 tbe 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, with the range of P:B values used in the model, results in ecological efficiencies and total consumption rates which are in agreement with the previously mentioned values.

Seabirds

Studies by the Fish and Wildlife Service indicate that the following seabirds are found in abundance 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*; wedge-tailed shearwater, *Puffinus pacificus*; Laysan albatross, *Diomedea immutabilis*; and black-footed albatross, *D. nigripes*. 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 to 50 percent of the birds (mean individual weight of 0.31 kg) feed in the 1,200 km^2 area around FFS (Harrison et al., 1983). Thus, the estimated mean density for seabirds is 15.4 kg/km^2. Their diet composition vector is 0.68 small pelagics, 0.15 reef fishes, 0.10 jacks, 0.02 nearshore scombrids, and 0.05 zooplankton, and they consume an average of 80 times their biomass annually (Harrison et al., 1983).

Monk Seal

The second apex species is the Hawaiian monk seal. The estimate of biomass for the seal population in the 1,200 km^2 region around FFS, obtained from a visual census, is 75,500 kg, which results in a density of 63 kg/km^2 (W.G. Gilmartin, 1982: personal communication). The diet is estimated to consist of 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 its weight in food per year to support growth and maintenance (W.G. Gilmartin, 1982: personal communication).

Tiger Shark

The tiger shark is the predominant apex predator at FFS. The stomach contents of 27 tiger shark suggest a diet vector consisting of 0.30 seabirds, 0.01 tiger shark, 0.28 reef fish, 0.01 turtles, 0.08 monk seal, 0.14 lobsters, 0.05 jacks, 0.08 small pelagics, 0.03 reef sharks, and 0.02 nearshore scombrids (DeCrosta, 1981). The tiger shark population at FFS is estimated at 504 individuals with a mean individual weight of 100 kg (DeCrosta, 1981). These values result in a density of 42 kg/km^2 for tiger shark biomass over the 1,200 km^2 area at FFS.

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 also work their way into 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, squid, and octopuses. Based on an analysis of stomach contents (DeCrosta, 1981), their diet is estimated as 0.90 reef fishes, 0.05 lobsters, and 0.05

jacks. Mortality estimates are not available for reef sharks in the NWHI. However, Holden (1977) presented 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 Hawaiian green sea turtle, Chelonia mydas. The diet of the green turtle is estimated at 0.90 benthic algae and 0.10 zooplankton (G.H. Balazs, 1982: personal communication). 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, 1982: 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_∞ = 27 cm and k = 0.215 for akule in Hawaii (Kawamoto, 1973), M = 0.65 was estimated. The growth parameters for opelu in Hawaii are estimated at L_∞ = 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 as 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, Sphyraena barracuda. This group is found both in the reef and nearshore regions. Based on an analysis of stomach contents (Sudekum, 1981) 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 Seriola dumerili of L_∞ = 149 cm and k = 0.31 (J.H. Uchiyama, 1982: personal communication), M is estimated as 0.52 and this is used as the P:B estimate.

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 fishes (J.D. Parrish, 1981: personal communication). Typically, members of this group have a relatively high natural mortality. For the kumu, *Parupeneus porphyreus*, the growth parameters are estimated at L_∞ = 49 cm and k = 0.54 (Moffitt, 1979) which yields an estimate of M = 1.0. The butterflyfish, *Chaetodon miliaris*, has growth parameters L_∞ = 12.7 cm and k = 1.13 (Ralston, 1976) which yields an estimate of M = 2.3. As a rather arbitrary average the value of M = 1.5 was used as the P:B estimate for this large reef fish species group.

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 the spiny lobster, *P. marginatus*, at FFS has been estimated from tagging studies as 0.32 for males and 0.71 for females (C. MacDonald, 1982: personal communication). An average value of M = 0.52 is taken as the P:B estimate for this group. The diet of this group is 100 percent heterotrophic benthos. Production and consumption rates were estimated for the spiny lobster, *P. homarus*, on a reef off South Africa by 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.

Bottomfishes

This is a commercially important group of food fishes including opakapaka, *Pristipomoides filamentosus*; kalekale, *P. sieboldii*; gindai, *P. zonatus*; onaga, *Etelis coruscans*; ehu, *E. carbunculus*; uku, *Aprion virescens*; hapuupuu, *Epinephelus quernus*; kahala, *Seriola dumerili*, and butaguchi, *Pseudocaranx dentex*. Fishermen report that these bottomfishes are caught predominantly between depths of 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 were examined for the predominant species lex, and a mean diet vector for this group is estimated as 0.125 small pelagics, 0.469 reef fishes, 0.018 lobsters and crabs 0.026 bottomfishes, 0.104 zooplankton, and 0.258 heterotrophic benthos (S.V.D. Ralston, 1982: personal communication).

A detailed analysis of growth and mortality for the opakapaka, provided an estimate of M = 0.32 (Ralston, 1981). This mortality estimate is used for the bottomfish species group P:B estimate.

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, an inshore pelagic fish, 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 yielded 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 a species group diet vector of 0.91 small pelagics and 0.09 zooplankton.

Preliminary estimates of growth parameters for kawakawa are L_∞ = 58.0 cm and k = 0.42 (J.H. Uchiyama, 1982: personal communication). The estimated M = 0.66 from these growth estimates served as the estimate of the P:B ratio.

Zooplankton (including fish larvae)

The P:B ratio for zooplankton is size-specific, ranging from 18 to 91 (J. Hirota, 1982: personal communication). The geometric mean for this range is 40, the value used for the P:B ratio. The zooplankton diet is 0.95 phytoplankton and 0.05 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 (J. Hirota, 1982: personal communication).

Heterotrophic Benthos

This group consists of all the invertebrates, bacteria, and protozoans living on the benthic substrate. The P:B ratio is estimated at 3.0 (J. Hirota, 1982: personal communication). The diet is 0.15 heterotrophic benthos and 0.85 benthic algae.

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 (J. Hirota, 1982: personal communication).

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

RESULTS AND DISCUSSION

The ECOPATH estimates of mean annual biomass and annual production for the species group at FFS are provided in Table 3 and a simplified ecosystem food web is schematically presented in Figure 1. As might be expected the reef fishes group is the largest in terms of biomass after the primary producers and heterotrophic benthos. The biomass and production for this group of reef fishes can be checked from current field studies on reef habitat and reef transects at FFS (H. Okamoto and Hobson, 1979: personal communication; R.W. Grigg and J.D. Parrish, 1979: personal communication). These studies suggest that 12 percent of the area from the 0 to 18 m (0 to 10 fathoms) depth is rich in reef fishes, 17 percent is moderate, and 71 percent is sparse. It is assumed that the area in depths from 18 to 55 m (10 to 30 fathoms) is entirely a sparse habitat. A total of 36 transects produced estimates of fish biomass as follows: for a rich habitat 163,666 kg/km^2; for a moderate habitat 16,815 kg/km^2; and for a sparse habitat 1,569.4 kg/km^2. This gives an average density of reef fishea at FFS of 15,000 kg/km^2 which compares with the model estimate of 24,163 kg/km^2 over the reef habitat. Production of fishes from a reef in Bermuda was estimated at 22,000 kg/km^2/yr (Bardach, 1959) which is also comparable with the model estimate of 36,244 kg/km^2/yr (Table 3).

Although an estimate of density for bottomfishes is not available to check the model value, an estimate for maximum sustainable yield (MSY) of bottomfishes 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 kg/nmi of 100-fathom isobath (Ralston and Polovina, 1982). Using Gulland's formula $MSY = 1/2\ M\ B_O$, with the value $M = 0.32$ used in the model and the model estimate of $B_O = 387$ kg/km^2, an estimated MSY of 62 kg/km^2 is obtained. Since the bottomfish habitat is approximately 300 km^2 and the length of the 100-fathom contour at FFS is 65 nmi, the estimated MSY of 62 kg/km^2 is equivalent to an MSY of 286 kg/nmi of 100-fathom isobath which is in agreement with the Penguin Bank value.

TABLE 1. DIET (PERCENTAGE BY SPECIES GROUP) OF SPECIES GROUPS AT FRENCH FRIGATE SHOALS

Birds	
Small pelagics	68
Jacks	10
Reef fishes	15
Nearshore scombrids	2
Zooplankton	5
Tiger sharks	
Birds	30
Monk seals	8
Tiger sharks	1
Reef sharks	3
Turtle	1
Small pelagics	8
Jacks	5
Reef fishes	28
Lobster and crabs	14
Nearshore scombrids	2
Small pelagics	
Small pelagics	6
zooplankton	94
Reef fishes	
Reef fishes	12.3
Zooplankton	17
Heterotrophic benthos	45.9
Benthic algae	24.8
Bottomfishes	
Small pelagics	12.5
Reef fishes	46.9
Lobsters and crabs	1.8
Bottom fishes	2.6
Zooplankton	10.4
Heterotrophic benthos	25.8
Monk seals	
Reef fishes	85
Lobsters and crabs	15
Reef sharks	
Small pelagics	5
Reef fishes	90
Lobsters and crabs	5
Turtles	
Zooplankton	10
Benthic algae	90
Jacks	
Small pelagics	8
Reef fishes	80
Lobsters and crabs	12
Lobsters and crabs	
Heterotrophic benthos	100
Nearshore scombrids	
Small pelagics	48
Reef fishes	8
Bottom fishes	8
Zooplankton	36
Heterotrophic benthos	
Heterotrophic benthos	15
Benthic algae	85
Zooplankton	
Phytoplankton	91
Benthic algae	9

TABLE 2. INPUT PARAMETERS FOR THE ECOPATH MODEL

Species Group	Production/ Biomass	Food for Production Biomass	Food for Maintenance Biomass	Nonpredatory Mortality	Biomass for Apex Species (kg/yr^2)
Birds	5.40	15	2	--	15.4
Monk seals	3.00	15	2	--	63.0
Tiger shark	0.25	10	2	--	42.0
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	1.50	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	40.00	7	2	0.024	--
Phytoplankton	70.00	--	--	0.024	--
Heterotrophic benthos	3.00	5	2	0.024	--
Benthic algae	12.50	--	--	0.024	--

TABLE 3. MEAN ANNUAL BIOMASS AND ANNUAL PRODUCTION ESTIMATE FROM ECOPATH 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
Birds	15	83	1,200.00	0.07	83.0
Monk seals	63	189	1,200.00	0.06	47.0
Tiger sharks	42	11	1,200.00	0.06	4.5
Reef sharks	38	7	1,200.00	0.05	3.8
Turtles	15	2	1,200.00	0.04	3.5
Small pelagics	1,883	2,071	1,200.00	0.15	7.5
Jacks	421	147	1,200.00	0.09	3.8
Reef fishes	24,163	36,244	700.00	0.16	9.5
Lobsters and crabs	2,327	1,210	700.00	0.06	8.2
Bottom fishes	387	124	300.00	0.09	3.6
Nearshore scombrids	62	41	900.00	0.12	5.3
Zooplankton	912	36,486	1,200.00	0.14	282.0
Phytoplankton	3,345	234,157	1,200.00	0.00	0.0
Heterotrophic benthos	289,181	867,543	700.00	0.19	52.0
Benthic algae	342,598	4,282,471	700.00	0.00	0.0
Total biomass	390,604				
Total production		3,294,960			

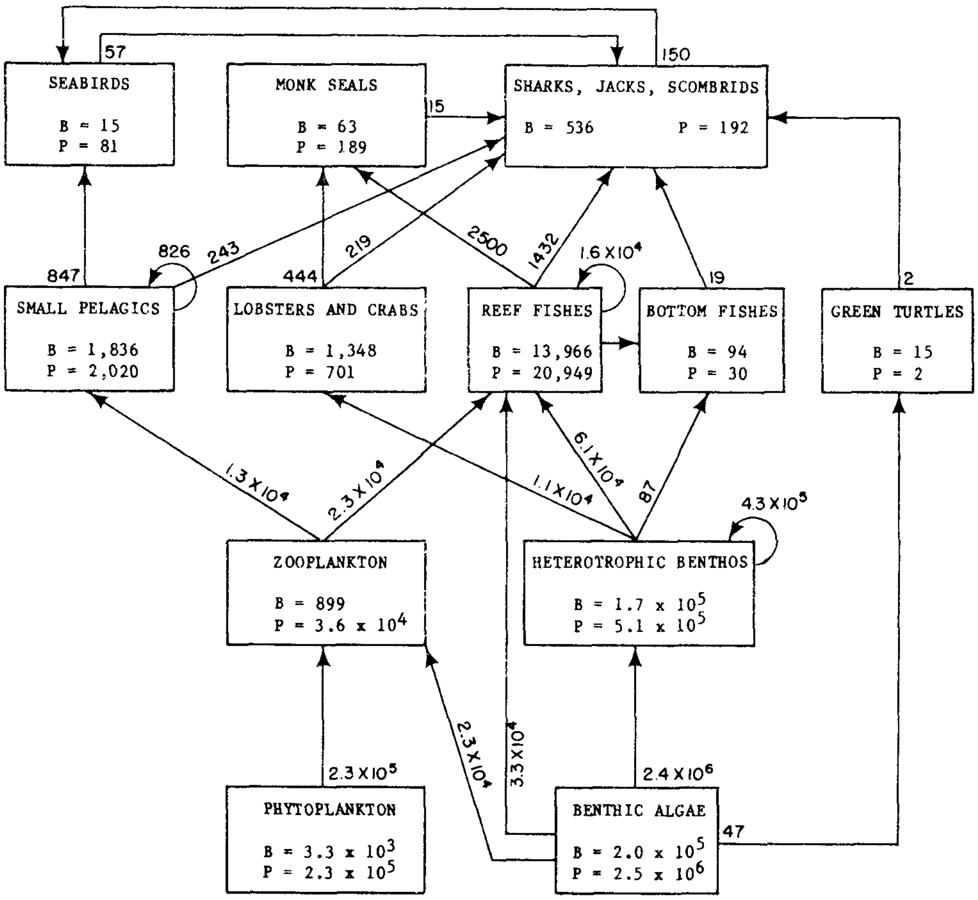

Figure 1. Biomass budget schematic for major prey-predator pathways. Annual production denoted as P and mean annual biomass as B with values in units of kg/km^2 based on a habitat area of 1,200 km^2 for purposes of trophic comparisons and will differ from estimates of B and P given in Table 3 when the habitat area is less than 1,200 km^2.

An estimate of the biomass of the reef shark population 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 population of galapagos shark at 703 individuals and the gray reef shark at 826 individuals. With these population estimates and estimated mean weight of 60 kg for the galapagos shark and 20 kg for gray reef shark, the estimated biomass for the reef shark population is determined to be 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 in the NWHI at 670 metric tons (MT) biomass/ km^2/yr. The model estimates that 234 $MT/km^2/yr$ of phytoplankton production is needed to support life in the reef and nearshore ecosystem.

An estimate of net benthic primary production over a 700 km^2 habitat at French Frigate Shoals based on field measurements is 4.1×10^6 $kg/km^2/yr$ (see expanded abstract in this proceedings by R. Grigg). The model estimates the net benthic algal production necessary to support the ecosystem at French Frigate Shoals at 4.3×10^6 $kg/km^2/yr$ (Table 3).

The biomass of prey consumed by each predator is presented in Table 4. From Figure 1 and Table 4, it can be determined, for example, that monk seals consume most of the lobster and crab production but that they still constitute only a small portion of the monk seal diet compared with the portion of reef fishes.

SENSITIVITY ANALYSIS

To determine the sensitivity of the mean annual species group biomass estimated by the ECOPATH model to uncertainty or error in the inputted parameter estimates, a simple sensitivity analysis was performed. The set of input parameters used for the FFS biomass estimation served as the baseline values.

For a specific parameter, say the P:B value, the parameter for species group i was perturbed by a percentage p with all other parameters fixed at their baseline values, and the mean annual biomass for species group i was computed based on the perturbed parameter. The percentage of change of this new mean annual biomass from the baseline biomass for species group i was computed. This procedure was repeated for all i where each time the parameter for a new species group, say i + 1, was perturbed, the parameter value for species group i was returned to the baseline value. Let B_{io} represent the baseline mean annual biomass for species group i and B_{ip} represent the mean annual biomass for species group i when one of the input parameters was perturbed by p percent. Then a measure of the sensitivity of the estimate of mean annual biomass to a p percentage of change in a specific input parameter is the average absolute value of the change in mean annual biomass averaged over all species groups (avg B)

TABLE 4. PREDATOR CONSUMPTION VECTOR (KG/KM^2) BASED ON A HABITAT AREA 1,200 KM

<u>Birds</u>	
Small pelagic	869
Jacks	128
Reef fishes	192
Nearshore scombrids	26
Zooplankton	64
<u>Tiger sharks</u>	
Birds	57
Monk seals	15
Tiger sharks	2
Reef sharks	
Turtles	2
Small pelagics	15
Jacks	10
Reef fishes	53
Lobsters and crabs	27
Nearshore scombrids	4
<u>Small pelagics</u>	
Small pelagics	847
Zooplankton	13,272
<u>Reef fishes</u>	
Reef fishes	16,470
Zooplankton	22,763
Heterotrophic benthos	61,461
Benthic algae	33,208
<u>Bottomfishes</u>	
Small pelagics	15
Reef fishes	163
Lobsters and crabs	6
Bottomfishes	9
Zooplankton	36
Heterotrophic benthos	90
<u>Monk seals</u>	
Reef fishes	2,517
Lobsters and crabs	444
<u>Reef sharks</u>	
Pelagics	7
Reef fishes	127
Lobsters and crabs	7
<u>Turtles</u>	
Zooplankton	5
Benthic algea	47
<u>Jacks</u>	
Small pelagics	126
Reef fishes	1,263
<u>Lobster and crabs</u>	
Heterotrophic benthos	11,187
<u>Nearshore scombrids</u>	
Small pelagics	117
Reef fishes	20
Bottomfishes	20
Zooplankton	88
<u>Heterotrophic benthos</u>	
Heterotrophic benthos	260 x 10
Benthic algae	1.5 x 10
<u>Zooplankton</u>	
Phytoplankton	234 x 10
Benthic algae	23 x 10

where

$$\text{avg B} = \sum_{i=1}^{15} |B_{io} - B_{ip}| / 15\ B_{io} .$$

Similarly the sensitivity of the estimated total ecosystem mean annual biomass (TB) to change in the input parameters can be measured by the average change in TB when a specific parameter is perturbed for one species group at a time. If TB_{ip} represents the total ecosystem mean annual biomass when a parameter for species group i is perturbed by p percent, and if TB is the total ecosystem mean annual baseline biomass, then a measure of the sensitivity of the total biomass to change in a single parameter is the average absolute change in total biomass (avg TB) where:

$$\text{avg TB} = \sum_{i=1}^{15} |TB - TB_{ip}| / 15\ TB .$$

The values of avg B and avg TB for changes in P:B, d, a, b, and the apex B's are given in Table 5. The estimate of mean annual biomass and total ecosystem biomass is relatively insensitive to change in the input parameters a, b, d, and the apex B's. For example, an increase in the value of a, the ratio of food required for growth, by 25 percent only results in a 1.8 per cent change in the average mean annual biomass and a 2.8 percent change in total biomass. However, the estimate of mean annual biomass is quite sensitive to changes in the P:B value. A 25 percent increase for a specific species group results in almost a 22 percent change in the average mean annual biomass, and a 25 percent decrease results in almost a 40 percent change. Fortunately, this sensitivity is restricted only to the species group for which the parameter is being perturbed since the average change in total ecosystem biomass is relatively small for the P:B parameter.

Thus far a parameter has been perturbed for only one species group at a time. The sensitivity of the estimated annual species group biomass and total ecosystem biomass to perturbation in the P:B value and food required (a and b together) for 10 percent changes in all species groups simultaneously is given in Table 6. Due to the prey-predator interactions a 10 percent change in all food consumption values or a 10 percent change in all P:B values can have a substantially greater effect on the estimated species group biomasses and the estimated total ecosystem biomass.

TABLE 5. AVERAGE CHANGE IN MEAN ANNUAL BIOMASS AND TOTAL ECOSYSTEM BIOMASS AS A FUNCTION OF CHANGE IN INPUT PARAMETERS

	Perturbation Relative to Baseline Value							
	0.75	0.80	0.85	0.90	1.10	1.15	1.20	1.25
				Parameter a				
avg B	0.016	0.013	0.010	0.006	0.007	0.011	0.014	0.018
avg TB	0.026	0.021	0.016	0.011	0.011	0.017	0.022	0.028
				Parameter b				
avg B	0.046	0.038	0.030	0.021	0.026	0.041	0.059	0.080
avg TB	0.049	0.040	0.031	0.021	0.024	0.038	0.053	0.070
				Parameter d				
avg B	0.014	0.011	0.008	0.006	0.006	0.009	0.012	0.015
avg TB	0.005	0.004	0.003	0.002	0.002	0.003	0.004	0.005
				P:B ratio				
avg B	0.394	0.292	0.204	0.127	0.101	0.144	0.183	0.219
avg TB	0.076	0.056	0.039	0.024	0.019	0.027	0.034	0.040
				Apex B's				
avg TB	0.083	0.067	0.050	0.033	0.033	0.050	0.067	0.083

TABLE 6. CHANGE IN MEAN ANNUAL BIOMASS AND TOTAL ECOSYSTEM BIOMASS AS A FUNCTION OF SIMULTANEOUS CHANGES IN A PARAMETER FOR ALL SPECIES GROUPS

	Perturbation Relative to Baseline Value	
	0.90	1.10
	Parameter Jointly a and b	
avg B	0.14	0.19
avg TB	0.23	0.32
	Parameter P:B	
avg B	0.25	0.17
avg TB	0.32	0.21

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