

PRELIMINARY RESULTS FROM ECOSYSTEM MODELING
AT FRENCH FRIGATE SHOALS

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ABSTRACT

The marine ecosystem at French Frigate Shoals is discussed and preliminary results of the modeling work are presented. Application of the Bulk Biomass Model produces biomass estimates and turnover rates for species groups at French Frigate Shoals which consist of seabirds, monk seals, tiger sharks, small sharks, turtles, small pelagics, carangids, reef fishes, lobsters, snappers and groupers, shrimps, nearshore scombrids, and benthos.

French Frigate Shoals
ecosystem modeling
Bulk Biomass Model

INTRODUCTION

The objective of our ecosystem modeling is to draw on the expertise and results of the people and projects of the Northwestern Hawaiian Islands (NWHI) program to develop a quantitative and dynamic model of the marine ecosystem around French Frigate Shoals (FFS) in the NWHI. Because the model is dynamic, it may prove to be useful as a management tool and may also help to identify components of the ecosystem where additional research attention is needed.

Our approach to modeling begins with the top carnivores and works down to the primary producers. We have identified 13 species groups which form the components of our ecosystem. Rather than initially try to model the entire NWHI, we have restricted our modeling work to the ecosystem at FFS.

METHODS

The mathematical Bulk Biomass Model, which is described in detail by Laevastu and Favorite (1978), served as the tool for our ecosystem

modeling. This model produces estimates of the biomass of the species groups in the ecosystem which is at equilibrium, based on growth, mortality, and consumption values specified by the user. The ecosystem is said to be at equilibrium conditions when the biomass of a species group is unchanged from one year to the next, although seasonal changes within a year are permitted. This is achieved when biomass growth equals its removal due to predation, natural mortality, and fishing mortality.

The population size of species which are the apex predators, typically birds and mammals, are considered fixed and are not changed during iterations of the model. The biomass of all other species groups are varied during the iterations until equilibrium conditions are met. The biomass values for species groups estimated at equilibrium conditions are heavily dependent on accurate estimates of the quantitative composition of the diet for each species group (Livingston, 1978). This report will deal only with the application of this tool to the ecosystem at FFS.

The ecosystem

We have defined 13 species groups which represent the components of the reef and nearshore ecosystem. These groups which will subsequently be described in detail are: seabirds, monk seals, tiger sharks, small sharks, turtles, small pelagics, carangids, reef fishes, lobsters, benthos, snappers and groupers, nearshore scombrids, and shrimps.

French Frigate Shoals

French Frigate Shoals is located at 166°10'W, 24°50'N, approximately midway along the chain of islands and banks comprising the NWHI. It is described by Bakus (in Bryne, 1979) as a "crescent-shaped reef on a circular submerged platform about 18 miles 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, ~ 1 acre) near the center of the platform. The highest elevation is generally 5 feet above sea level except for La Perouse Pinnacle (135 feet 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 our modeling is the reef and nearshore community. We have defined the reef habitat as the area from 0 to 55 m (0 to 30 fathoms) (Gosline and Brock, 1976). The nearshore community is defined as the area ranging from 55 to 365 m (30 to 200 fathoms). These definitions applied to FFS yield a reef habitat of 761.6 km² and a nearshore habitat of 407.7 km². The sum of these regions consists of a circular area centered at FFS with a radius of approximately 20 km (Table 1).

Seabirds

Studies from the U.S. Fish and Wildlife Service (FWS) 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; wedge-tailed

TABLE 1. AREA BY DEPTH AT FRENCH FRIGATE SHOALS

Reef Habitat		Nearshore Habitat	
Depth (fathoms)	Area (km ²)	Depth (fathoms)	Area (km ²)
0-10	461.5	30-40	34.9
10-20	264.9	40-50	37.3
20-30	35.2	50-100	95.7
Total	761.6	100-200	239.8
		Total	407.7

shearwater, *Puffinus pacificus*; Laysan albatross, *Diomedea immutabilis*; and black-footed albatross, *D. niaripes*. The total seabird population is estimated by FWS to be 320,000 birds (C. Harrison, U.S. Fish and Wildlife Service, Honolulu, Hawaii 96850, personal communication, October 1979). Detailed studies of stomach contents of birds in the NWHI have been undertaken jointly by the National Marine Fisheries Service (NMFS) Honolulu Laboratory and FWS. Based on this information, we estimate the diet of the birds to be 65% small pelagics including flyingfish, opelu, and squid, 10% juvenile tunas; 10% juvenile carangids; 10% juvenile snappers; and 5% zooplankton.

Monk seals

A census of the Hawaiian monk seal indicates a population of about 200 adults and pups in 1978 (Fiscus et al., 1978). Stomach contents of dead seals, regurgitated samples, and feces have been studied to determine their diet (National Marine Fisheries Service). Based on this work, we estimate that their diet is 85% reef fishes including eels and octopus, 5% lobsters, and 10% benthos. The extent of predation on seals by sharks is uncertain. While numerous seals are seen with scars which could have been caused by shark attacks, observations at Laysan provide little direct evidence of such attacks even though sharks are abundant in the shallow waters (B.W. Johnson and P.A. Johnson, National Marine Mammal Laboratory, National Marine Fisheries Service, Seattle, Washington 98115, personal communication, October 1979).

Tiger sharks

The tiger shark, *Galeocerdo cuvier*, is the predominant apex predator at FFS. Analysis of stomach contents from tiger sharks caught in the NWHI suggest that their diet consists of 45% reef fishes, 20% seabirds, 24% smaller sharks, 4% small pelagics, 4% lobsters, 2% turtles, and 1% monk seals (M. DeCrosta, Hawaii Cooperative Fishery Research Unit, University of Hawaii, Honolulu, Hawaii 96822, personal communication, December 1979).

A measure of the relative abundance of tiger sharks in the NWHI was obtained by Taylor and Naftel (1978). Eighteen sets of shark longlines at Pearl and Hermes Reef and FFS with a total of 388 hooks produced a catch rate of 10.31 tiger sharks/100 hooks. A report on shark fishing

around Oahu suggests that a catch rate of six tiger sharks/100 hooks represented a density of 1.21 tiger sharks/km of 10-fathom contour (Lawrie, 1977). Extrapolating this density estimate for the NWHI catch rate, we obtain a figure of 2.08 tiger sharks/km or a total of 415 tiger sharks at FFS. We feel that most of these sharks would feed in the reef habitat where food is more abundant.

Small sharks

This is a group of nearshore warmwater sharks other than the tiger shark. Based on observations and catches at FFS, this group includes the grey reef shark, Carcharhinus amblyrhynchos, the galapagos shark, Carcharhinus 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 great 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 fish, bottom-dwelling fish, stingrays, crustaceans, squid, and octopus. Based on analysis of stomach contents (M. DeCrosta, personal communication, December 1979), we estimate their diet as: 75% reef fishes, 5% lobsters, 10% small pelagics, 5% carangids, and 5% snappers and groupers in the reef habitat; and 58% small pelagics, 20% carangids, 15% snappers and groupers, 5% small sharks, and 2% reef fishes in the nearshore habitat.

Relative abundance for this group of sharks has been estimated in the NWHI at 9.8 sharks/100 hooks, based on longline catches (Taylor and Naftel, 1978). Around Oahu, a catch rate of 2.3 sharks/100 hooks was estimated to correspond to a density of 0.7 sharks/km along the 10-fathom contour (Lawrie, 1977). Extrapolating this density based on the catch rate for NWHI, we estimate a density of 2.9 sharks/km along the 10-fathom contour or 597 sharks at FFS. Visual observations of researchers who have worked at FFS suggest that this number is too low. We have arbitrarily chosen density figures of 10 sharks/km² for the reef habitat and 5 sharks/km² for the nearshore habitat. Based on a mean weight of 30 kg, we obtain biomass estimates of 300 kg/km² for the reef habitat and 150 kg/km² for the nearshore habitat.

Turtles

This group consists of the green turtle. Census counts indicate a population of 50 to 100 resident adult and 100 to 200 resident juvenile turtles at FFS (Balazs, 1979). However, during the breeding season, the population increases from 200 to 500 adults. Their diet consists principally of the following types of algae: Codium arabicum, Caulerpa racemosa, Turbinaria ornata, Spyridia filamentosa, Rosenvingea orientalis, and Lobophora variegata (Balazs, 1979). Their main predator is the tiger shark.

Small pelagics (small pelagic fishes and mollusks)

This group consists of small surface pelagic fishes and squid including flyingfish, exocoetids, opelu, Decapterus spp., akule, Trachurops

crumenophthalmus, needlefish, belonids, and halfbeaks, hemiramphids. We estimate the diet of this group to be 80% zooplankton, 7% phytoplankton, and 13% small pelagics. Information which would enable direct biomass estimation is very limited. We have reliable figures on the seabird population of FFS and the bird diet. Based on this information, the minimum biomass of small pelagics necessary to meet bird predation would be 3,000 kg/km² in the nearshore habitat and 300 kg/km² for the reef habitat.

Carangids (carangids and large carnivores)

This is a group of active, fast-swimming carnivores which includes the white ulua, Caranx ignobilis; omilu, C. melampygus; ulua, Carangoides ferdau; kahala, Seriola dumerili; uku, Aprion virescens; and barracuda, Sphyraena barracuda. These carangids are found both in the reef and nearshore regions. Based on an analysis of stomach contents (M. DeCrosta, personal communication, December 1979), we estimate the diet of this group to be 15% zooplankton, 60% reef fishes, 15% lobsters, and 10% carangids in the reef region; and 15% zooplankton, 60% small pelagics, 5% reef fishes, 10% snappers, and 10% carangids in the nearshore region.

Researchers have remarked on the apparent low abundance of carangids at FFS relative to other banks in the NWHI. The biomass estimate of 400 kg/km² for both reef and nearshore habitat used for this area is based on very limited fishing data and transect dives (H. Okamoto, Hawaii Division of Fish and Game, Honolulu, Hawaii 96813, personal communication, December 1979; and E. Hobson, Southwest Fisheries Center Tiburon Laboratory, National Marine Fisheries Service, NOAA, Tiburon, California 94920, personal communication, December 1979).

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).

Studies of the reef habitat and transects are currently ongoing at FFS (H. Okamoto and E. Hobson, personal communications, December 1979; R.W. Grigg, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii 96744; and J. Parrish, U.S. Fish and Wildlife Service, Honolulu, Hawaii 96850, personal communications, October 1979). These observations suggest that 12% of the area from 0 to 18 m (0 to 10 fathoms) is rich in reef fishes, 17% is moderate, and 71% is sparse. We will assume 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/km² (1,460 lb/acre); for a moderate habitat 16,815 kg/km² (150 lb/acre); and for a sparse habitat 1,569.4 kg/km² (14 lb/acre). This gives an average density of reef fishes at FFS of 15,000 kg/km² (134 lb/acre).

The density estimates of 163,666 kg/km² (1,460 lb/acre) for a rich habitat is in agreement with two estimates of standing crop determined from a rotenone study in Kaneohe Bay of 123,310 kg/km² (1,100 lb/acre) and 92,819 kg/km² (828 lb/acre) (Brock et al., 1979). Further, Goldman and

Talbot (1975) concluded from a survey of the literature that a maximum standing crop in a coral reef is about 201,780 kg/km² (1,800 lb/acre).

Estimates of the composition of reef fishes by weight from the Great Barrier Reef indicate that 10% are planktivores, 36% benthic feeders, and 54% carnivores (Goldman and Talbot, 1975).

Lobsters (lobsters and crabs)

This group includes the spiny lobsters, Panulirus marginatus and P. penicillatus, the slipper lobster, Scyllarides squammosus, and various crabs. The abundance of lobsters appears to be relatively low at FFS. Trapping data and transect studies indicate that the lobster population here is very low compared to other regions in the NWHI (R. Uchida, Southwest Fisheries Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812, personal communication, October 1979). Based on this information, we selected a density of 200 kg/km² in the reef region and 50 kg/km² in the nearshore habitat. Lobsters are bottom feeders which prey primarily on benthos.

Benthos

The benthic community is typically rich, diverse, and well-developed. Organisms in this community include the sponges, algae, benthic fish, gastropods, bivalves, holothuroids, annelids, asteroides, ophiuroids, echinoids, crustaceans, and anthozoans. Members of the benthos may be carnivores, herbivores, or detritivores. An ongoing project is studying this community at FFS (R. Grigg and J. Parrish, personal communication, October 1979).

Snappers and groupers

This is a commercially important group of food fishes including opakapaka, Pristipomoides filamentosus; kalikali, P. sieboldii; gindai, P. zonatus; onaga, Etelis carbunculus; ehu, E. marshi; uku, Aprion virescens; hapu'upu'u, Epinephelus quernus; and butaguchi, Caranx cheilio. Fishermen report that these bottomfishes are caught predominantly between 75 and 220 m (40 and 120 fathoms). They are all active, carnivorous fish which prey on small fish, shrimp and other crustaceans, and macrozooplankton. Based on analysis of stomach contents, we estimate their diet to be 15% zooplankton, 60% benthos, 5% snappers, and 20% shrimps (R. Humphreys, Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, Hawaii 96812, personal communication, December 1979).

Based on our analysis of an intensive bottomfishing experiment in Guam (Ikehara et al., 1972), we arrived at an estimate of bottomfish biomass as 4.3×10^3 kg/nmi of the 100-fathom contour. We estimate the length of the 100-fathom contour at FFS to be 85 nmi and assume that 90% of the snapper and grouper biomass are in the nearshore region. We obtain estimates of snapper and grouper density in the reef region as 48 kg/km² and in the nearshore region as 808 kg/km².

Shrimps

This group, consisting primarily of Heterocarpus ensifer and Penaeus spp. is found in abundance between 225 and 375 m (125 and 200 fathoms). Estimates of density from trapping and trawling in the main islands are 50 kg/km² over this habitat range (Struhsaker and Yoshida, 1975). They are detritivores.

Nearshore scombrids (nearshore scombrids and carnivores)

This is a group of commercially important tunas and tunalike fish, and includes skipjack tuna, Katsuwonus pelamis; kawakawa, Euthynnus affinus; yellowfin tuna, Thunnus albacares; and ono, Acanthocybium solandri. Mahimahi, Coryphaena hippurus, and the rainbow runner, Elagatis bipinnulatus, also belong in this group. 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). Based on stomach content analysis, we estimate the diet of this group to be 20% zooplankton and 80% small pelagics.

The input data required by the Bulk Biomass Model are summarized for all species groups in Tables 2, 3, and 4.

TABLE 2. GROWTH AND FOOD CONSUMPTION RATES IN PERCENTAGE OF BODY WEIGHT PER MONTH

Species Group	Growth Rate	Food Consumption Rate
Tiger sharks	--	48
Monk seals	--	240
Seabirds	--	450
Small sharks	6	48
Turtles	3	180
Small pelagics	8	30
Carangids	4	60
Reef fishes	10	30
Lobsters	6	23
Benthos	6	24
Snappers and groupers	3	30
Shrimps	5	30
Nearshore scombrids	6	30

Note: Natural mortality due to factors except predation is 0.2%; fishing mortality = 0.

TABLE 3. INITIAL DENSITY ESTIMATES USED AS INPUT

Apex Species	Reef Habitat (Number)	Nearshore Habitat (Number)
Seabirds	40,000	280,000
Monk seals	150	50
Tiger sharks	250	150

Prey Species	Reef Habitat (Biomass (kg/km ²))	Nearshore Habitat (Biomass (kg/km ²))
Small sharks	300	150
Turtles	7	7
Small pelagics	300	3,000
Carangids	400	400
Reef fishes	15,000	500
Lobsters	200	50
Benthos	15,000	3,000
Snappers and groupers	50	800
Shrimps	5	50
Nearshore scombrids	50	350

TABLE 4. FOOD COMPOSITION (PERCENTAGE OF DIET BY SPECIES GROUPS)

Reef Habitat	Nearshore Habitat
Small sharks: 75% Reef fishes 10% Small pelagics 5% Lobsters 5% Carangids 5% Snappers and groupers	Small sharks: 58% Small pelagics 20% Carangids 15% Snappers and groupers 5% Small sharks 2% Reef fishes
Turtles: 100% Benthos	Turtles: 100% Benthos
Small pelagics: 80% Zooplankton 13% Small pelagics 7% Phytoplankton	Small pelagics: 80% Zooplankton 13% Small pelagics 7% Phytoplankton
Carangids: 60% Reef fishes 15% Lobsters 15% Zooplankton 10% Carangids	Carangids: 60% Small pelagics 10% Snappers and groupers 10% Carangids 5% Reef fishes 15% Zooplankton

TABLE 4. FOOD COMPOSITION (PERCENTAGE OF DIET BY SPECIES GROUPS)
(Continued)

Reef Habitat	Nearshore Habitat
Reef fishes: 54% Reef fishes 36% Benthos 10% Zooplankton	Reef fishes: 54% Reef fishes 36% Benthos 10% Zooplankton
Lobsters: 100% Benthos	Lobsters: 100% Benthos
Benthos: 50% Zooplankton 30% Phytoplankton 20% Benthos	Benthos: 50% Zooplankton 30% Phytoplankton 20% Benthos
Snappers and groupers: 60% Benthos 20% Shrimps 15% Zooplankton 5% Snappers and groupers	Snappers and groupers: 60% Benthos 20% Shrimps 15% Zooplankton 5% Snappers and groupers
Shrimps: 100% Benthos	Shrimps: 100% Benthos
Nearshore scombrids: 70% Small pelagics 25% Zooplankton 5% Nearshore scombrids	Nearshore scombrids: 70% Small pelagics 25% Zooplankton 5% Nearshore scombrids
Seabirds: 65% Small pelagics 10% Nearshore scombrids 10% Carangids 10% Snappers and groupers 5% Zooplankton	Seabirds: 65% Small pelagics 10% Nearshore scombrids 10% Carangids 10% Snappers and groupers 5% Zooplankton
Seals: 85% Reef fishes 10% Benthos 5% Lobsters	Seals: 85% Reef fishes 10% Benthos 5% Lobsters
Tiger sharks: 54% Reef fishes 30% Small sharks 7% Lobsters 7% Small pelagics 2% Turtles	Tiger sharks: 54% Reef fishes 30% Small sharks 7% Lobsters 7% Small pelagics 2% Turtles

RESULTS AND DISCUSSION

The estimates of biomass, consumption, and turnover presented in Table 5 are based on computer runs simulating 80 years of ecosystem time with the input data from Tables 2, 3, and 4. There are still slight time trends in the biomass values for several of the species groups so these results do not yet represent an equilibrium solution; however, they are probably sufficiently close to an equilibrium solution to be useful for the purposes of discussing the model and input values. We have used relatively low food consumption rates for all species groups so the resulting biomass values represent the minimum sustainable biomass (Laevastu and Favorite, 1978).

TABLE 5. AVERAGE BIOMASS (IN WET WEIGHT, KG/KM²) (B), ANNUAL CONSUMPTION (PRODUCTION) (IN WET WEIGHT, KG/KM²) (C), AND TURNOVER (T = C/B) FOR REEF AND NEARSHORE REGIONS

Species	Reef Region			Nearshore Region		
	B	C	T	B	C	T
Small sharks	63.7	54.0	0.85	18.7	16.2	0.87
Turtles	9.3	3.6	0.39	3.5	0.7	0.20
Small pelagics	537.9	593.6	1.10	4,942.7	5,878.6	1.19
Carangids	157.0	135.1	0.86	937.4	1,022.0	1.09
Reef fishes	14,395.5	17,370.7	1.21	521.0	760.3	1.46
Lobsters	178.1	141.4	0.79	44.3	42.0	0.95
Benthos	9,580.9	13,981.6	1.46	1,235.3	1,970.3	1.60
Snappers and groupers	133.3	88.7	0.67	1,058.8	1,173.6	1.11
Shrimps	22.4	24.0	1.07	30.3	18.5	0.61
Nearshore scombrids	59.9	54.0	0.90	425.8	378.0	0.89
Total	25,138.0	32,446.7	1.29	9,217.8	11,260.2	1.22
Zooplankton	--	32,130.0	--	--	22,571.0	--

For most of the species groups, the estimated biomass values in Table 5 are not far from the initial estimates. This is particularly reassuring for reef fishes where we feel we have a reliable initial estimate. One exception is the estimated shark biomass, which appears low. This is due to heavy and perhaps, an unrealistic estimate of predation on smaller sharks by tiger sharks.

Data compiled after our computer work, which quantifies the distribution and relative abundance of benthos at FFS, coupled with standard production computation suggest that the production of benthos in the reef habitat should be about three times the value we obtained (R. Grigg, personal communication, February 1980). This information will be used to change our input estimates for future computer work. In the nearshore habitat, our estimated production agrees with his calculations.

Our estimated annual production for the reef region, excluding the benthic, zooplankton, and phytoplankton production, is 18,465.1 kg/km². This agrees with an estimated production of 22,000 kg/km²/yr for a similar community on a reef in Bermuda (Bardach, 1959).

We have not attempted to model the phytoplankton and zooplankton production for the ecosystem. The computer program does, however, determine the total ecosystem zooplankton requirement based on the inputted diet composition values for all the species groups. The annual zooplankton consumption for the reef region is 32,130 kg/km² and for the nearshore region is 22,571 kg/km². Based on a transfer coefficient of 10%, this zooplankton production requires a phytoplankton production of 321,300 kg/km² and 225,710 kg/km² in the reef and nearshore regions, respectively. Primary production for the nearshore region has been estimated as 365,000 kg/km² (J. Hirota, Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii 96744, personal communication, December 1979).

The predation on the species groups by seabirds, seals, and tiger sharks is approximately twice as high in the nearshore region as in the reef region (Table 6). This is due to the predation of birds on small pelagics in the nearshore region.

TABLE 6. ANNUAL CONSUMPTION BY APEX PREDATORS (SEABIRDS, MONK SEALS, AND TIGER SHARKS) IN KG/KM²

Species	Reef Region	Nearshore Region
Small sharks	43	9
Turtles	3	1
Small pelagics	288	1,967
Carangids	48	273
Reef fishes	871	145
Lobsters	53	7
Benthos	83	10
Snappers and groupers	43	303
Shrimps	0	0
Nearshore scombrids	43	302
Total	1,475	3,017

FUTURE RESEARCH

There are two directions for future research. First, research directed toward improving estimates of biomass, growth rates, food composition, and food conversion is needed to improve the accuracy of the input to the model. Some of this research is already planned as part of the specific projects in the NWHI investigation. However, in some cases, specific projects are being proposed at NMFS to obtain the necessary data. One example of this is an intensive bottomfishing experiment we are planning at a small and isolated bank to estimate the standing stock of snappers and groupers per nautical mile of a given depth contour.

The second aspect of future research consists of model sensitivity analysis, simulation, and modification. We will vary input parameters to reflect our degree of certainty about the input values and observe the changes in equilibrium biomass values. We will simulate various fishing strategies to observe their impact on the ecosystem. Finally, we will consider modifications of some of the mathematical relationships in the model to incorporate our best understanding of the biological processes at French Frigate Shoals.

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