The Role of Sharks and Longline Fisheries in a Pelagic Ecosystem of the Central Pacific

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ABSTRACT

The increased exploitation of pelagic sharks by longline fisheries raised questions about changes in the food webs that include sharks as apex predators. We used a version of Ecopath/Ecosim models to evaluate changes in trophic interactions due to shark exploitation in the Central North Pacific. Fisheries targeted on blue sharks tend to produce compensatory responses that favor other shark species and billfishes, but they have only modest effects on the majority of food web components. Modest levels of intraguild predation (adult sharks that eat juvenile sharks) produce strong, nonlinear responses in shark populations. In general, analysis of the Central North Pacific model reveals that sharks are not keystone predators, but that increases in longline fisheries can have profound effects on the food webs that support sharks.

Key words: sharks; blue shark; food web; models; ecosystem; pelagic ecosystem; fisheries; predation; predator–prey interactions; conservation; Pacific Ocean.

INTRODUCTION

A number of recent publications have documented a growing concern about the widespread decline of shark populations (Smith and others 1998; Walker 1998; Musick 1999; Stevens and others 2000). Many shark species are at or near the apex of a trophic structure that supports them. It is often suggested that sharks may also function as keystone predators (Hinman 1998; Stevens and others 2000) and that they might be essential to the maintenance and stability of food webs. Thus, the question of the consequences of shark exploitation extends from traditional population biology to the domain of eco-

system issues. Addressing that larger scale poses significant challenges, and meeting those challenges is now an imperative that requires a more comprehensive view of sharks and shark fisheries in an ecosystem context (Botsford and others 1997; Dayton 1998; NRC 1998; NMFS 1999).

In tropical and subtropical seas, pelagic sharks are commonly members of a trophic guild that includes large tunas and billfishes (Figure 1), all of which are vulnerable to longline fisheries (Boggs 1992; Boggs and Ito 1993). Prior to about 1990, most pelagic longline fisheries treated sharks as bycatch; they were discarded and released, with relatively low consequent mortality (He and Laurs 1998). In the 1990s, the development of shark fin markets raised the mortality rate such that more than 80% of sharks caught were killed (WPFMC 1998; Camhi 1999).

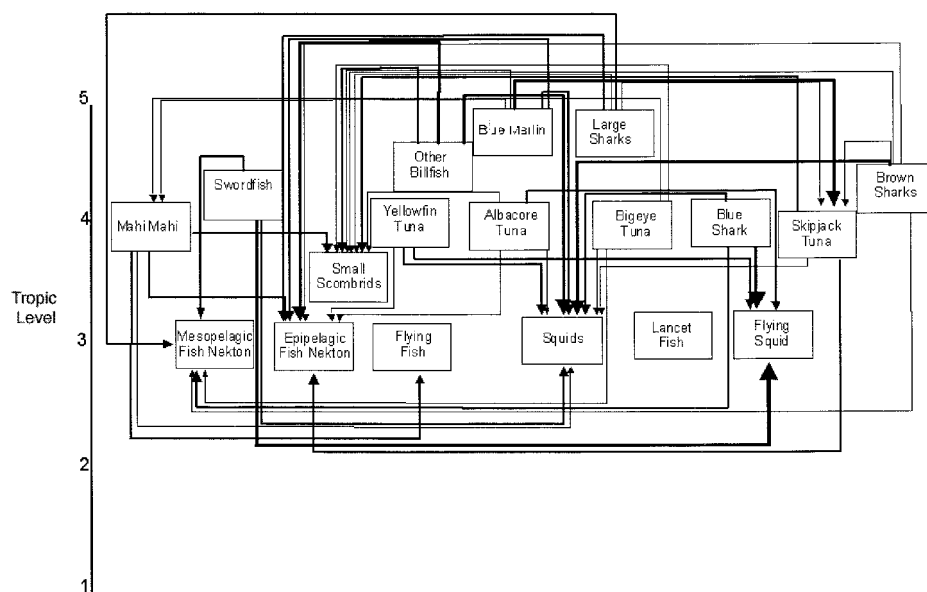In response to growing concern over shark con-

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Figure 1. Food web of higher trophic levels used in the Ecosim model for the Central North Pacific (CNP 8).

servation, both the United States and Australia have enacted recent (2000–01) legislative bans on landings of shark fin. This type of legislation will probably result in a significant reduction in mortality rates for coastal sharks from the (Extended Economic Zone (EEZ) of countries that limit shark landings. However, there will be a much more modest reduction in mortality rates for pelagic sharks taken in longline gear because Asian fleets dominate these fisheries in the international waters of all of the world's oceans. For example, only about 2% of the Central Pacific longline fleet is under US registry; the remaining 98% is dominated by Japan, Korea, and Taiwan. Thus, questions continue about the ecological effects arising from the increasing mortality rates for pelagic sharks and/or the consequences of concerted international attempts to protect them.

In this paper, we develop a whole-ecosystem model for sharks in the context of a Central North Pacific food web. This model allows estimates of the role of changing exploitation rates and their ecological effects. In general, pelagic shark populations are more strongly affected by exploitation than many other fishes at the top of the food web; however, changes in shark exploitation rates do not yield profound ecological effects for other components of the ecosystem.

METHODS

Model Structure and Inputs

We delimit the Central North Pacific ecosystem as pelagic waters bounded by the Equator to the south, the lower edge of the Transition Zone (the mixing zone between subtropical and subarctic waters, approximately 35–40°N), and the longitudinal boundaries of 150°W and 130°E. Our analyses are based on the Ecopath model developed by Polovina (1984) and modified by Christensen and Pauly (1992, 1993). The Ecopath model has been used to estimate the linkage between primary production and fish production for the world's oceans (Pauly and Christensen 1995) and as the basis for evaluating changes in trophic structure due to fishery exploitation in both marine and freshwater systems (Pauly and others 1998). The derivation and application of the Ecopath model will be summarized only briefly here because there are now applications of Ecopath to more than 100 different ecosystems (D. Pauly personal communication). The software is available without cost at http://www.fisheries.com, and a recent user's guide offers an extensive description of the model-building process (Christensen and others 2000).

The core of an Ecopath model is the balance of production and losses of biomass for each component of an ecosystem:

Production– + Immigration–Predatory losses

–Nonpredatory mortality–Harvest–Emigration = 0

$$(1)$$

In other words, the system is set to equilibrium based on estimates of rates for each of the terms in Eq. (1). This initial condition allows analyses of flows between trophic levels and individual state variables. An important component of this process

is that the ratio of production to biomass (P/B) is equal to the sum of all sources of mortality—those due to predation, exploitation, and other causes. Thus, the system is set to equilibrium based on the current levels of mortality, biomass, and production. Any change in exploitation rates produces a new steady-state condition.

Walters and others (1997) developed Ecosim as a dynamic simulation model that represents the effects of changes in initial steady-state condition for an Ecopath model. User inputs can alter the initial conditions for exploitation rates, predator–prey interactions, and/or external changes in the environment as applied to any state variable in the Ecopath model. Ecosim then calculates the time course for consequent change in all other state variables for the ecosystem and produces a new equilibrium condition. Derivation of the Ecosim model is detailed in Walters and others (1997) and Christensen and others (2000).

The master equation for Ecosim predicts changes in the biomass (B) pools according to:

$$dB/dt = Production-Predatory\ losses-Harvests$$

$$-Other\ (nonpredatory)\ losses \quad (2)$$

All Ecopath variables are embedded in a food web. Thus, simulation of changes in state variables may be expressed in other components of the food web. The resultant dynamics depend on the linkages stated in the trophic flow matrix and in the parameters that are used to define each. Response to manipulation is generally proportional to the biomass for a given component and the turnover rates estimated for it. For example, organisms with large P/B values (for instance, zooplankton) respond rapidly to perturbation and achieve new steady-state values quickly. Those with low P/B values (for example, sharks), which are indicative of K-strategy life histories or low turnover rates, respond slowly and with substantial lags (Apollonio 1994; Musick 1999). However, sharks occupy the apex of the food web, so changes in their biomass may cascade through the trophic system (Hinman 1998; Camhi 1999).

The CNP 8 Ecosim model

With both Ecopath and Ecosim, a diversity of options and alternative functions are available to the user. The original version of our Ecopath/Ecosim model was called Central North Pacific 6 (CNP 6). Its parameter set is available at http://www.fisheries.com and from Kitchell and others (1999). CNP 6 was constructed with an interest in the role of intraguild predation, so there were split pools assigned to the adults and juveniles of all apex predators. That form proved to be cumbersome and, more importantly, difficult to evaluate and parameterize because the data derived from typical fisheries analyses either do not include juveniles or do not treat them as a separate state variable. To make better use of the traditional fisheries data, we reduced the complexity of the model to create a version that focused entirely on aggregated biomass pools. The new version, CNP 8, also differs from CNP 6 through the addition of another pool for sharks. We distinguish three types of sharks: the blue shark, which is the most common shark in the Central Pacific; a pool for "large sharks" that has vital rates (for example, P/B, mortality rates, and so on.) similar to those for large lamnid sharks such as the mako shark and white shark; and a pool for smaller, carcharinid sharks ("brown sharks") such as oceanic white tip and silky sharks. CNP 8 also differs from the CNP 6 model by representing fish nekton as two pools—mesopelagic nekton and epipelagic nekton. We also removed the juvenile pool for each of the tuna species in CNP 6 and created a new group called "small scombrids," which includes juveniles of the tuna species (bigeye, yellowfin, albacore, and skipjack) as well as mackerels and other smaller scombrids such as *Auxis* spp.. As a consequence of aggregating the model for the adult pools of each apex predator, changes were made in key Ecopath inputs. The Appendix provides a brief synopsis of the new input parameters and their sources.

In the initial version of this modeling effort (CNP 6), we employed the default conditions provided with the software. That included a value of 0.5 for the vulnerability parameter, which modifies the intensity of the predator–prey interaction (Walters and others 1997). A more recent optimization analysis by Walters and others (2000) demonstrates that this parameter (v) should be generally lower but within the range of 0.3–0.5. Accordingly, we set the interaction term to a value of 0.4 for the simulations presented here. The effect of this change is to gradually decouple predation rate from predator abundance as predator biomass rises to high levels.

Parameter tables and scientific names for the CNP 8 Ecopath inputs are presented in Table 1. The diet composition used for the base case version of the model is summarized in Table 2. In combination, these sets of inputs were used to define the Baseline scenario, which was manipulated to simulate consequences of alternative fishery management practices. As described in the following section, a second scenario was developed as a means for testing the

Table 1. Ecopath Parameters for the Baseline Scenario of CNP 8

Group Name	Trophic Level	Biomass (mt/km^2)	Prod./Biom.	Cons./Biom.	Ecotrophic Efficiency
Bigeye tuna (*Thunnus obesus*)	4.0	7.0	0.8	16.0	0.68
Yellowfin tuna (*Thunnus albacares*)	4.0	17.36	1.2	18.0	0.62
Albacore tuna (*Thunnus alalunga*)	4.0	6.98	0.6	12.0	0.58
Blue shark (*Prionace glauca*)	4.0	9.54	0.3	2.8	0.5
Blue marlin (*Makaira mazara*)	4.6	3.42	0.3	4.0	0.5
Large sharks	4.6	0.5	0.25	2.5	0.5
Brown sharks	4.2	8.76	0.3	2.8	0.5
Swordfish (*Xiphias gladius*)	4.2	3.75	0.4	5.0	0.5
Other billfish	4.3	2.13	0.5	5.0	0.5
Mahimahi (*Coryphaena hippurus*)	3.9	30.45	3.0	20.0	0.5
Small scombrids	3.5	243	2.0	10.0	0.9
Flying squid	3.3	18.23	5.0	50.0	0.9
Skipjack tuna (*Katsuwonus pelamis*)	3.9	41.57	1.9	20.0	0.55
Lancetfish (*Alepisaurus ferox*)	3.2	35.9	0.3	2.9	0.9
Squids	3.1	410	2.5	25.0	0.9
Flying fish	3.0	85	2.0	10.0	0.9
Mesopelagic fishes	3.0	781	1.5	6.0	0.9
Epipelagic fishes	3.0	1010	1.5	6.0	0.9
Epipelagic micronekton	2.0	1518	10.0	50.0	0.8
Mesopelagic micronekton	2.0	1978	7.0	35.0	0.8
Phytoplankton	1.0	2903	100.0	—	0.5
Detritus	1.0	1.0	—	—	—

Trophic level of a group is an output of the model. Biomass of each tuna is an input. All other biomasses are outputs based on specified inputs.

greatest possible magnitude of ecosystem effects owing to sharks.

Increasing Predation by Sharks: The Apex Shark Scenario

In the basic CNP 8 model, sharks and other large fishes forage over a very broad range of trophic levels, which is represented in a recent compilation of food habits studies on members of the Chondrichthyes (Cortes 1999). Simulations of shark removal resulted in very little perturbation of the ecosystem with this model, partly because sharks have low rations and low P/B ratios and partly because sharks do feed on a wide range of prey types. These results contradict a popular vision of sharks as apex predators that regulate prey population stability and system biodiversity.

We must acknowledge that fisheries have been pursued for many years in much of the pelagic habitat. The resultant changes in shark populations, their effects on prey populations, and the consequent ecosystem effects may have developed long before scientific records were begun. Accordingly, the possibility of a greater role for sharks as keystone predators was explored by simulating a greater predation by sharks at the trophic vertex. To do this, we created two, alternative Ecopath diet matrices. The Baseline scenario (Table 2) was one alternative; it adhered to documented fractions of sharks in the diets of other sharks (see, for example, Cortes 1999). The resulting CNP 8 model is a relatively conservative descriptor of trophic dynamics on two counts. First, it assumes an equilibrium as the initial condition so that perturbations of the

Table 2. Prey/Predator Matrix for Baseline Scenario of CNP 8

Prey	Predator 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 Bigeye tuna	0.1	0.1	0.1		2	3		1	2											
2 Yellowfin tuna	0.1	1	0.1		7	10	7		2											
3 Albacore tuna	0.1					3		1												
4 Blue shark				0.4		10														
5 Blue marlin						1														
6 Large sharks						1														
7 Brown sharks						4	1													
8 Swordfish					1	1														
9 Other billfish					1	2														
10 Mahimahi	5	10	5		10	5	2	10	5											
11 Small scombrids	4	14	12		13	15	14	5	20	20			30							
12 Flying squid	15		20	35	20	5	40		5											
13 Skipjack tuna	3	5	3		30	10	2		15											
14 Lancetfish	5		3			3	3	3												
15 Squids	15	10	10	20	20	5	30	20	30	15	20	20	10							
16 Flying fish		10								20										
17 Mesopelagic fishes	33	15	7	25		10	15	20			10	4	5	15	6					
18 Epipelagic fishes	5	15	15	10	16	13	17	9	28	28	20	6	25	5	4					
19 Epipelagic micronekton	5	10	10	5		10	20			10	35	30	20	15	40	100	20	80		
20 Mesopelagic micronekton	10	10	15	5		10	10			10	15	40	10	65	50		80	20		
21 Phytoplankton																			100	100

Symbol defines each group name as prey or predator. Columns are percentage by mass of the diet for each predator.

model tend to cause responses that return to equilibrium; and second, it uses the most recent descriptions of shark biology as inputs and therefore underrepresents conditions of the past when sharks and their prey were probably more abundant and of larger average size. To compensate, we constructed a set of inputs that represented ecological conditions that would be potentially similar to those before the advent of modern fisheries. This second alternative (The Apex Shark scenario) used the same estimates of ration (Q/B) for sharks, but it focused piscivory by sharks on large fishes such as billfishes and tunas, eliminated small fish as prey, and allowed intraguild cannibalism to increase so that sharks became a larger component of the shark diet (Tables 3 and 4). The purpose of the second scenario was to simulate likely ecological effects if current shark populations were allowed to expand to prefishery levels. The Appendix details the sources of parameters for CNP 8 and both the Baseline and Apex Shark scenarios.

The Apex Shark diet alternatives were constructed to account for more of the natural mortality of sharks, billfishes, and tuna than is indicated in the literature on their diets. In the Baseline model and in a previous Ecopath model for this system

(CNP 6), fishing mortality (F) and predation mortality (M2) accounted for only about 50% of the mortality experienced by large predators. Ecotrophic efficiency (EE) for large fish was around 0.5, causing unexplained natural mortality (M0) to be a large fraction of total mortality, Z, where M0/Z = 1–EE. In other words, the model provided specific accounting for only 50% of the mortality for apex predators. A high natural mortality (M = M0 + M2) was required for model consistency with fishery exploitation levels in the realm of F<M. Unless a large M0 was set by using a low EE, the documented diets of top predators included so little of the trophic vertex that F≫M0 + M2. For example, if the recommended default EE value of 0.9 was used, then M0 was 10% of Z, fisheries appeared to be overexploited (F/M≫1.0), and modeled changes in F produced exaggerated responses in top predator biomass.

For the increased apex predation diet models (Apex Shark Scenario), the M2 values for sharks, billfishes, and tunas were increased in an attempt to achieve high EE values while keeping F/M as close as possible to the original inputs (Table 5). We eliminated shark predation on small scombrids, lancetfish, and fish nekton from the Apex Shark diet

Table 3.   Ecopath Parameters for the Apex Shark Scenario of CNP 8

Group Name	Trophic Level	Biomass (mt/km^2)	Prod./Biom.	Cons./Biom.	Ecotrophic Efficiency
Bigeye tuna	4.0	7.0	0.8	16.0	0.89
Yellowfin tuna	4.0	17.36	1.2	18.0	0.87
Albacore tuna	4.0	6.98	0.6	12.0	0.92
Blue shark	4.4	11.98	0.3	2.8	0.9
Blue marlin	4.6	4.07	0.3	4.0	0.9
Large sharks	5.1	0.5	0.25	2.5	0.9
Brown sharks	4.7	9.86	0.3	2.8	0.9
Swordfish	4.2	3.78	0.4	5.0	0.9
Other billfish	4.3	1.85	0.5	5.0	0.9
Mahimahi	3.9	17.0	3.0	20.0	0.9
Small scombrids	3.5	211	2.0	10.0	0.9
Flying squid	3.3	15.8	5.0	50.0	0.9
Skipjack tuna	3.9	41.6	1.9	20.0	0.74
Lancetfish	3.2	33.1	0.3	2.9	0.9
Squids	3.1	353	2.5	25.0	0.9
Flying fish	3.0	55	2.0	10.0	0.9
Mesopelagic fishes	3.0	683	1.5	6.0	0.9
Epipelagic fishes	3.0	871	1.5	6.0	0.9
Epipelagic micronekton	2.0	1291	10.0	50.0	0.8
Mesopelagic micronekton	2.0	1717	7.0	35.0	0.8
Phytoplankton	1.0	2493	100.0	—	0.5
Detritus	1.0	1.0	—	—	—

Inputs as outlined in the text and Table 1

matrices (Table 4). These components totaled about 35%–50% of shark diets in the basic model. They were replaced with increased predation on sharks, billfishes, and tunas. In the Baseline diet matrices (Table 2), the percentages of shark predation on sharks was kept at about that reported in the literature—15% for large sharks, 1% for brown sharks, and 0.5% for blue shark. In the Apex Shark model, predation on sharks by sharks was allowed to increase to 30% for large sharks, 7% for browns sharks, and 5% for blue shark (Table 4).

In the Apex Shark diet matrix, large shark predation on billfishes (blue marlin, swordfish, and other billfish) was increased from 4% (Baseline model) to 10% and brown shark predation on billfishes was increased from 0% to 5%. Large shark predation on tunas (bigeye, yellowfin, albacore, and skipjack) was increased from 26% in the Baseline model to 46% in the Apex Shark model. Brown shark predation on tunas increased from 9% in the Baseline model to 49% in the Apex Shark model. Blue sharks were assumed to feed lowest on the food web of the three shark groups. They did not consume billfishes or tunas in the Baseline model, but we assumed that they could consume 30% tuna in the Apex Shark model. (It is worth noting that blue shark have not been reported to consume tuna in any of the studies published to date.)

In the Baseline model, cannibalism by small sharks (that is, brown sharks on brown sharks) was less than 1%. In the Apex Shark model, cannibalism was increased to 5% in all three shark groups. Making sharks eat more sharks, and in particular making them more cannibalistic, proved to be the only way to provide sufficient predation mortality on sharks to balance the F/M ratio at EE = 0.9. Furthermore the increased cannibalism in the Apex Shark model increased the shark biomass solution in Ecopath and made them more important predators on billfishes and tunas, even though the proportion of tunas in their diet decreased.

Obviously, many combinations of changes in inputs could be made, and few, if any, are based on solid quantitative evidence. We do not (and cannot) know the prefishery abundance or diets of sharks or other fishes in the Central North Pacific. We do know that sharks are among the species most vulnerable to changes as fisheries develop. Our Apex Shark scenario is simply a guess at what ecological conditions might have been like before longline fisheries began and therefore what they might become if those fisheries were removed.

Table 4. Prey/Predator Matrix for Apex Shark Scenario of CNP 8

Prey	Predator 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1 Bigeye tuna	0.1	0.1	0.1		2	7	4	1												
2 Yellowfin tuna	0.1	1	0.1	8	7	20	14		2											
3 Albacore tuna	0.1					6	5	1												
4 Blue shark				5		12	8													
5 Blue marlin					4	2														
6 Large sharks						5														
7 Brown sharks					13	5														
8 Swordfish						1	4	2												
9 Other billfish					1	2	1													
10 Mahimahi	5	10	5		10	5	2	1	5											
11 Small scombrids	4	14	12		13			5	20	20			30							
12 Flying squid	15		20	35	2	5	40		5											
13 Skipjack tuna	3	5	3	22	30	13	26		15											
14 Lancetfish	5		3					3												
15 Squids	15	10	10	20	20	5	30	20	30	15	20	20	10							
16 Flying fish		10								20										
17 Mesopelagic fishes	33	15	7					20			10	4	5	15	6					
18 Epipelagic fishes	5	15	15		16			9	28	20	20	6	25	5	4					
19 Epipelagic micronekton	5	10	10	5		1	2			10	35	30	20	15	40	100	20	80		
20 Mesopelagic micronekton	10	10	15	5		10	10			10	15	40	10	65	50		80	20		
21 Phytoplankton																			100	100

Symbol defines each group name as prey or predator. Columns are percentage by mass of the diet for each predator.

RESULTS

Both the Baseline scenario and the Apex Shark scenario were used as the basis for evaluating the management approaches expressed in two different types of ecological context. In the first case, manipulations were exclusively focused on ecological effects that might derive from the shark fishery components of the system. Ecological effects expressed in the shark components derive from one of two management actions: (a) increasing the current finning rate to levels that would double shark mortality (2× Finning), or (b) eliminating the practice of finning (Ban Finning).

The second case was built to simulate ecological responses that might be evoked if the longline fishery and all of the species it harvests were subjected to one of two management actions: (a) increasing fishing by twofold (2× Fishing), which would produce exploitation rates in the Central North Pacific similar to the current intensity of longline fisheries in the north Central Atlantic, Carribean, and Gulf of Mexico; or (b) eliminating the longline fishery in the Central North Pacific (Ban Fishing). Both management actions were simulated under Ecopath in-

puts of the Baseline scenario and again for those of the Apex Shark scenario.

Each of the simulations was conducted for a 50-year period. At year 10, the management perturbation was introduced and responses of the model were tracked for the remaining 40 years as a new equilibrium was established. Model output is normalized to the Ecopath equilibrium with changes in response to perturbation expressed graphically as departures from the ratio of the initial conditions. Declines in a state variable are plotted through time as reductions expressed in the ratio of start:end biomasses and increases as the ratio of end:start biomass. One figure (Figure 2) is presented as a summary of time dynamics for the simulation of 2× Fishing under the Baseline scenario. For clarity, the state variables presented are those that exhibited strongest responses (50% change or more). Other figures (Figures 3 and 4) are summaries of the net change in the major predators and their prey for each combination of scenarios and manipulations.

Responses by modeled biomass pools usually reached a new equilibrium within a 10–20 year period after manipulation. The response to 2× Fishing under the Baseline scenario (Figure 2) demon-

Table 5. Mortality Rates Used for the Baseline and Apex Shark Scenarios

Group	Baseline Scenario				Apex Shark Scenario		
	Z	F	M2	M0	F	M2	M0
Large shark	0.25	0.10	0.025	0.125	0.1	0.125	0.025
Brown shark	0.3	0.116	0.034	0.15	0.103	0.167	0.03
Blue shark	0.3	0.126	0.024	0.15	0.1	0.17	0.03
Blue marlin	0.3	0.146	0.004	0.15	0.123	0.147	0.03
Other billfish	0.05	0.174	0.076	0.25	0.2	0.25	0.05
Bigeye tuna	0.8	0.4	0.144	0.256	0.4	0.315	0.085
Yellowfin tuna	1.2	0.384	0.364	0.452	0.384	0.657	0.159
Albacore tuna	0.6	0.3	0.048	0.252	0.3	0.25	0.05
Swordfish	0.4	0.16	0.04	0.2	0.159	0.207	0.034
Mahimahi	3.0	0.066	1.434	1.5	0.118	2.582	0.3
Skipjack tuna	1.9	0.38	0.669	0.851	0.38	1.018	0.502
Small scombrids	2.0	0.0	1.8	0.2	0.0	1.8	0.2
Flying squid	5.0	0.0	4.5	0.5	0.0	4.5	0.5
Lancetfish	0.3	0.007	0.263	0.25	0.0	2.25	0.25
Squids	2.5	0.0	2.25	0.25	0.0	2.25	0.25
Flying fish	2.0	0.0	1.8	0.2	0.0	1.8	0.2
Mesopelagic fishes	1.5	0.0	1.35	0.15	0.0	1.35	0.15
Epipelagic fishes	1.5	0.0	1.35	0.15	0.0	1.35	0.15

Symbols for mortality types are those used in text.
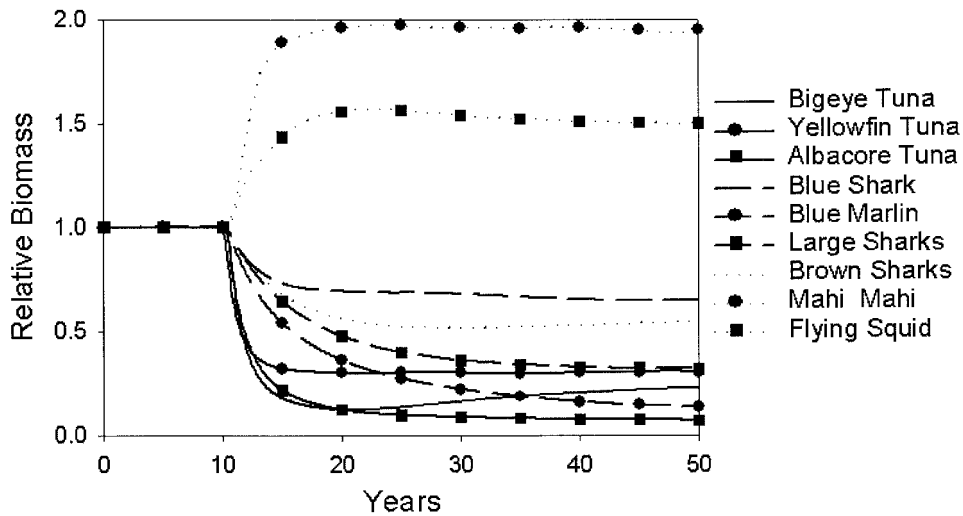
Figure 2. Time course of responses to manipulation of CNP 8. The Baseline scenario is for a doubling of the longline fishery (2× Fishing) at 10 years into a 50-year simulation.

strates the time course of changes for representative state variables that were most responsive to a doubling of mortality owing to longline fisheries. Figure 3 presents a summary of net responses to increased exploitation for each of the major predator groups. Nearly all apex predators declined; large and slowly maturing fishes were most affected by increased fishing. In order of greatest decline, those species were blue marlin, large sharks, albacore tuna, brown sharks, and bigeye tuna. Lancetfishes, mahimahi, and flying squids increased as a result of reductions in their predators and/or competitors.

Rates of change demonstrate the effect of life history attributes described by the parameters of the Ecopath inputs; species with low P/B (for example, blue marlin and large sharks) show greater lags and greater total change.

The removal of longline fisheries produced opposite responses, but they were not directly equivalent. Blue marlin and large sharks increased strongly, while lancetfishes decreased greatly. Yellowfin tuna, swordfish, and blue sharks were the least responsive species among the apex predator guild. Skipjack tuna, squids, and small scombrids
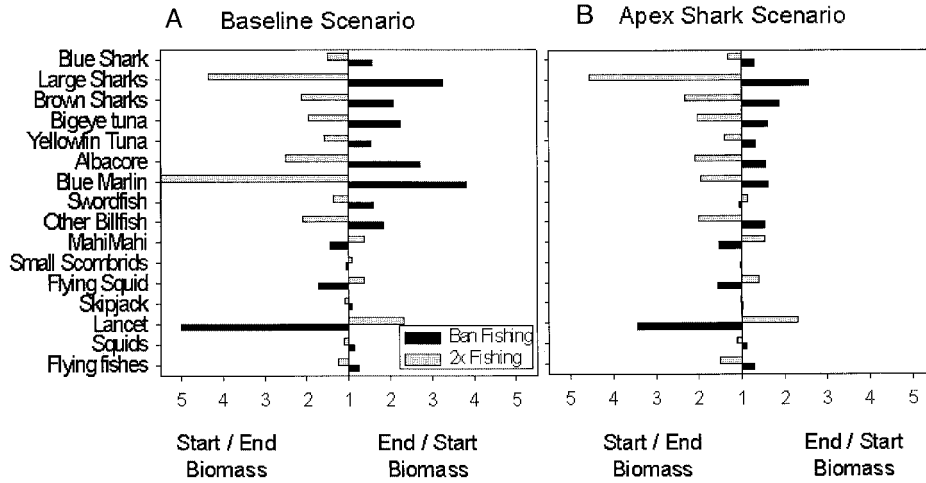
Figure 3. Changes in the CNP 8 state variables under the **A** Baseline or **B** Apex Shark scenario and in response to manipulations that double fishing rates for all components (2× Fishing) or remove all fishery exploitation (Ban Fishing). Manipulations were imposed at 10 years into a 50-year simulation. Final biomasses are plotted as the ratio of start/end for those that decreased and as end/start for those that increased.
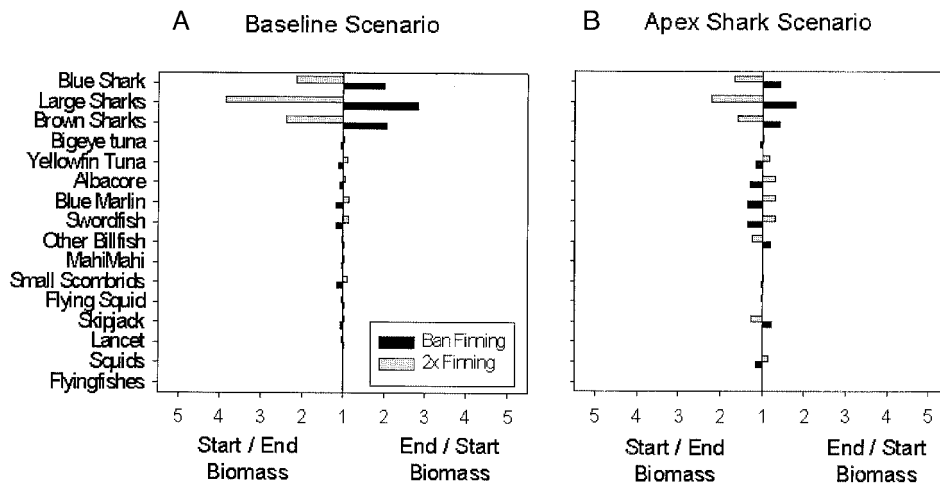

Figure 4. Changes in the CNP 8 state variables under **A** the Baseline or **B** Apex Shark scenario and in response to manipulations that double fishing rates for all sharks (2× Finning) or remove all shark exploitation (Ban Finning). Manipulations were imposed at 10 years into a 50-year simulation. Final biomasses are plotted as the ratio of start/end for those that decreased and as end/start for those that increased.

were little affected by either an increase or a decrease in longline fishery effects. These animals have very high P/B values and appear to tolerate high levels of exploitation or predation.

Equivalent manipulations of the model under the Apex Shark scenario produced somewhat different results from those of the Baseline responses. Large sharks and brown sharks were most affected. All other members of the apex predator guild were more resilient to perturbation because sharks in this Ecopath version are depicted as the dominant predator in the system and a major cause of natural mortality for other exploited members of the food web. Increases or decreases in fishing mortality create compensatory responses in mortality (M2) due to changes in predation by sharks and because fisheries also remove shark prey.

If management actions are focused exclusively on shark finning in the Baseline condition, a twofold increase in shark finning produces strong declines in all three shark components (Figure 4). Banning shark finning produces a similar and opposite re-

sponse. Little or no change occurs in the remaining components of the food web. Similar manipulations in the Apex Shark scenario produce less decline in the sharks and a somewhat greater response among the other components of the food web. Reductions or increases in sharks produce opposite but only modest responses in tunas and billfish. For that reason, their shared prey are little affected. Keystone predator effects are not apparent in either the Baseline or the Apex Shark cases.

DISCUSSION

An important lesson emerged from the Apex Shark version of the Ecopath model. Increasing the amount of cannibalism produced very strong responses in the food web. If other sharks are as little as 1% of the shark diet, strong effects arise and spread to both the prey and competitors of sharks. If that 1% were juvenile sharks, then population effects might be much more important than those indicated by a biomass-based model such as Ecosim.

Many lines of evidence and arguments point to predator avoidance as a component in the selection pressures for habitat choice and migratory behaviors in shark life history patterns (Walker 1998). Given that, strong interactions may have been historically important and less readily apparent in contemporary observations because migrations and antipredatory behaviors effectively sequester and reduce the interactions to very-low-frequency events.

We believe that greater attention should be paid to the potential role of cannibalism among sharks. The Ecosim model contains a structure for simulating the effect of predator avoidance, but the available literature on cannibalism and intraguild predation by sharks is not sufficient to allow us to implement that simulation without some quantitative guidance and the expertise of experienced observers. The continued monitoring of the effects of shark removal programs offers an analogous opportunity (van der Elst 1979).

The Ecosim model allowed us to evaluate potential fishery management actions as a manipulation of the food web involving sharks and their competitors. The CNP 8 model does demonstrate strong predator-removal effects when yellowfin or bigeye tunas are heavily harvested. When either one is fished intensively, reciprocal changes are evident among many of the competitors and prey pools. The responses are similar to those documented in the CNP 6 model (Kitchell and others 1999). As made evident in Figure 3, increasing or banning longline fishing in the Baseline scenario has profound effects at many levels of the food web. Like the CNP 6 modeling analyses, we conclude that the keystone predator in this system is, in fact, the longline fishery. Although the two models have rather different trophic structures, they produce similar results because of the similarity in the basic characteristics of their respective Ecopath inputs for each state variable.

Ecopath models require an initial assumption of equilibrium conditions based on contemporary empirical observations. This allows Ecosim to forecast outcomes for alternative fishery management scenarios. A comparison of Ecosim results with the known historical trends in data would require stock assessments that produced an Ecopath for some time in the past. Although we have not attempted to construct that Ecopath, we can compare Ecosim results with data based on general characteristics. For example, Ecosim results say that an increase in longline fisheries causes declines in billfishes and large tunas. Their prey, such as mahimahi, should increase accordingly. In fact, that observation is widely confirmed by increases of mahimahi in the catch records for many of the world's tropical seas. At this writing, adequate historical records of abundance are not available for many of the key components in the CNP. As those data become available, we would encourage the use of traditional stock assessment methods as a way to hindcast the structure of an Ecopath model for the prefishery system. That model could then be used as a basis for quantitative evaluation of changes in the relative importance of mortality owing to predation and the effects of fishery development on apex predator populations.

We also encourage fishery managers to acknowledge that a decade or more may be required for some species to show evidence of the results of sudden changes in fishing rates. This model produces long lags owing to trophic effects and their consequent expression in biomass dynamics. In an analogous way, a strong or weak year class of an important predator would require many years before its full effects were expressed in the food web. Such lags are generally proportional to life history characteristics and would be most pronounced for the long-lived, slow-maturation characteristics of most shark species.

Keystone predator effects are known to occur in many systems (Kitchell and others 1999). In more recent reports, they were evident in cases where a relatively rare predator (killer whales) imposed selective predation on sea otters and produced dramatic results at many levels in kelp forest systems (Estes and others 1998). Although our Apex Shark scenarios created a much greater predatory impact, the CNP 8 model does not exhibit keystone effects when harvest rates on sharks are substantially different. Although this result does not eliminate the prospect that other sharks in other places may have important ecosystem effects through selective predation, the relatively low biomass, modest feeding rates, and slow population turnover times of pelagic sharks make their sympatric competitors (tunas and billfishes) a more important component of the apex predator guild in this Central North Pacific food web.

At the ecosystem scale, both the CNP 6 and CNP 8 versions of the model demonstrate that fishing for sharks has profound effects on the sharks but much more limited effect on other components of the Central North Pacific food web. Although severe reduction or removal of sharks from this large pelagic system is possible, it does not lead to a catastrophic change in the structure and function of the ecosystem that produces sharks. Based on these models, we see no evidence of strong trophic cas-

cades (Carpenter and Kitchell 1993; Shiomoto and others 1997) or keystone predator effects owing to sharks in the Central North Pacific system.

We defined the CNP as a single system. In fact, its huge areal extent includes substantial gradients in temperature and nutrient supply, plus strong, localized productivity effects owing to island wakes, sea mount upwellings, oceanic fronts, and so on. In addition, many of the members of the food web engage in large-scale, intra-annual spawning and/or feeding migrations that cover great distances. None of that spatial or temporal heterogeneity is expressed in this version of the model. Although not reported herein, we have constructed two CNP versions using the Ecospace software (Walters and others 1999). One of those models used simple diffusive movement and broad thermal habitat preferences (north vs south regions) to represent heterogeneity; another simulated convergence zone dynamics that concentrates fish, fishing, and production from larger areas adjacent to those convergence areas (C. H. Boggs unpublished). Neither of these models yielded predictions that were substantially different from what we obtain using CNP 8. In other words, the consequences of aggregation and its stronger trophic interactions are already represented implicitly via the diet composition parameters. The development of other, more detailed levels of complexity will require greater resolution of spatial and temporal differences in predator–prey interactions as represented in the diet matrix of Ecopath.

Our modeling results are probably representative of those that might be derived in any tropical or subtropical pelagic system where sharks are associated with an abundant and diverse group of tunas and billfishes. The food habits and life histories of the scombrid and xiphoid fishes make them capable of rapid compensatory responses if shark populations are reduced through exploitation. As a consequence, food web structure and trophic dynamics in the CNP are only modestly responsive to the removal of sharks.

In systems where tunas and billfishes play a lesser role, sharks may be important keystone predators. Stevens and others (2000) conducted shark removal simulations on Ecosim models for the Northeast Venezuela Shelf, the Alaska Gyre, and the French Frigate Shoals. Complex responses emerged from the Northeast Venezuela model. The removal of sharks allowed increases in many—but not all—shark prey and a series of "strong and unforseen changes in the abundances of many species" (Stevens and others 2000). The Alaska Gyre and a similar model for Prince William Sound showed strong responses to the removal of sharks because they are significant predators of salmon, Pacific cod, pollock, and/or marine mammals. (Stevens and others 2000; KK. Aydin personal communication).

The original Ecopath model was developed for the French Frigate Shoals ecosystem (Polovina 1984). A recently implemented Ecosim model for this system demonstrated that shark removal can have complex effects. When tiger sharks were selectively removed in the model, green turtles and albatrosses (Laysan and black-footed) increased dramatically because both are preyed upon by tiger sharks. Reef sharks and the Hawaiian monk seal also increased due to the release of competitive interactions (Stevens and others 2000; J. Polovina personal communication). Although turtles generally comprise a very small proportion of shark diets (Marquez 1990; Fergusson and others 2000), that mortality source may be important for animals, such as sea turtles, that have low population densities, slow turnover rates, and very low levels of natural mortality.

The examples developed here reveal interesting trophic interactions among the species that may be the focus of conservation interests—billfishes, sharks, sea turtles, sea birds, and marine mammals. When considered from the perspective of an ecosystem context, complex outcomes can derive from tradeoffs that arise from predator–prey and/or competitive interactions involving rare or endangered forms. Those outcomes cannot be foreseen if one maintains a single-minded focus on the population dynamics of individual species, as is so commonly expressed in the literature of conservation organizations (Camhi and others 1998; Camhi 1999). In a policy context analogous to that of the single-species focus, there have been strident calls for the closure of US longline fisheries (Hinman 1998). Currently, boats in US registry constitute less than 2% of the Pacific longline fleet; therefore, closure of the US longline fisheries would produce only very small changes in the mortality rates for pelagic sharks. More important, their closure would eliminate the only reliable source of information on the status of the populations of pelagic sharks and other fishes taken on longline gear.

Because budget constraints allow only a very modest research effort by the National Marine Fisheries Service, our active fisheries are our windows to international waters. Closing those windows might offer some comfort to an ecological conscience and have the merit of a highly principled political position, but it requires the tradeoff of becoming progressively less well informed about the status of these pelagic ecosystems. In addition, there

would be no means of providing incentives for the development of methods (such as set sites, timing, duration, gear types, and so on) that could reduce the mortality rates for bycatch species such as billfishes, turtles, sea birds, and sharks. In our view, the tradeoff is one of principle (closed fisheries) for ignorance (no data). In cases where a reduction in fishery mortality is essential, we believe that a reduced, yet properly monitored and active fishery is a preferable alternative and that it could serve as the research surrogate needed to develop fishing methods that accomplish conservation goals.

Several of the Ecopath models available through the University of British Columbia include sharks. When perturbed through a keystone predator test, some of those models also produce strong ecological responses to the removal of sharks. Logically, we should expect that systems will differ in the relative importance of sharks based on their abundance, trophic position, and prey. We should also attend to the adequacy of parameter estimates used to represent sharks in a food web context. There are now more than 100 Ecopath models representing different types of marine ecosystems. A recent assembly of those models provides access to a diversity of prospects for exploring the ecological importance of sharks and their interactions in a food web context (Christensen and others 2000).

The conservation of sharks centers on two main issues. One of them is focused on biodiversity arguments and the unique evolutionary history expressed in the lineage of sharks. That, alone, is a strong and significant basis for concerns about fishery effects on shark populations. The second set of issues commonly includes questions about the importance of sharks in the larger context—that is, as predators that may regulate community structure and ecosystem function (Hinman 1998). The Ecosim modeling approach puts sharks in a larger context—that of an entire ecosystem. Like all models, this one includes simplifications and assumptions that some may find questionable. However, the basic inputs of the Ecopath model should offer greater credibility because they represent a number of known entities that are unique to sharks—their diets, growth rates, mortality schedules, biomass, and population turnover rates. The software is available at http://www.fisheries.com. The Ecopath inputs summarized herein can be modified and tested if users choose to evaluate alternative model structures, inputs, or basic assumptions. We encourage those developments for the modeling of other systems and, importantly, as a means of evaluating basic questions about the ecological importance of sharks that have yet to be resolved.

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Appendix   Parameter Estimates for the CNP 8 Model

The following provides documentation of parameter estimates and diet composition for several apex predator components of the CNP 8 model that have been updated from CNP 6. Some changes derive from reorganizing the state variables specified for CNP 6 by Kitchell and others (1999). Others derive from recently published reviews, which are as cited in the text.

Symbols and their definitions derive from the original Ecopath documentation: Z = total mortality, F = mortality due to fishing, M = natural mortality, which includes $M0$ = unexplained mortality and $M2$ = mortality explained within the model as due to predation. The ratio of annual production (P) to mean biomass (B) is P/B, which is often approximated as equal to Z. The total annual food consumed by a predator is represented as Q and the annual ration as Q/B. The ecotrophic efficiency (EE) scales from 0 to 1 and represents the total amount of production accounted for within the model due to the combination of F and M2 (that is, $EE \bullet P/B = F + M2$).

1. Bigeye tuna (*Thunnus obsesus*). Estimates of natural mortality are highly variable for bigeye tuna. Hampton and others (1996) estimate $M = 0.52$. Hampton (personal communication) estimates $M = 1.2$ near the Equator, and $M = 0.6$ for the Coral Sea (where a bigger size range of fishes was tagged). Hampton (personal communication) also estimated $F = 0.14–0.24$, and Hampton and others (1996) estimate $F = 0.23$ for juvenile bigeye taken in the Western Pacific purse seine fishery. We chose $M = 0.4$ and $F = 0.4$ as input into the model, which implies that the present population is fully exploited. Total mortality $(F + M = Z)$ was used as the approximation of P/B based on the stock assessment of Miyabe (1995). Current bigeye harvest was taken from Lawson (1999), who estimated total Western Pacific harvest equal to 168,459 mt. We divided this by 2 (to get harvest above the Equator) and converted to t/km^2 by dividing by 30,000 km^2 (the approximate area of the model). We estimated total biomass (B) by dividing this harvest by F $(F = 0.4)$. We let Ecopath estimate EE from the input of B, P/B, harvest, and losses to predation specified in Ecopath, instead of specifying EE and estimating biomass. Diet composition for bigeye was mostly derived from the CNP 6 diet matrix; but because two fish nekton pools were now available, we made bigeye eat a high proportion of mesopelagic fish. Proportions were 0.327 for mesopelagic fish nekton and 0.05 for epipelagic fish nekton. Small scombrids comprised 0.04 of diet, which represented the sum of juvenile scombrids in diet from CNP 6. We introduced cannibalism and predation on yellowfin and albacore to make the EE output for these groups exceed 0.5. Cannibalism for bigeye was small (0.001 of diet).

2. Yellowfin tuna (*Thunnus albacares*). Bayliff (1971) estimated $M = 0.8$ in the Eastern Pacific Ocean (EPO) based on analysis of tagging data. Analysis of tagging data in the Western Pacific Ocean (WPO) indicated that M ranged from 0.36 (60–70 mm fish) to 6.3 (20–30 mm fish) (SPC 1997). We used an age-integrated average value of $M = 1.0$ and the estimate of $F = 0.2$ from the same analysis to get $Z = 1.2$. Current yellowfin harvest was taken from Lawson (1999), who estimated an average of 373,910 mt for the period 1990–98. We assumed 200,000 mt of that was within the Central North Pacific (CNP), which gives harvests of 6.667 t/km^2. Total biomass was estimated by dividing this value by F $(F = 0.2)$. As was the case for bigeye, we estimated EE from the specified biomass. Diet composition for yellowfin was also derived from the CNP 6 diet matrix. We pooled all predation on juvenile scombrids into the "small scombrids" group. We divided consumption of fish nekton equally between epipelagic and mesopelagic pools. We assumed that mahimahi comprised 0.1 of yellowfin diet.

3. Albacore tuna (*Thunnus alalunga*). We used the estimate of $M = 0.3$ presented by Shaw and Bartoo (1997), although estimates of tagging data from the South Pacific suggest that M is much less (Sibert pers. comm.). The same analysis indicated the current harvest (approximate 62,850 mt/y) is close to the estimated maximum sustainable yield (MSY) (78,000–86,000 mt/y). For simplicity, we made albacore fully exploited by making $F = M$. We again derived estimates of density by dividing harvest by F. Albacore diet composition was also derived from the CNP 6 diet matrix. We pooled all predation on juvenile scombrids into the "small scombrids" group. Pre-

dation on mahimahi was set slightly lower than the previous estimate of predation on juvenile mahimahi.

4. Blue shark (*Prionace glauca*). We updated the P:B and Q:B substantially. We estimated M = 0.2 based on regression of von Bertalanffy parameters (Nakano and Seki 1999), which agrees with the estimate provided by Smith and others (1998) based on maximum age. We assumed that F = 0.1 to make Z = 0.3. Blue shark harvest was taken from He and Laurs (1998). Q:B was set to 2.78, based on the bioenergetics model of Schindler and others (2002) (in press). We introduced a small amount of cannibalism (0.004), which matched the proportion of sharks in diets described by Cortes (1999). Squid (0.2) and flying squids (0.35) were the dominant components of the diet, with a high proportion of mesopelagic fish nekton (0.246), as taken from Cortes (1999).

5. Blue marlin (*Makaira mazaras*). Parameters were not changed from CNP 6. Goodyear (1998) estimated M = 0.1–0.25 for blue marlin in the Atlantic Ocean, justifying our use of Z = 0.3 here.

6. Large sharks (for example, mako and white sharks). We estimated M = 0.16, based on Von Bertalanffy Growth Function (VBGF) parameters provided in Cailliet and others (1983) for shortfin mako, and then assumed Z = 0.25. We made Q:B equal to 2.5, so that growth efficiency equaled 0.1. This low value was targeted to reflect the endothermic nature of these sharks. We used the standardized diet composition data described by Cortes (1999). Small scombrids (0.15) and epipelagic fish nekton

(0.13) were the two most important diet items. Yellowfin and skipjack tuna were both important (0.1), as were blue sharks (0.1). High consumption rates on yellowfin were introduced in an attempt to explain a higher proportion of their diet. This number may be unrealistic. High values of blue sharks were chosen because they appear to be more abundant than other groups.

7. Brown sharks (for example, oceanic whitetip and silky sharks). We assumed that M = 0.2, based on regression of the oceanic whitetip VBGF parameters in Seki and others (1998). We assumed that Z = 0.3 and set Q:B equal to blue shark Q:B (2.78). The diet composition of silky and oceanic whitetip sharks described in Cortes (1999) and Seki and others (1998) indicates that only 1% of the diet is sharks, so this was allocated to cannibalism. Squids were represented by 30% squid and 5% flying squids. Predation on fishes was dominated by small scombrids (0.14), epipelagic fish nekton (0.17), mesopelagic fish nekton (0.16), and yellowfin tuna (0.07).

8. Swordfish (*Xiphias gladius*). P:B, Q:B, and harvest were not changed from CNP 6. VBGF parameters fit to Pacific swordfish suggest that M = 0.3–0.4 for males and M = 0.22–0.28 for females (Sun and others 1999). From this, we assumed M = 0.3 and Z = 0.4. Swordfish diet was dominated by flying squid (0.4), squids (0.2), and mesopelagic fish nekton (0.2). These numbers were derived from the diet analysis by Hernandez-Garcia (1995) of east Central Atlantic swordfish. The relative proportions of flying squids and squids were based on the depth distribution of swordfish.