

MAXIMAL YIELDS FROM MULTISPECIES FISHERIES SYSTEMS: RULES FOR SYSTEMS WITH MULTIPLE TROPHIC LEVELS

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Abstract. Increasing centralization of the control of fisheries combined with increased knowledge of food-web relationships is likely to lead to attempts to maximize economic yield from entire food webs. With the exception of predator–prey systems, we lack any analysis of the nature of such yield-maximizing strategies. We use simple food-web models to investigate the nature of yield- or profit-maximizing exploitation of communities including two types of three-species food webs and a variety of six-species systems with as many as five trophic levels. These models show that, for most webs, relatively few species are harvested at equilibrium and that a significant fraction of the species is lost from the web. These extinctions occur for two reasons: (1) indirect effects due to harvesting of species that had positive effects on the extinct species, and (2) intentional eradication of species that are not themselves valuable, but have negative effects on more valuable species. In most cases, the yield-maximizing harvest involves taking only species from one trophic level. In no case was an unharvested top predator part of the yield-maximizing strategy. Analyses reveal that the existence of direct density dependence in consumers has a large effect on the nature of the optimal harvest policy, typically resulting in harvest of a larger number of species. A constraint that all species must be retained in the system (a “constraint of biodiversity conservation”) usually increases the number of species and trophic levels harvested at the yield-maximizing policy. The reduction in total yield caused by such a constraint is modest for most food webs but can be over 90% in some cases. Independent harvesting of species within the web can also cause extinctions but is less likely to do so.

Key words: *constraint of biodiversity conservation; food web; Kyoto Declaration; management of fisheries; maximizing revenue and/or yield; omnivory; sustainability.*

INTRODUCTION

Historically, the field of fisheries management has been based on models of single-species exploitation. This is reflected in the fact that fisheries textbooks from the previous decade (Clark 1990, Hilborn and Walters 1992, Quinn and Deriso 1999) devote at most a few pages to management of multispecies systems. Recent years have seen a rapidly growing popularity of multispecies models (e.g., Hollowed et al. 2000, Walters et al. 2000, Yodzis 2001, Latour et al. 2003, Walters and Martell 2004), often under the rubric of “ecosystem management.” Unfortunately, there is almost no general theory to suggest the likely outcome of different types of multispecies management approaches. Harvesting in marine systems is known to have greatly altered their trophic structure (Pauly et al. 1998), and it would be desirable to know whether such alterations would have been more or less likely under an explicitly multispecies approach.

Our goal is to establish what community consequences are expected when a multispecies system is

exploited with the goal of maximizing yield or profit from the food web as a whole. Such strategies are likely to have been applied in the past in the case of multispecies aquaculture in ponds. This approach of maximizing yield from entire communities is the motivation for some proposals to harvest marine mammals. It is increasingly likely to be applied to natural systems in the future, as control of different fisheries is consolidated into a small number of national or corporate groups, and as knowledge of food-web relationships increases. Our analysis suggests that this “whole web” approach is likely to produce severe reductions or extinctions of a large number of species. Up to this point, this question has apparently only been formally analyzed for the case of the simplest multispecies system, a two-species predator–prey system (May et al. 1979, Clark 1990).

The food-web models we employ here represent some of the simplest possible types of multispecies models. The per capita growth rate of each species is assumed to be a linear function of its own population size, and the population sizes of its predators and foods. Analogous assumptions form the foundation of much of the theory based on single-species approaches (e.g., Roughgarden 1998). Clark (1990) and May et al. (1979)

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have investigated the simplest version of this multi-species problem, in which there are homogeneous populations of a predator and a prey species. In Clark's (1990) analysis, the predator's growth rate is entirely determined by its intake rate of prey. To maximize the total sustainable yield or revenue from a predator-prey system, either the predator should be eliminated and only the prey exploited, or, if the predator is sufficiently valuable, only it should be exploited (Clark 1990).

Both of the previous analyses of yield-maximizing exploitation of predator-prey systems have the potential to result in extinction of one of the two species. In theory, yield- or revenue-maximizing exploitation of a single species will only result in extreme overexploitation (or extinction) of a target species when (1) the harvesting policy is based on a flawed model of population dynamics; (2) competition between independent exploiters results in exploitation rates that exceed the optimum (the tragedy of the commons); or (3) investment of revenues from destructive harvesting yields a higher rate of return than maintaining the resource; i.e., there is a high discount rate (Clark 1976, 1990). When only one species is harvested, a single omniscient and rational exploiter pursuing yield maximization would not cause extinction or near extinction of that species.

There is an international consensus supporting reconciliation between sustainable use and the conservation of biological diversity, which appears in the United Nations-sponsored 1992 Convention on Biological Diversity (*available online*).⁴ If this idea is applied to the type of predator-prey system modeled by Clark (1990), it would mandate that predator abundance be maintained above a threshold, such that extinction risk was negligible on some time scale of interest. The adoption of such minimum densities for all species in a larger food web is what we refer to as a "constraint of biodiversity conservation." It is not clear how often a constraint of biodiversity conservation is likely to be needed in multi-species systems where whole-web profit or yield maximization is pursued. That question, and the question of how large a reduction in yield is likely to occur as the result of such a constraint, are both examined here. Some top predators in marine ecosystems are often marine mammals and birds, which are frequently protected from any commercial harvesting. Thus, there are some cases where a partial constraint of biodiversity conservation already applies to some of the species in an ecosystem.

We explore the revenue- or biomass yield-maximizing policies for food-web models with more than two species. Specifically, we considered three types of dynamical models: (1) a two-prey, one-predator model, (2) a three-species-three-trophic-level model that may include omnivory, and (3) a community model with six species and up to five trophic levels. These models

provide a variety of food-web configurations that we use to address the following questions: (1) Is culling of unharvested top predators economically beneficial? (2) Do yield maximizing policies typically involve harvest of many species or many trophic levels? and (3) Do yield maximizing solutions entail extinction of species, and, if so, why do they go extinct? We use the six-species models to investigate the impact of a constraint of biodiversity conservation on both the optimal harvest policy and the yield or revenue that it produces.

METHODS

Model description

We model populations using ordinary differential equations, and we neglect population structure. This simplified approach is adopted because it is the logical starting point for modeling, given that there is no general multispecies theory currently available. The analysis of harvesting a species with simple logistic population growth has formed an essential underpinning for the development of more detailed single-species models (Clark 1976, 1990, Lande et al. 1997). We view the models presented here as providing an essential starting point for analyzing questions of multispecies harvest. As mentioned above, we assume that the per capita growth rates of each species depend linearly on the abundance of some subset of the species in the web. We include a harvesting term for each species, where the per capita harvest rate is the product of a fishing effort, e_i for species i , and a catchability term (catch per unit effort per unit stock abundance), q_i .

The rate of change in the abundance of species i , dn_i/dt is

$$\frac{dn_i}{dt} = \left(r_i + \sum_{j=1}^s a_{ij}n_j - q_i e_i \right) n_i \quad (1)$$

($i = 1, 2, \dots, s$), where r_i is the per capita rate of population change when all species have densities approaching zero; a_{ij} is the effect of an individual of species j on the per capita population growth rate of species i ; e_i is the fishing effort for species i ; q_i is the catchability for species i ; and s is the number of species in the biological community. For simplicity, we assume that a_{ij} is constant, implying that the per capita growth rate is a linear function of population abundances. For a consumer species ($i > 2$), r_i is negative, and represents a density-independent per capita death rate. The effect of an individual of species i on the per capita growth rate of species j , a_{ij} , is negative if species j exploits i or if species i and j compete directly with each other; a_{ji} is positive if species j exploits i and $a_{ji} \leq -a_{ij}$, where $m_{ji} = -a_{ji}/a_{ij}$ (1) is the energy conversion rate from prey i to predator j . Our analysis consists of determining the set of fishing efforts that maximize the value of the harvest. Readers who are not concerned with how this set of efforts was determined may skip to the *Results* section, below. For simplicity, we refer to all

⁴ (<http://www.biodiv.org/convention/araticles.asp>)

maximal solutions as “MSR,” or maximum sustained revenue. In simulations without harvest costs, this may actually be a biomass- or gross revenue-maximizing strategy, while in cases with costs it represents maximum sustained net revenue.

General methods of analysis

The MSR depends on the equilibrium abundances of species that still exist under the set of fishing efforts chosen. The coexistence equilibrium (with positive densities of all species), denoted by $\mathbf{n}^* = (n_1^*, n_2^*, \dots, n_s^*)^\top$, is given by $\mathbf{n}^* = -\mathbf{A}^{-1}(\mathbf{r} - \mathbf{q}\mathbf{e})$, or

$$\begin{pmatrix} n_1^* \\ n_2^* \\ n_3^* \\ \vdots \\ n_s^* \end{pmatrix} = \begin{pmatrix} a_{11} & a_{12} & a_{13} & \cdots & a_{1s} \\ a_{21} & a_{22} & a_{23} & \cdots & a_{2s} \\ a_{31} & a_{32} & a_{33} & \cdots & a_{3s} \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ a_{s1} & a_{s2} & a_{s3} & \cdots & a_{ss} \end{pmatrix}^{-1} \begin{pmatrix} r_1 - q_1 e_1 \\ r_2 - q_2 e_2 \\ r_3 - q_3 e_3 \\ \vdots \\ r_s - q_s e_s \end{pmatrix} \quad (2)$$

where the superscript \top means the transpose of a vector; \mathbf{A}^{-1} means the inverse matrix of \mathbf{A} ; \mathbf{A} is a matrix whose (i, j) th element is a_{ij} , $\mathbf{r} = (r_1, r_2, r_3, \dots, r_s)^\top$; $\mathbf{q}\mathbf{e} = (q_1 e_1, q_2 e_2, q_3 e_3, \dots, q_s e_s)^\top$. The equilibrium is feasible if all population sizes are positive.

The equilibrium is stable if all eigenvalues of the community matrix \mathbf{C}^* have negative real parts, where n_i^* is the equilibrium abundance of species i , and \mathbf{C}^* is

$$\mathbf{C}^* = \begin{pmatrix} a_{11}n_1^* & a_{12}n_1^* & a_{13}n_1^* & \cdots & a_{1s}n_1^* \\ a_{21}n_2^* & a_{22}n_2^* & a_{23}n_2^* & \cdots & a_{2s}n_2^* \\ a_{31}n_3^* & a_{32}n_3^* & a_{33}n_3^* & \cdots & a_{3s}n_3^* \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ a_{s1}n_s^* & a_{s2}n_s^* & a_{s3}n_s^* & \cdots & a_{ss}n_s^* \end{pmatrix}. \quad (3)$$

If the community matrix has a pair of conjugate imaginary eigenvalues with a positive real part, the equilibrium is an unstable focus, and these species may coexist, but their populations fluctuate permanently. If the community matrix has a real and positive eigenvalue, the equilibrium is a saddle point and the full set of species is unlikely to persist.

The feasibility of an equilibrium and its local stability depend on the fishing efforts on all species, \mathbf{e} because \mathbf{n}^* depends on \mathbf{e} . The mean total rate of revenue acquisition, denoted by Y , from all s species is

$$Y = \frac{1}{T} \int_0^T \left\{ \sum_{i=1}^s [p_i q_i n_i(t) - c_i] e_i \right\} dt \quad (4)$$

where T is a sufficiently large time interval, p_i is the value of an individual catch of species i , and c_i is the cost of a unit of fishing effort on species i . Value is generally the economic price, but our approach is consistent with any measure of value (biomass, protein content, etc.). We do not adopt a discounting factor in calculating yield, because it is not clear that such a factor should be used if noneconomic values are used, and because having such a factor does not greatly

change the optimal policy, unless some species has such a slow growth rate relative to the discounting factor that immediate harvest of all individuals is optimal. We assume that q_i , p_i , c_i , and e_i are independent of time, regardless of any stock fluctuations. Because of the linearity of the per capita growth-rate functions, the long-term average abundances in cycling systems are identical to the equilibrium abundances (see Hofbauer and Sigmund 1988). Therefore, the long-term yield given by Eq. 4 is

$$Y = \sum_{i=1}^s (q_i p_i n_i^* - c_i) e_i \quad (5)$$

where n_i^* is the equilibrium abundance of species i . The fishing policy that maximizes Y (maximum sustainable revenue, MSR, denoted by Y_{MSR}) must satisfy

$$dY_{\text{MSR}}/de_i = 0 \quad \text{if } e_i > 0 \quad (6a)$$

$$dY_{\text{MSR}}/de_i \leq 0 \quad \text{if } e_i = 0 \quad (6b)$$

for each species i . Solution types were defined by whether each e_i was positive or zero, and the set of Eq. 6a for nonzero efforts was solved numerically.

Some of the original set of s species may go extinct at the MSR harvesting policy. If k species belonging to a set of species, denoted by $S = \{i_1, i_2, \dots, i_k\}$, persist in the community and the other $(s - k)$ species go extinct under the MSR policy, any equilibrium must satisfy $dn_i^*/dt = 0$ for extant species i and $n_j^* = 0$ for extinct species j . Suppose that there is a particular set of remaining species, denoted $S = \{i_1, i_2, \dots, i_k\}$, at the MSR. Construct matrices and vectors analogous to the original \mathbf{n}^* , \mathbf{A} , \mathbf{r} , and $\mathbf{q}\mathbf{e}$, that consist of only these k species. These are denoted \mathbf{n}_S^* , \mathbf{A}_S , \mathbf{r}_S , and $\mathbf{q}_S \mathbf{e}_S$, respectively. The unique set of equilibrium densities for which these k species persist and the other $(s - k)$ species go extinct, is given by

$$\mathbf{n}_S^* = -\mathbf{A}_S^{-1}(\mathbf{r}_S - \mathbf{q}_S \mathbf{e}_S) \quad (7)$$

which is obtained by following the same steps that led to Eq. 2. If the abundance of any species at the equilibrium is negative, the species set S is not feasible. From a linear stability analysis, the equilibrium is locally stable if the community matrix \mathbf{C}_S^* does not have any eigenvalues with a positive real part, and if, for all extinct species,

$$\left(\frac{1}{n_j} \right) \left(\frac{dn_j}{dt} \right) = r_1 - q_j e_j + \sum_{i \in S} a_{ji} n_i^* < 0 \quad (8)$$

at $\mathbf{n}_S = \mathbf{n}_S^*$ and $n_j = 0$. Inequality 8 guarantees that species j cannot invade once it is extinct in the local system. Condition 8 is not needed for stability unless there is a potential source of immigrants of the locally extinct species. In the tables that summarize our results, we implicitly assume that there is no immigration, so excluding a species does not require continued fishing effort after the population drops to zero.

There are $(2^s - 1)$ candidate equilibria consisting of a non-empty subset of the original s species. The feasibility of each equilibrium again depends on the fishing effort vector \mathbf{e} . We obtain these equilibria from Eq. 7. For a given subset of k extant species, there are $2^k - 1$ candidate solutions that satisfy conditions 6a and 6b. If the equilibrium when the fishing effort \mathbf{e} satisfies conditions 6a and 6b is a saddle point, we exclude this solution. We then search for the average yield that is maximal among all the feasible solutions that are either stable or cyclic (i.e., unstable focus) equilibria. This solution will depend on the prices, p_i , of the species.

Analysis of different food-web systems

We now consider three types of food webs using the above framework for analysis.

Two-prey, one-predator systems.—Because the predator does not persist if both prey go extinct, there are six subsets of species consisting of 1 or 2 or 3 extant species. Some of these are functionally equivalent. For example, the set of systems with the predator and prey number 1 has identical average properties to the set of systems with the predator and prey 2, since the parameters for each prey species are randomly selected from the same range. We number the distinct systems according to which species are present and which species are harvested; the different possibilities for harvest result in 11 community–harvest combinations, labeled C1–C11. The biological systems under maximum sustainable revenue have four potential configurations: (i) a single prey (prey number 1 or 2) without predator; (ii) both prey species without predator; (iii) the predator and either prey 1 or 2; and (iv) all three species. If the MSR solution has a single prey species, that species must be harvested; this combination is labeled C1. If both prey are present without the predator, the potential solutions are to harvest one (C2) or both (C3). If there is one predator and one prey, the possible solutions are to harvest only the prey (C4), only the predator (C5), or both species (C6). If all three species are present, the potential solutions are to harvest one prey (C7), both prey (C8), one prey and one predator (C9), only the predator (C10), or all three species (C11). We examine whether these solutions are feasible (population abundances and fishing efforts are nonnegative and the equilibrium is either locally stable or an unstable focus). We determine the MSR for each feasible combination of species presence and harvesting, and compare these 11 solutions to determine which produces the maximum sustainable revenue (i.e., the global MSR).

Equilibrium solutions that maximize sustainable revenue for two-prey, one-predator systems were determined for five variations of the basic model for community dynamics: (i) without interspecific competition or direct density effect in the predator ($a_{12} = a_{21} = 0$ and $a_{33} = 0$); (ii) with weaker interspecific than intraspecific competition ($a_{11} < a_{12} < 0$ and $a_{22} < a_{21} < 0$);

and $a_{33} = 0$); (iii) with stronger inter- than intraspecific competition; (iv) with no competition but with direct predator-density effects ($a_{12} = a_{21} = 0$ and $-1 < a_{33} < 0$); and (v) with relatively weak interspecific competition, and a direct predator density effect ($a_{11} < a_{12} < 0$ and $a_{22} < a_{21} < 0$ and $-1 < a_{33} < 0$). These inter- and intraspecific competition parameters are seldom measured, so it is important to determine how different assumptions about their presence and/or magnitude affected the global MSR. In determining the frequencies of different types of solutions, we do not distinguish cases where a different (single) prey species was extinct or harvested. For each of the five sets of assumptions listed above, we examined 1000 randomly chosen parameter sets that have a feasible equilibrium consisting of three species in the absence of any fisheries. For simplicity we assume that $a_{12} = a_{21}$ and $a_{13} = a_{31}$, i.e., we set the conversion efficiency from prey to predator equal to 1. This somewhat unrealistic assumption does not appear to affect the main qualitative conclusions presented below. We also assume that q_i is 1, because q and p affect the optimal solution similarly. Other parameter values are chosen by independent draws from a uniform distribution between 0 and 1 for r_i , p_1 and p_2 , and between 0 and 10 for p_3 because predators usually fetch a higher price than prey species. When the Japanese sardine was abundant in 1992, the average price of tunas (861 yen/kg) was 30 times larger than that of sardine (29 yen/kg) in Japan and the sardines were mostly used as fish meal. We ignored the cost of fishing effort, so $c_i = 0$. The potential effects of a cost to fishing effort are considered in the six-species model.

Three-species food chain.—The second type of three-species system we consider is one consisting of three trophic levels either with or without omnivory (intraguild predation). A potential fisheries example is the system consisting of anchovy, squid, and the northern Pacific minke whale. However, the model applies to any three-level system including those in which the top predator consumes the lowest level. Species are numbered according to their trophic level, with species 3 being the top predator. Because higher trophic levels do not persist if the bottom prey populations go extinct, there are four solutions with different species composition: only species 1 exists; species 1 and 2 exist in the absence of the top predator; species 1 and 3 exist but species 2 goes extinct (only possible with omnivory); and all three species coexist. The 14 candidate solutions for the optimal fishing effort are listed on Table 2, and range from species 1 present and harvested (C1) to all species present and all are exploited (C14). We again examine whether these solutions are feasible (population abundance and fishing effort are nonnegative and the equilibrium is a locally stable point or an unstable focus).

We obtained the maximum sustainable revenue among the feasible solutions. We randomly chose parameter values under four different assumptions about

omnivory and direct density dependence in the consumer trophic levels: (i) systems lacking both direct density effects at higher trophic levels and omnivory, i.e., $a_{22} = a_{33} = 0$ and $a_{13} = a_{31} = 0$ in Eq. 1, (ii) systems with omnivory but no direct density dependence, i.e., $a_{22} = a_{33} = 0$ and $-1 < a_{13} \leq a_{31} < 0$ in Eq. 1, (iii) systems with direct density effects at higher trophic levels, but without omnivory, i.e., $a_{22} = a_{33} = -0.1$ and $a_{13} = a_{31} = 0$ in Eq. 1, and (iv) systems with direct density effects and omnivory, i.e., $a_{22} = a_{33} = -0.1$ and $0 < a_{31} \leq a_{13} < 1$ in Eq. 1. Parameter values were chosen by independent draws from a uniform distribution between 0 and 1 for $-a_{ij}$ ($i > j$) and r_i between 0.8 and 1 for $m_{ji} = -a_{ji}/a_{ij}$ ($i < j$), between 0 and 10 for p_2 , and between 0 and 100 for p_3 , where p_1 is set to be 1. We again ignored the cost of fishing effort, so $c_i = 0$.

Six-species food webs.—Recall that our six-species systems always include two prey species on the lowest trophic level (these producer species are designated species 1 and 2). The rest of the web is constructed by sequentially adding species, allowing each new species to consume each of the already present species with a constant probability. This produced webs having between two and five trophic levels. We assume that the diagonal elements a_{ii} are -1 for bottom-level species and are either 0 or are drawn randomly from a uniform distribution between 0 and -1 for consumer species (3 through 6). We also assume that $a_{ij} = a_{ji}$ when i and j are prey, a_{ij} is negative when species j eats species i ($j > i$), a_{ij} is 0 with probability of 50% and its absolute value is between 0 and 1 with probability of 50%. We consider (i) systems without direct density effects at higher trophic levels, i.e., $a_{ii} = 0$ for $i \geq 3$, and (ii) systems with direct density effects for all species, i.e., $-1 < a_{ii} < 0$ for $i \geq 3$. (Recall that species 1 and 2 are the two basal species). Some of the assumptions regarding parameter ranges are by necessity somewhat arbitrary, because so little is known about the magnitudes of these interaction coefficients. However, preliminary work has not revealed cases where the major qualitative conclusions presented below depend on these assumptions.

We construct an interaction matrix \mathbf{A} from randomly chosen parameter values, and seek a vector of growth rates \mathbf{r} that gives a feasible equilibrium without any fishery ($\mathbf{e} = 0$) using a type of genetic algorithm, i.e., r_i 's change slightly and simultaneously by "mutation" and if the minimum (negative) abundance among six species given by a "mutant" \mathbf{r} is larger than that given by the original \mathbf{r} , we exchanged the two vectors \mathbf{r} and tried further mutations. A feasible \mathbf{r} is sought until we either find a feasible equilibrium or fail to find one for 1000 "mutant" \mathbf{r} 's. In the latter case, we discard the original interaction matrix. We repeated this process 1000 times. Therefore, we base our analysis on 1000 food webs having an equilibrium with all six species present in the absence of fishing. The equilibrium is

either locally stable or an unstable focus. For each food web, we obtain a solution, which is a set of fishing efforts \mathbf{e}^* that maximizes the total yield given a set of randomly chosen prices (specified by the price matrix \mathbf{p}). The price matrix is different for each food web. We assumed that cost of fishing effort, c_i , is chosen from the uniformly random variable between 0 and 1 for all species. We investigated the feasibility and the total rate of revenue gain of 2915 types of solutions using Mathematica 5.0 (Wolfram 2003).

We calculate the number of extant species and the number of trophic levels under the MSR solution. We also calculate the number of trophic links, both in the absence of fisheries and under the MSR solution. We count the number of exploited species and the number of extant species that are not consumed by any predator and are not harvested. We also determine which extinct species would need to be harvested to keep them out of the MSR community if there was immigration from outside the system. The trophic level of a predator species is here defined as one greater than the number of feeding links along the longest path from one of the prey (either species 1 or 2) to that predator species.

The fishing effort that maximizes the total yield may not guarantee persistence of all species. To reconcile maximum sustainable revenue with biodiversity conservation, we obtained the fishing effort that maximizes the total yield when all species persist. Under this "constraint of biodiversity conservation" the optimal fishing effort is the vector \mathbf{e} that maximizes

$$\Psi = Y - \sum_{i=1}^s \log \left[1 + \left(\frac{0.1n_i^{**}}{n_i^*} \right)^{10} \right] \quad (9)$$

where n_i^{**} is the equilibrium of species i without fisheries. The second term on the right-hand side of Eq. 9 is close to 0 when $n_i^*/n_i^{**} \gg 0.1$ and otherwise becomes negative with a large magnitude. This has the effect of preventing the harvest of rare species, and might be implemented by an appropriately scaled tax on landings of such species (Roughgarden 1998). The maximum total yield without the constraint of biodiversity conservation ("unconstrained MSR") is never smaller than the total yield with constraint of biodiversity conservation ("constrained MSR"). We calculate the ratio of constrained MSR to unconstrained MSR for identical systems with same \mathbf{A} , \mathbf{r} , and \mathbf{p} .

RESULTS

Two-prey, one-predator systems

Table 1 displays the maximum sustainable revenue (MSR) solutions of 1000 randomly generated examples for each of five different types of two-prey, one-predator models. Even for the simplest case, where systems lack both direct density dependence in predator growth and interspecific competition between the prey (column (i)), there are three types of solutions for the MSR: (C3) two prey are exploited and the predator goes ex-

TABLE 1. Equilibrium solutions and frequencies of these solutions that maximize sustainable revenue for two-prey, one-predator systems under different types of competition and predator effects.

Community– harvest combinations†	Variable value‡						Solution frequencies (%)				
	n_1	n_2	n_3	e_1	e_2	e_3	(i)	(ii)	(iii)	(iv)	(v)
C1	+	0	0	+			0	16	26	0	19
C2	+	+	0	+	0		0	0	0	0	0
C3	+	+	0	+	+		48	32	0	48	32
C4	+	0	+	+		0	0	0	0	0	0
C5	+	0	+	0		+	0	24	74	0	12
C6	+	0	+	+		+	0	0	0	0	1
C7	+	+	+	+	0	0	0	0	0	0	0
C8	+	+	+	+	+	0	0	0	0	0	0
C9	+	+	+	+	0	+	12	11	0	15	15
C10	+	+	+	0	0	+	41	19	0	34	18
C11	+	+	+	+	+	+	0	0	0	3	3

Notes: Results are from 1000 sets of randomly chosen parameter values. The three columns headed by n_i (species abundance) define the composition of the community, while the columns headed e_i (the fishing effort) define the species harvested. Columns (i)–(v) each sum to 100% and represent different equilibrium solutions: (i) without either interspecific competition or predator direct density effects, (ii) with weaker inter- than intraspecific competition, (iii) with stronger interspecific competition, (iv) with direct density effects of the predator, and (v) with weak interspecific competition and direct predator-density effects.

† For further explanation, see *Methods: Two-prey, one-predator systems*.

‡ A “+” means the variable in that column has a positive value at the solution. A blank cell means fishing is infeasible because the species is extinct.

tinct; (C10) only the predator is exploited and the two species coexist and support the predator’s population; and (C9) one prey and one predator are exploited and the three species coexist. As the model is made more complicated, by adding competition between prey or direct competition within the predator, a wider range of species–harvest combinations enter into the list of potential MSR solutions.

A number of generalizations emerge from the results in Table 1. The first is that it is never optimal to have the predator present but unharvested (combinations C2, C4, C7, and C8); this is true for all five of the variations of this food web that were analyzed. If a predator is not itself valuable, it should be eliminated to increase yield from the lower trophic level. The second generalization is that harvesting of both levels in this two-trophic-level system may maximize the total yield, although this still represents a small fraction (from 0 to 18% for the five different classes of models) of the optimal solutions. Systems with harvest of both trophic levels are cases where the harvested prey contributes relatively little to predator growth, or the nonharvested prey has a low monetary value, p , but contributes significantly to the growth of a valuable predator. Harvesting of all three species only occurred when there was direct density dependence in the predator (columns (iv) and (v)), and, even then, only occurred in 3% of the random webs. A final generalization is that extinction of one or more species characterized MSR solutions for a large fraction of the food webs; from 47% of the webs in models with no competition or direct density dependence, to 100% in models with stronger inter- than intraspecific competition. In most cases, the

predator was absent from the MSR web if either prey represented a more valuable resource, and the less valuable prey was absent when it competed strongly with the more valuable prey. In these cases, the absence could be a result of either intentional elimination, or exclusion by the remaining species because of changes in their abundance as the result of harvesting other species. Direct density dependence and interspecific competition between prey both had significant effects on the distribution of community–harvest combinations among the MSR webs.

Three species systems with three trophic levels

Table 2 shows the classification of 1000 MSR solutions for each of four different types of three-species, tritrophic systems. We again summarize these results by highlighting results that characterize the vast majority of parameter combinations examined. As in the case of the two-prey, one-predator system, at an MSR a top predator was never both present and not harvested (combinations C2, C5, C8, C9, C11). As in the previously discussed web, a top predator that is not itself valuable necessarily reduces the yield from the rest of the web. The MSR solutions usually involved harvest of only a single trophic level. This was true for every single web in the case of a food chain with no direct consumer density dependence and no omnivory (column (i)). In the remaining three classes of models, the fraction of webs where only one level was harvested at MSR ranged from 75% (with both omnivory and direct density effects) to 96% (with omnivory but no direct density effects). Harvesting all three trophic levels only occurred in webs with direct density depen-

TABLE 2. Equilibrium solutions and the frequencies of solutions that maximize sustainable revenue for three-trophic-level systems.

Community–harvest combinations	Variable value†						Solution frequencies (%)‡			
	n_1	n_2	n_3	e_1	e_2	e_3	(i)	(ii)	(iii)	(iv)
C1	+	0	0	+			49	60	62	41
C2	+	+	0	+	0		0	0	0	0
C3	+	+	0	0	+		25	21	17	6
C4	+	+	0	+	+		0	0	11	7
C5	+	0	+	+		0	0	0	0	0
C6	+	0	+	0		+	0	5	0	27
C7	+	0	+	+		+	0	0	0	5
C8	+	+	+	+	0		0	0	0	0
C9	+	+	+	0	+	0	0	0	0	0
C10	+	+	+	0	0	+	26	10	3	1
C11	+	+	+	+	+	0	0	0	0	0
C12	+	+	+	+	0	+	0	0	0.2	0.1
C13	+	+	+	0	+	+	0	3	5	12
C14	+	+	+	+	+	+	0	0	1	1

Notes: Results are from 1000 sets of randomly chosen parameter values. See Table 1 for an explanation of the format.

† A “+” means that the variable in that column has a positive value at the solution. A blank cell means fishing is infeasible because the species is extinct.

‡ Solutions: (i) without omnivory or direct density effects of higher trophic levels, (ii) with omnivory, (iii) with direct density effects of all species, and (iv) with omnivory and direct density effects for all species.

dence, and then only occurred in 1% of the cases (combination C14 in columns (iii) and (iv)). In every case examined, the combination of species composition and harvesting that characterized the largest number of webs was a system that only contained the bottom trophic level (C1). In some of these cases, harvesting that level had the indirect effect of eliminating the top two levels, but in a large fraction of cases, it was necessary to intentionally harvest one or both of the higher levels to extinction.

As in the case of the two-prey, one-predator webs, the presence of direct density dependence in predatory species caused a large shift in the distribution of MSR solutions among the different potential categories. Omnivory by the top-level predator also changed the distribution of solutions. This was to be expected because solutions in which the mid-level consumer is absent and the top-level consumer is present (C6) cannot occur in the absence of omnivory.

Six-species systems with multiple trophic levels

We start by describing systems that lack any harvesting. The average number of trophic links in these communities (7.9) was slightly larger than the 7 that would be expected from our 50% link probability, because webs with fewer links had to be discarded more often as a result of lack of species persistence. The number of links in six-species communities (two prey and four consumers) must be equal to or larger than 4. The mean number of trophic levels in the unharvested systems (one plus the length of the longest food chain) was 3.9.

At the MSR solution, the remaining food web was usually considerably reduced in size. The number of

extant species ranged from 1 to 6, and the number of trophic links ranged from 0 to 9 (Table 3). Table 3 also compares the MSR policies for systems with (B) and without (A) direct density dependence in consumer species in the absence of a cost of fishing effort. The MSR policies for systems with direct density dependence in consumer species and with a cost of fishing effort are shown in Table 3C. Taking costs into account produced one new class of outcomes—because of the high costs of all fishing efforts in those webs, there were 12 cases where no species were exploited. However, the remaining 988 webs had MSR policies qualitatively similar to those for comparable webs without fishing costs (Table 3B). It is clear that, in most webs in all three situations shown in Table 3, the numbers of extant species and links are both decreased significantly by fisheries that maximize sustainable revenue from the entire system. The average number of species that were extinct at the MSR solution was 2.92 (no costs or density dependence), 2.60 (no costs with density dependence), and 3.93 (with costs and density dependence). The number of exploited species and the number of trophic levels that are exploited ranged from 1 to 3 and 1 to 2, with and without density dependence, respectively. The presence of costs significantly decreased the mean number of exploited species and levels, as well as the number of species present. For all three cases, there were no unconstrained MSR policies that involve a fishing ban on one or more top-predator species. Top predators were either exploited or removed at the unconstrained MSR solution.

Table 3 also summarizes the nature of MSR policies under a constraint of biodiversity conservation. Such a constraint significantly altered the MSR policy in a

TABLE 3. Resultant food webs and fishing efforts from 1000 randomly constructed six-species systems, with and without direct density effects of predators, are shown in parts (A) and (B), respectively. (C) Results corresponding to part (B), but with a cost-of-fishing effort, c_i , assuming that c is randomly chosen between 0 and 1.

Entry number	Initial food web		Unconstrained MSR				Constrained MSR	
	Chain length	No. links -4	No. species	No. links	No. exploited species	No. trophic levels	No. exploited species	No. trophic levels
A) With direct density effects of predators (no. of links minus 4)								
0	0	2	0	3	0	0	0	0
1	0	46	0	308	880	896	34	96
2	0	132	299	247	119	104	285	444
3	298	229	407	237	1	0	465	382
4	507	236	214	95	0	0	198	78
5	195	208	71	72	0	0	17	0
≥6	0	95	9	38	0	0	1	2.44
Average	3.90	7.93	3.08	2.51	1.12	1.10	2.88	1000
B) Without direct density effects of predators (no. links minus 3)								
0	0	18	0	41	0	0	0	0
1	0	80	19	251	482	552	14	46
2	7	175	247	172	371	376	166	402
3	326	336	304	177	114	65	453	437
4	498	229	227	99	29	7	306	107
5	169	122	148	105	4	0	58	8
≥6	0	40	55	155	0	0	3	0
Average	3.829	6.215	3.403	3.176	1.702	1.527	3.237	2.629
C) Without direct density effects of predators (no. links minus 3), with fishing-effort cost								
0	0	11	0	372	12	0	12†	12†
1	0	71	323	369	646	728	25	51
2	5	133	380	127	293	238	75	284
3	332	225	204	72	54	21	241	459
4	522	233	71	27	7	1	372	169
5	141	185	8	14	0	0	237	13
≥6	0	142	2	7	0	12	26	0
Average	3.799	3.779	2.031	1.066	1.422	2	3.727	2.737

Notes: Columns show the frequency distribution of the food-chain length and the number of trophic links in initial food webs, the number of extant species, the number of trophic links (number of links minus 4 or 3; e.g., the frequency of initial webs with five links are 46 and 175 in parts A and B, respectively), and the number of species and trophic levels that are exploited at unconstrained MSR (maximum sustainable revenue) solutions. For details, see *Results: Six-species systems with multiple trophic levels*.

† No species were exploited in 12 webs.

large fraction of the food webs. Obviously species and feeding links were not eliminated under such a system. Systems with a harvesting ban on the top predator appeared in 3% and 12% of constrained MSR solutions without and with direct density dependence, respectively.

Fig. 1a–e shows five examples of systems at the unconstrained MSR solution for situations without costs of fishing effort. Although there were rare cases where all six species persisted (as in Fig. 1a), it was more common for both the number of species or trophic levels to be reduced, as in Fig. 1b–e. Fig. 1f–j show the same five systems at the constrained MSR solutions. We should note that, assuming extinctions are local rather than global, some extinct species would reinvade the MSR community if there was no harvesting effort directed at those species (e.g., species 4 and 5 in Fig. 1e). In these cases, the MSR policy might include harvesting effort directed at, but minimal actual harvest of, these species. If the species becomes extinct globally (or if there is no immigration from other areas), then harvesting effort on species that are intentionally

removed from the community could end after those species disappeared. The examples in Fig. 1 show that it is possible for the constrained MSR policy to involve harvesting from more (Fig. 1c and e), fewer (Fig. 1d), or the same (Fig. 1a and b) number of trophic levels as in the unconstrained solution. Similarly there can be more (Fig. 1b, c, and e), fewer (Fig. 1d) or equal (Fig. 1a) numbers of species harvested at the constrained solution. On average, more species and more trophic levels are harvested at the constrained solution. The constrained MSR must be identical to the unconstrained MSR (assuming the cost term given by Eq. 9 is insignificant) for the relatively rare cases where no species goes extinct at the unconstrained MSR solution (see Fig. 1a and f). The number of exploited species at the constrained MSR solutions is larger than the number at the unconstrained MSR solutions for the large majority of systems (945/1000 for webs without direct consumer density dependence and 857/1000 with density dependence). The number of species harvested was larger in unconstrained systems in only 2/1000 cases without consumer density dependence, and in

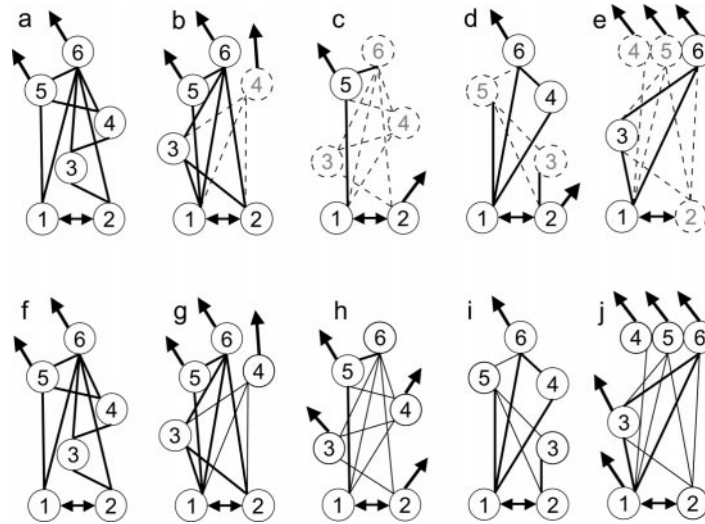


FIG. 1. MSR (maximum sustainable revenue) solutions, not including the costs of fishing effort, for five examples of the six-species food-web systems: (a–e) unconstrained by a fishing ban on one or more top predators; and (f–j) constrained by a ban. Panels (f–j) are identical systems to panels (a–e), respectively. Circles represent species; arrows represent fisheries. The lines between circles represent trophic links from lower-numbered species to higher-numbered species. Dotted circles and lines mean that these species and trophic links went extinct at the unconstrained MSR solution. See *Results: Six-species systems with multiple trophic levels* for details.

11/1000 systems with density dependence (including the systems shown in Fig. 1d and i). The ratios of constrained MSR to unconstrained MSR were 100%, 92%, 61%, 12% and 6% for systems shown in panels a:f, b:g, c:h, d:i and e:j of Figs. 1(a–e) and 1(f–j), respectively. The average ratio of constrained MSR to unconstrained MSR among 1000 systems was approximately 63% and 76%, without and with direct density dependence, respectively.

An important aspect of the MSR solutions is whether species are extinct as the direct result of harvesting them, in which case their per capita growth rate in the absence of harvest would be positive at the MSR solution, or if they are extinct as the indirect result of exploitation of their food species at the MSR, in which case their per capita growth rate is negative. Here we summarize the results for systems without harvesting costs. In 9 of the 1000 systems without direct density dependence, no species went extinct. In 58 systems, every extinction was due to harvesting other species. The average number of extinct species in these webs was 2.17. In 226 systems, every extinction was intentional. The average number of extinct species in these webs was 2.18. In the remaining 707 systems, both types of extinction occurred at the MSR; the average numbers of intentionally and unintentionally eliminated species are 1.59 and 1.66, respectively. In 55 of the 1000 systems with direct density dependence, no species went extinct. In 66 systems, all extinctions were unintentional, while in 289 systems all of the extinctions were intentional. The average numbers of extinct species in these two classes of webs were 1.91 and

1.87, respectively. In the remaining 590 systems there was a mix of negative and positive per capita growth rates among extinct species at MSR, with averages of 1.66 unintentional and 1.62 intentional extinctions.

In comparing the revenue from constrained and unconstrained MSR solutions, the type of extinction had a large effect. If active harvesting was required for all missing species (i.e., they were intentionally driven extinct), the ratio of the unconstrained MSR to constrained MSR was 91% in systems without direct density dependence of consumers. When some species went extinct due to the indirect effects of harvesting, there was a smaller ratio of MSR in constrained to unconstrained solutions, 55%. With direct density dependence in the predator species, these percentages were 86% (instead of 91%) and 74% (instead of 55%).

DISCUSSION

We designed this study to provide a basis for understanding some of the potential consequences of harvesting to maximize the economic or biomass yield from an entire food web. In the past, this goal is likely to have been used primarily in multispecies aquaculture, and strategies are likely to have been developed empirically, by comparison of the yields from different mixes of species with different rates of harvesting. However, consolidation of the control of exploitation of aquatic resources is likely to lead to increasing attempts to apply the same approach to natural systems, both freshwater and marine. Given the global importance of such resources, understanding the potential consequences of different exploitation strategies is be-

coming increasingly important. One of our main results is that yield or profit maximization, combined with greater knowledge of food-web interactions, will create a pressure to cull non-harvested top predators. Yodzis (2001) discussed the question of culling of non-harvested top predators, noting that this has been considered repeatedly in the case when seals are the top predators. Of course, most fish species that are top predators have been and are being heavily exploited because of their high market value. The issue of multispecies harvesting in general is becoming increasingly relevant, as overexploitation of species on higher trophic levels has prompted the development or expansion of harvest of previous non-exploited species on lower trophic levels (Pauly et al. 1998). Roughgarden and Armsworth (2001) have discussed this issue in connections with biodiversity preservation in communities of competitors. They suggest that “weeding” of less valuable species presents a risk for preservation of biodiversity.

The models we examined are simple in their structure and in the linear form of their component functions. Furthermore, they were analyzed by sampling from a uniform distribution of parameters that produced persistent communities. Thus, the conclusions that are most likely to apply to natural systems are qualitative rather than quantitative, and are those that characterize the vast majority of the webs and parameter space that we explored. We chose ranges of each parameter for just mathematical ease: the magnitude of intraspecific competition is 0 or between 0 and 1. We assumed price that depends on trophic levels as mentioned above. Another simplification that we assumed is no energy loss between trophic interactions, or $a_{ij} = a_{ji}$ for all trophic interactions. All of these assumptions are likely to alter the quantitative results. For example, our analysis of adding costs of harvesting revealed that this significantly increased the number of extinctions in our six-species webs. However, the fact that our main qualitative results are similar for three different types of food webs and for multiple variations within these webs suggests that they are likely to be fairly general. The assumption of 100% conversion efficiencies is likely to have resulted in higher numbers of extinctions of intermediate-level predators in systems with omnivory, which is likely to be true of more realistic conversion efficiencies. Because of this and the simplicity of our models, we are not suggesting that quantitative results are likely to apply to real food webs. However, a number of qualitative results seem relatively unaffected by the food-web structure or by the parameter ranges used.

The general conclusions that fit these criteria are: (1) in most cases, harvesting under the food-web MSR (maximum sustainable revenue) is restricted to one or two trophic levels; (2) in most cases, a large fraction of the species go extinct under the food-web MSR; (3) in all cases examined, an unharvested top predator is never part of the food-web MSR (if the top predator is not itself valuable, it should be eliminated to increase

the yield of other, more valuable species in the food web); (4) the presence of direct density dependence in consumer species has a major impact on the form of the MSR solution, on average increasing the number of species and trophic levels harvested. Changing the range of parameters examined did not qualitatively change any of these conclusions. Changing parameters such as the relative price of top predators generally had straightforward quantitative effects; e.g., more top predators were extinct at the MSR when their mean price was lower.

In the remainder of this section we first discuss previous theory related to these conclusions, and then discuss their implications for regulating exploitation of systems where the goal of food-web MSR seems likely to be followed. In connection with the last point, we discuss the impact of applying a constraint of biodiversity conservation on the maximum harvest from the web. We then discuss how the conclusions of this analysis might be changed if additional or alternative biological or economic features were added to the models.

Some of our conclusions echo those of Clark's (1990) analysis of predator-prey systems. He showed that the MSR from the entire web was obtained by harvesting only one of the two species. If that species was the prey, it was always optimal to eliminate the predator. Thus, extinction was a common outcome, and it was never optimal to have an unharvested top predator. May et al. (1979) had also analyzed a predator-prey model and found some cases where both levels should be harvested. The contrast between these two analyses was a consequence of the assumed direct density dependence in the predator growth rate in the model employed May et al. (1979). This again shows the importance of trying to estimate this much-neglected component of population dynamics.

Our third conclusion (MSR involves eliminating unharvested top predators) contrasts with a series of articles by Yodzis (1994, 1996, 2001). He used a rather different analysis of a much larger and more complicated web to suggest that harvesting seals had a high probability of failing to increase the hake population in the Benguela ecosystem. There are several possible explanations for this difference. The most likely is that Yodzis did not consider the possibility of harvesting competitors or lower level predators of the focal species in addition to harvesting the top predator. In fact, Yodzis (2001) suggests that a competing fish species that was not harvested, but that was susceptible to seal predation, was responsible for most of the potential positive impact of seals on the heavily exploited species of hake. Other differences in methods may have contributed to the difference in results. Yodzis only examined the effect of a small change in harvesting, whereas we look at the consequences of any level of harvesting. In addition, Yodzis only examined the impact on a single prey species, while we examine the

impact on yield from the entire web. A third possibility is that much more complicated systems might yield different outcomes in our analysis. Of the three possibilities, the last seems least likely, since we generated a wide range of trophic structures in the six-species models, and the MSR never included a harvest-free top predator.

MSR harvest in our models with three or more trophic levels generally involved harvest of only one or two trophic levels. This contradicts the advice of the 1995 Kyoto Declaration and Plan of Action on the Sustainable Contribution of Fisheries to Food Security (*available online*),⁵ which recommends (in Article 14) that multiple trophic levels should be harvested. Webs in which only the top predator is harvested were characterized by at most a small number of extinctions, but this was decidedly not the case when many species were harvested.

The extinctions of many less-valuable species under the MSR policy was another robust conclusion of our analyses. Although management of a single species based on MSR can cause some extinctions when that species is embedded in a food web (Clark 1990), our analysis predicts that, in a typical food web managed for whole-web MSR, a large fraction of the relatively less valuable species should be driven to extinction to increase yields from others. In our analysis of six-species webs, close to half of the species were absent at the average MSR solution, and roughly half of the absent species were eliminated intentionally to increase yields from other species. In natural systems, the predicted extinctions are often likely to be changed to drastic reductions in abundance, due to the difficulty and/or expense of eliminating the last few individuals of a rare species (but see discussion below, and Clark [1976]). It is noteworthy that close to half of the extinctions we observed are due to indirect effects transmitted through the food web; it is probable that many of these extinctions would occur if each of the harvested species was managed independently. Both our models of multispecies harvesting, and comparable single-species harvesting often predict “unintentional” extinctions, for example, predator extinctions due to decreased abundance of prey from the direct or indirect effects of harvesting. While we do not know of documented examples, the decline in Northern fur seals has been attributed to the walleye pollock fishery (see Etnier 2004 for a recent discussion of various hypotheses), and some of the declines in Great Lakes fish species have been attributed to indirect food-web effects of invaders (Mills et al. 2003).

Large predators have been heavily overexploited in many systems (Pauly et al. 1998). This is not because of negative effects on more valuable species at lower trophic levels, but because of the economic benefit of harvesting top predators, due to their greater price.

Such predators have been overexploited under past, single-species fisheries management due to the failure of management to achieve a true maximum sustainable revenue. There is a good chance that some of these species would increase in abundance if food webs were actually managed in a manner to maximize profit from the entire system. However, others might go extinct due to reductions in their prey.

The presence of direct density dependence in the consumer populations greatly altered the distribution of MSR harvesting strategies in our models. There is no reason to believe that this result is restricted to models with the linear functional forms assumed here. If it is general, then it has important implications for any attempt to pursue the goal of maximizing yields from food webs, because very little is known about the presence or strength of such direct density dependence in natural communities. These terms can arise from cannibalism, foraging interference, resources other than food, or species-specific diseases. The presence of significant direct density dependence usually decreases the number of species that are driven to extinction by the policy that maximizes yield from the entire web.

Under the constraint of biodiversity conservation, a harvesting ban on top predators may be part of the policy that maximizes the total economic yield. There are some webs where a constraint of biodiversity conservation reduces the MSR by more than 90%. However, in the large majority of webs where at least some of the extinctions were the result of intentional elimination of the extinct species, the constraint of biodiversity conservation reduced yield by less than 20% on average. The reduction in yield caused by the biodiversity constraint is particularly small when the consumers in the web experience direct density dependence.

How robust are the findings of this analysis? This is an important question because of the simplicity of the biological and economic aspects of the model employed here. We should comment on the potential impact of biological or economic features that are missing from the model. Most fisheries systems have many more species, are likely to involve nonlinear interaction functions, have temporal variation in parameter values, and have significant size or spatial structure. Each of these is likely to have an important impact on some aspects of food-web dynamics. However, it is unclear why any of these would be likely to qualitatively change the four generalizations highlighted in the third paragraph of this *Discussion* section. The results for a more limited analysis of predator-prey systems with nonlinear predator functional responses (H. Matsuda, *unpublished manuscript*) suggest that exceptions to the “harvest-one-level” generalization are likely to be somewhat more common in multispecies systems if the functional responses in those systems are allowed to be nonlinear. Spatially structured populations are often

⁵ <http://www.fao.org/fi/agreem/kyoto/kyoe.asp>

less susceptible to extinction than unstructured populations, so predictions of extinction may be changed to predictions of very low population size in such models. Future work on extensions of the biological model used here should clarify some of these potential effects.

In the realm of economics, our analysis has assumed that each type of fishing effort is directed at a single species, and only catches that species. Prices (values) are assumed constant. Higher prices as a consequence of lower harvests tend to lower the stock size at MSR (Clark 1976), but would likely have a small effect on the economic yield at MSR. It is also unlikely that cases where multiple species are caught using the same gear would greatly change the outcome of our analysis, although the exact solution would change. If two valuable species were caught using the same gear, effort would be most influenced by the more valuable of the two. The possibility of catching "uneconomical" species as bycatch when harvesting others would reduce or eliminate the cost of harvest of those species. Competitors and predators of valuable species typically have not been harvested to near extinction in the past. One possible reason for this discrepancy is that our MSR policy assumes that a single decision maker possessing perfect information controls the harvesting efforts. This does not characterize most current fisheries, although control of fishing effort is becoming increasingly centralized, and, presumably, knowledge of population biology is increasing.

Given many competing individual fishers, it is unlikely that elimination, or even significant overexploitation, of uneconomical fish species will occur, unless they can be eliminated with little or no cost. If there is an extra cost to harvest such species, then the interests of individual fishers will often not coincide with the interests of the group; "cheaters" who avoid harvesting an unmarketable top predator, for example, will make a greater profit than those who do not. This represents a type of reverse "tragedy of the commons." It is the common property aspect of most food webs that may have saved some uneconomical species from either very low densities or extinction. As our knowledge of food-web interactions increases, this positive role of competition among exploiters of common property resources is also likely to increase.

In conclusion, (1) we feel that multispecies models should be used more widely in fisheries, regardless of what actual policy is adopted to guide harvesting; and (2) we do not advocate the type of whole-web MSR policies that we explore. We certainly do not support such policies in the absence of constraints that protect species from extinction. We view such whole-web MSR policies as likely future consequences of economic forces together with increasing consolidation of, or cooperation between, different groups of exploiters. However, elements of such whole-web policies are already present in the repeated demands to cull unexploited top predators. Our analysis shows that man-

aging entire systems to maximize total yield is likely to pose a threat to diversity that goes beyond the culling of predators. More centralized control of fishing efforts on multiple species, combined with better knowledge of the food web may lead to more attempts to eliminate or greatly reduce many species to improve yields from others. One of the main goals of our analysis is to alert managers to the additional risks of local extinction that follow from such whole-web management.

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