20 July 1979, Volume 205, Number 4403 SCIENCE

Management of Multispecies Fisheries

Robert M. May, John R. Beddington, Colin W. Clark
Sidney J. Holt, Richard M. Laws

Summary. With the overexploitation of many conventional fish stocks, and growing interest in harvesting new kinds of food from the sea, there is increasing need for managers of fisheries to take account of interactions among species. In particular, as Antarctic krill-fishing industries grow, there is a need to agree upon sound principles for managing the Southern Ocean ecosystem. Using simple models, we discuss the way multispecies food webs respond to the harvesting of species at different trophic levels. These biological and economic insights are applied to a discussion of fisheries in the Southern Ocean and the North Sea and to enunciate some general principles for harvesting in multispecies systems.

With the collapse of some major fisheries, the establishment of national and international zones for fishing, and the increased demand for food, there is growing interest in harvesting "unconventional" stocks of marine organisms (*1*). These species typically occupy lower trophic levels than currently harvested species, and in many cases they are the food supply (prey) of other harvested stocks.

One example of such a situation occurs in the Southern Ocean, where overexploitation of baleen whales has reduced their net biomass to around one-sixth its estimated pristine value (*2*). Simple estimates suggest there is consequently a "surplus" of the Antarctic krill, *Euphausia superba*, no longer consumed by baleen whales, amounting to roughly 150 million metric tons annually (*2, 3*). Recently, there has been much discussion about exploiting this "surplus" krill, and already something like 100,000 tons per annum are so harvested (*4, 5*). But *Euphausia superba* is the main food source for a large number of species—whales, seals, seabirds, penguins, fish, cephalopods—in the Antarctic (*4, 5*), and there is concern about the implications that a krill fishery may hold both for the depleted stocks of baleen whales and for other creatures (*6*). This concern underlies current efforts by the Antarctic Treaty countries to enact a Convention for the Conservation of Antarctic Marine Living Resources, aiming to reconcile the harvesting of krill and other species with the long-term preservation of the Antarctic ecosystem, complete with all its existing species.

Commercial fisheries in the North Sea also exhibit the effects of competition and prey-predator interactions among species. Over the past 10 years, the stock and catch of herring and mackerel have declined under heavy fishing, but the total catch of fish has remained roughly constant, probably because the populations of the large gadoids (cod, saithe, haddock, and whiting) and other smaller fish (Norway pout, sprat, and sand eels) have increased (*7-10*). A likely reason for this increase is that diminished stocks of herring and mackerel result in less predation on, and enhanced survival of, larval and juvenile stages of other fish species. Other examples of management problems that involve the interactions between species in different trophic levels include krill, cephalopods (squid), and sperm whales; gray seals and fish [gray seals off Britain consume more than 100,000 tons of fish, including cod and salmon, each year (*11*)]; seals, whales, and fish that eat herring in the Bering Sea (*12*); harp seals, cod, and capelin (*13*); cod that eat herring and sprat in the Baltic (*14*); and otters and abalone off California (*15*). Further studies, where the multispecies interactions are primarily competitive, have been conducted on herring and mackerel in the Gulf of St. Lawrence (*16*), sardine and anchovy in the Pacific (*17, 18*), and cod and redfish in the North Atlantic (*19*).

So long as a harvested stock can be regarded as a single, isolated population, the notion of maximum sustainable yield (MSY) is a useful basis for discussing management principles. Despite its many acknowledged shortcomings (*20-22*), MSY in principle has the twin virtues of focusing discussion on long-term management for sustainable yields (not discounting the future), and of indicating a level of exploitation that cannot be exceeded without depleting the stock to low levels incapable of high biological productivity (*23*). Clearly, however, MSY applied to each species individually cannot serve as a guiding principle when the harvested species have strong interactions; it may well be that baleen whales cropped the krill below its MSY level in the pristine system. What specific principles, then, should be espoused to manage a multispecies fishery in such a way as to "maintain the health and sta-

---

R. M. May is professor in the Biology Department, Princeton University, Princeton, New Jersey 08540; J. R. Beddington is lecturer in the Biology Department, University of York, Heslington, York, Y01 5DD, England; C. Clark is professor in the Mathematics department, University of British Columbia, Vancouver V6T 1W5, Canada; S. J. Holt is adviser on marine affairs to the Fisheries Department, United Nations Food and Agriculture Organization, Via delle Terme di Caracalla, 00100 Rome, Italy; R. M. Laws is director of the British Antarctic Survey, Madingley Road, Cambridge, CB3 0ET, England.

0036-8075/79/0720-0267$02.00/0

bility of the marine ecosystem" (*24*)? In this article we attempt to provide some preliminary answers (*25*).

To this end, we consider some simple, heuristic models for the harvesting of interacting populations. Because we are particularly interested in the insights for management of the Southern Ocean, the models are cast as highly simplified metaphors for major elements of the Antarctic ecosystem. Thus we consider first the simultaneous harvesting of prey and predator in a two-species system (krill–baleen whales); second, the harvesting of the prey along with one of two predator species (krill-whales-seals); and third, the harvesting of bottom and top species in a system with three trophic levels (krill-cephalopods-sperm whales). In all instances we discuss the interplay among the yields of the different species that can be obtained under various harvesting regimes, and the dynamic response of the system to changes in these harvesting regimes. Next, responses to harvesting in more complicated ecosystems are reviewed. The actualities of harvesting krill in the Southern Ocean and of the management of North Sea fisheries are then looked at in the light of these models. In the real world, management for sustained biological yield is usually clouded by economic considerations, which tend to discount future yields; some explicitly multispecies aspects of these economic complications are discussed. Finally, we summarize some tentative recommendations for the management of multispecies systems.

There already exist several detailed and complicated theoretical models for particular multispecies fisheries (*7, 12, 17, 26*). Our crude caricature of multispecies systems aims to create a basic framework that can be readily understood and that provides insight into the essential scientific problems. Ultimately, we hope that such general models [see also the energy budget estimates of Jones (*8*)] and very detailed ones will be mutually supportive, as is the case in more fully developed disciplines such as physics and engineering.

A Prey-Predator Model: Krill and Baleen Whales

The model. Consider a prey (krill) population, N_1, that sustains a predator (baleen whale) population, N_2. A simple model that describes the essential features of the prey dynamics is

$$dN_1/dt = r_1N_1[1 - N_1/K] - aN_1N_2 \quad (1)$$

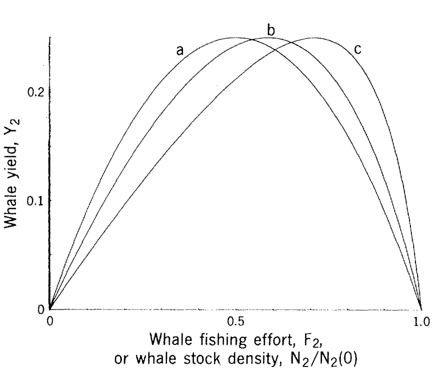


Fig. 1. Yield of whales, Y_2, is shown as a function of fishing effort, F_2, for three values of the parameter ν that characterizes predation intensity in our "krill and whale" model: (a) $\nu = 0$ (single species logistic); (b) $\nu = 1$; (c) $\nu = 5$. Alternatively, for this particular prey-predator model, the same curve depicts the relation between yield and stock density, referred to the unharvested density. (Since Y_2 involves an unspecified scaling factor, all curves have been drawn to have the same maximum value.) For further details see the text.

Here the prey has an intrinsic per capita growth rate r_1 at low population densities, and resource limitations slow population growth (in logistic fashion) to zero at $N_1 = K$ in the absence of predation. A crude Lotka-Volterra form of predation is assumed, with prey being consumed at a rate proportional to their density, aN_1, per predator. The dynamics of the predator population may be described by a logistic growth equation in which the carrying capacity is proportional to the amount of prey available

$$dN_2/dt = r_2N_2[1 - N_2/(\alpha N_1)] \quad (2)$$

Here r_2 is the intrinsic per capita growth rate of the predators, and the carrying capacity or natural equilibrium level is directly related to the prey abundance by the proportionality constant α. N_1 and N_2 can be taken to express either numbers or biomass; if the latter, α depends on the conversion efficiency of krill biomass into whales. The prey and predator populations could have been described by other equations, incorporating various refinements (*27–29*). But Eqs. 1 and 2 embody the essential elements of an interactive prey-predator system, and they are broadly representative of a wide class of models.

Suppose now that the krill population is harvested under a "constant effort" strategy (*30, 31*), at a rate r_1F_1; F_1 represents the constant fishing effort, rescaled so that $F_1 = 1$ corresponds to a fishing rate equal to the population's intrinsic growth rate, r_1. The consequent yield, Y_1, is conventionally assumed to be linearly proportional to this fishing effort times the stock density, N_1; in some appropriate units, we may write $Y^1 = r^1F^1N^1$. Harvesting of the kirll thus adds an extra mortality term, equal to $-r_1F_1N_1$, to the right-hand side in Eq. 1. Similarly, harvesting the whale population under "constant effort" at a rate r_2F_2 gives a yield $Y_2 = r_2F_2N_2$, and adds an extra mortality term, $-r_2F_2N_2$, to the right-hand side in Eq. 2.

As always, it is helpful to rewrite the population variables N_1 and N_2 in an appropriate dimensionless form, in order to highlight the combinations of parameters that are the key to the behavior of the system. Defining $X_1 = N_1/K$ and $X_2 = N_2/(\alpha K)$, and including the effects of harvesting, we can rewrite Eqs. 1 and 2 as (*32*)

$$dX_1/dt = r_1X_1[1 - F_1 - X_1 - \nu X_2] \quad (3)$$

$$dX_2/dt = r_2X_2[1 - F_2 - X_2/X_1] \quad (4)$$

Here the dimensionless parameter ν is defined as

$$\nu = a\alpha K/r_1 \quad (5)$$

Note that the equilibrium (static) properties of these equations depend only on the quantities F_1, F_2, and ν; the dynamics additionally involves r_1 and r_2 (*33*).

Equilibrium solutions and sustainable yields. The equilibrium values for krill and whale populations, X_1^* and X_2^* respectively, are obtained by putting $dX_1/dt = 0$ and $dX_2/dt = 0$ in Eqs. 3 and 4. So long as both F_1 and F_2 are less than unity, there is a unique, stable equilibrium solution:

$$X_1^* = \frac{1 - F_1}{1 + \nu(1 - F_2)} \quad (6)$$

$$X_2^* = \frac{(1 - F_1)(1 - F_2)}{1 + \nu(1 - F_2)} \quad (7)$$

If the harvesting of whales is maintained at a level in excess of their intrinsic growth rate, $F_2 > 1$, they are driven to extinction, and the system settles to the state $X_1^* = 1 - F_1$, $X_2^* = 0$. If the krill fishing rate is maintained at $F_1 > 1$, the entire system collapses to $X_1^* = 0$, $X_2^* = 0$. The biological yields $(Y_i = r_iF_iN_i)$ of krill and whales corresponding to the equilibrium populations of Eqs. 6 and 7 are

$$Y_1^* = \frac{(r_1K)F_1(1 - F_1)}{[1 + \nu(1 - F_2)]} \quad (8)$$

$$Y_2^* = \frac{(\alpha r_2K)(1 - F_1)F_2(1 - F_2)}{[1 + \nu(1 - F_2)]} \quad (9)$$

For the krill, putting $\nu = 0$ in Eq. 8 gives the conventional single-species result for harvesting a resource whose natural growth processes are logistic. The presence of krill-consuming whales has

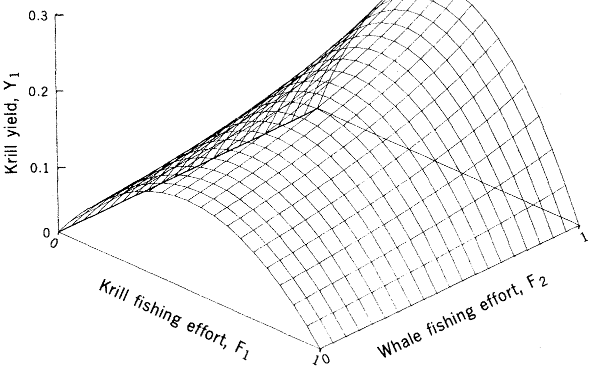


Fig. 2. Krill yield, Y_1, is shown as a function of fishing effort on krill, F_1, and on whales, F_2. (Here $\nu = 1$, and in Eq. 8 the scaling constant has been arbitrarily chosen $r_1K = 1$). The features of this figure are as discussed in the text.

the commonsense effect of diminishing the krill yield, Y_1^*, and depressing the equilibrium krill population, X_1^*, by an amount that increases as ν increases. Indeed, Eq. 6 in the absence of fishing ($F_1 = F_2 = 0$) gives $X_1^* = 1/(1 + \nu)$, which provides a simple biological interpretation for the quantity ν: if $\nu = 1$, the whales are harvesting the krill population exactly at its MSY point (that is, $X_1^* = {}^1/_2$, $N_1^* = {}^1/_2K$ for the logistic); if $\nu > 1$, the whales are harvesting in excess of MSY ($N_1^* < {}^1/_2K$); and if $\nu < 1$, whales are exploiting the krill at less than MSY levels ($N_1^* > {}^1/_2K$). Much ecological controversy surrounds the question of whether ν is to be expected to be around unity in natural prey-predator systems (*34*). For baleen whales exploiting krill there are not enough data to provide a reliable estimate of ν, although it seems unlikely that it is either very large or very small; for our numerical illustrations, we arbitrarily choose $\nu = 1$.

Note the difficulties that can beset the simple management principle "krill shall not be harvested below their MSY level." Whales may well have transgressed this in the pristine system.

Equations 7 and 9 show that the whale stocks and whale yields decrease linearly as the fishing effort for krill, F_1, increases. More interesting is the relation between yield, Y_2^*, and fishing effort for whales, F_2. Unlike all conventional single-species harvesting models, the yield-effort curve of Eq. 9 is not simply related to the recruitment relation (here the logistic Eq. 2) but rather is displaced backward by virtue of the factor $1/[1 + \nu(1 - F_2)]$. This feature (*35*), which is illustrated in Fig. 1, derives from the interactive character of the prey-predator situation; as harvesting levels on whales increase, the absolute abundance of krill increases, which has the effect of enhancing per capita growth rates for the remaining whales. Thus, for example, with $\nu = 1$ in our simple model the whale MSY is attained with $F_2 = 0.59$ and the stock reduced to 59 percent of its pristine level (*36*); this compares with figures of $F_2 = 0.50$ and a stock reduction to 50 percent in the corresponding single-species model with logistic growth (*37*). Such "backward-peaked" yield-effort curves are characteristic of the data for many whale (*38*) and some fish (*39*) and other (*40*) populations, and the above mechanism may be partly responsible (*41*).

Returning to the krill population, in Fig. 2 we show the krill yield as a function of the krill and whale fishing efforts, F_1 and F_2, respectively. For fixed F_2, the maximum krill harvest is achieved by $F_1 = 0.5$. This maximum sustainable krill yield increases as the whale fishing effort F_2 increases (depleting the whale population). Clearly the greatest possible krill harvest is attained when $F_2 = 1$, corresponding to extinction of the whales, so that they no longer compete with us for krill.

Considering the whale and krill yields jointly, we may ask what is the maximum krill yield consistent with a specified whale yield (that is, a specified whale quota)? Or, conversely, what is the maximum value of Y_2 subject to Y_1 having some given value? These questions are answered in Fig. 3. Combinations of krill and whale yields represented by points lying inside the shaded region in Fig. 3 are consistent with sustainable management of the stocks, and points outside the shaded region are not. In Fig. 3, the largest whale yields correspond to no fishing for krill ($Y_1^* = 0$ because $F_1 = 0$), whereas the largest krill yields are attained by exterminating whales ($Y_2^* = 0$ because $N_2^* = 0$). The details that underlie Fig. 3 are discussed elsewhere (*42-43*), but the basic message is very clear: A prey-predator system cannot be managed by applying MSY notions to each species individually.

In principle, a possible management criterion is to maximize the *total* sustainable yield of krill plus whales. Suppose the relative value of whales and krill is measured by γ (*44*), where this weighting factor γ can reflect, for example, relative economic value, processed weight, and protein content. The total weighted yield is then proportional to $Y = Y_1^* + \gamma Y_2^*$, whence Y can be written (up to some overall proportionality constant C)

$$Y = \frac{C[1 - F_1][F_1 + \beta F_2(1 - F_2)]}{1 + \nu(1 - F_2)} \tag{10}$$

Here β is the parameter combination

$$\beta = \gamma\alpha(r_2/r_1) \tag{11}$$

The symbol β has an illuminating interpretation as the effective value of unit whale biomass relative to unit krill biomass; it is the intrinsic relative value, γ, discounted by the biological conversion efficiency, α, and the relative intrinsic growth rates, r_2/r_1. The total sustainable yield Y may now be maximized with respect to F_1 and F_2 to find the global optimum. Three situations are possible (*45*). If β is small, the optimum solution is obtained by extinguishing the relatively valueless whales and harvesting only krill. If β is large, only whales should be sought, and their food supply should be left alone. Only for a narrow band of intermediate β values does the optimum solution involve both prey and predator. Quite apart from the practical difficulties inherent in seeking to optimize a total yield whose component elements of prey and predator are typically fished by different industries, the "all or nothing" nature of the global optimum will often make it inconsistent with preserving all species in the ecosystem.

Dynamics. Thus far, we have dealt with the sustainable yield that can be attained at equilibrium under various harvesting regimes. We now turn to the dynamics.

When the fishing efforts change, the system moves along a dynamic trajectory described by the differential Eqs. 3 and 4. For many prey-predator systems that are of interest to fishery managers, and for the krill-whale system in particular, the intrinsic growth rate for the prey population, r_1, is significantly larger than that for the predator population, r_2 (*46*). As a result, the prey population tends to respond to changes relatively fast, on a time scale set roughly by $T_1 \sim 1/r_1$; during this time the predator population will change little. Subsequently, the predator population will change relatively slowly, on the longer time scale $T_2 \sim 1/r_2$, and the entire system will settle to its new equilibrium.

To exemplify these ideas, Fig. 4 shows what happens in our metaphorical krill-baleen whale model (Eqs. 3 and 4) after krill harvesting is begun. Specifically, there is no krill fishing before time $t = 0$, and a constant krill fishing effort $F_1 = 0.5$, is maintained for $t > 0$. Other parameters remain constant, the values being shown in the legend (in particular, the whales here have been, and continue to be, heavily exploited at the rate $F_2 = 0.8$). Figure 4A depicts the trajectory the system follows in the prey-predator "phase plane"; The krill population changes relatively rapidly, on the T_1 time scale, to attain roughly the equilibrium value appropriate to the original whale density and the new harvesting regime; then both populations move relatively slowly, on the T_2 time scale, approximately along the krill "isocline" (where the krill population has the equilibrium value appropriate to the current value of the changing whale population), toward the final equilibrium point. Figure 4 also shows krill and whale populations as functions of time, further illustrating the above points. These changes take place relatively smoothly in Fig. 4; with other parameters, it is possible for the system to show damped oscillations as it relaxes to its new equilibrium.

The essential feature here is that, as krill harvesting starts up, the exploited population seems to adjust to a new steady value relatively quickly. But there are longer-term population changes controlled by slower components of the ecosystem. Once this is appreciated, it can be possible to get relatively quick indications of the reactions of the slower-changing populations (for example, by monitoring pregnancy rates). Basically, however, management must be geared to the slower time scales if the entire ecosystem is the unit of concern.

More generally, the way the system responds to environmental fluctuations will be altered by harvesting. The "characteristic return time," T_R, for recovery toward equilibrium after a small perturbation provides one crude measure of the robustness of the system (*47*), and T_R typically increases as either F_1 or F_2, or both, increase (*48*). That is, the harvested system typically takes longer to recover from environmental buffeting than does the pristine system. These effects become dramatically more severe as F_1 and F_2 increase toward unity. There are many qualifications and caveats that need to be appended to these simple generalizations (*49*), but it remains broadly true that harvested systems are typically less resilient.

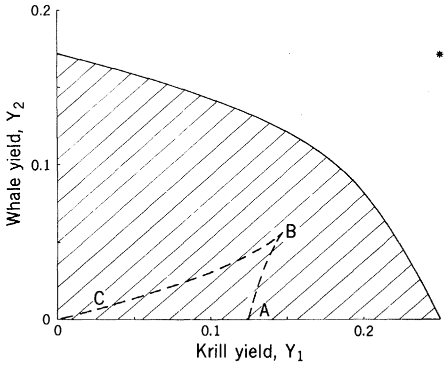
One Prey with Two Predators: Krill, Whales, and Seals

Krill are the food source for many species in the Antarctic. The effective removal of most baleen whale species does not therefore result in a simple increase in the abundance of krill, but rather some fraction of this increase is consumed by increased populations of other krill predators. Similar complications arise in other situations involving the harvesting of one of several species that prey on a common resource (*50*).

Some insight into the dynamics of such fisheries can be gained by extending our simple heuristic model to encompass two competing predators, only one of which is subject to significant harvesting. This krill-whale-seal model may serve as a crude metaphor for the interplay between populations of minke whales (not harvested until recently) and other baleen whales, or more broadly between seals, penguins, and other relatively unharvested animals and baleen whales.

In the extended model (*51, 52*), the competition between "whales" and "seals" is indirect, in the sense that the abundance of the resource (krill) that sustains them depends on the intensity of predation both by whales (measured by the familiar dimensionless parameter ν) and by seals (measured by an analogous parameter η). As the whale population decreases under exploitation, both the krill and the seal populations will benefit, but the details of how this benefit is apportioned between the two populations will depend on the magnitude of the parameters ν and η. Figure 5A illustrates some of these points, showing what happens in such a system when all harvesting ceases, given an initial equilibrium corresponding to heavy exploitation of whales. As the system settles to its original, unharvested state, the whale population increases while seal and krill populations decrease.

In general, the effects of competition result in the whale population relaxing toward the new equilibrium on a slower time scale than would be the case were there no competitors. There is a historical tendency, however, for the first exploited species to be the largest of the predators, and consequently for them of-



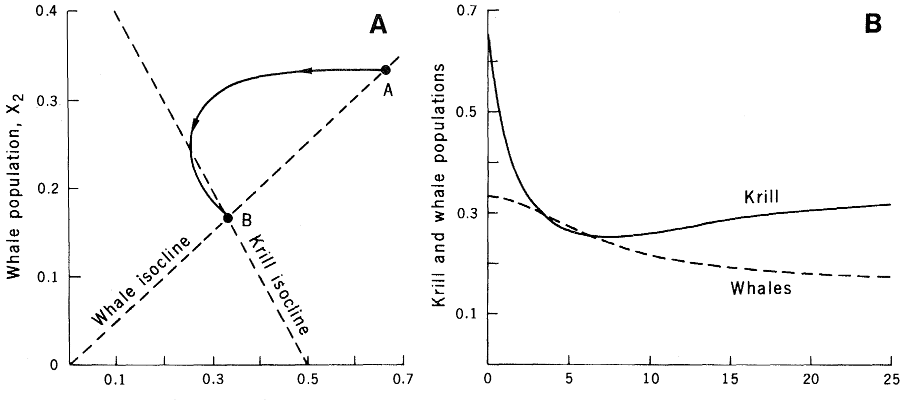


Fig. 3 (left). The boundary of the shaded area gives the maximum sustainable krill yield consistent with a prescribed whale yield (or, conversely, the maximum sustainable whale yield consistent with a specified krill yield), given that the krill-whale interaction is described by Eqs. 3 and 4 with $\nu = 1$ (and with the scaling constants in Eqs. 8 and 9 being $r_1K = 1$ and $\alpha r_2K = 1$). Combinations of yields inside the shaded area are therefore sustainable, and combinations outside it are not. In particular, the star in the top right-hand corner corresponds to krill and whale yields both having their individual MSY values; clearly these yields cannot both be sustained. The dashed curves *AB* and *BC*, and other details, are discussed in (*42*). Fig. 4 (right). The dynamic behavior of the krill-whale system (see Eqs. 3 and 4 in text) after a change in the harvesting regime. In (A) the dynamic trajectory is shown in the krill-whale population "phase plane"; the system moves from the old equilibrium state *A*, to the new equilibrium *B*, along a path whose general features are discussed in the text (the dashed lines are the krill and whale "isoclines," along which $dX_1/dt = 0$ and $dX_2/dt = 0$, respectively). In (B) the krill (solid) and whale (dashed) populations are shown as functions of time. Specifically, the parameters in Eqs. 3 and 4 here have the values: $\nu = 1$; $r_1 = 1$; $F_2 = 0.8$; $F_1 = 0$ for $t < 0$, and $F_1 = 0.5$ for $t > 0$.

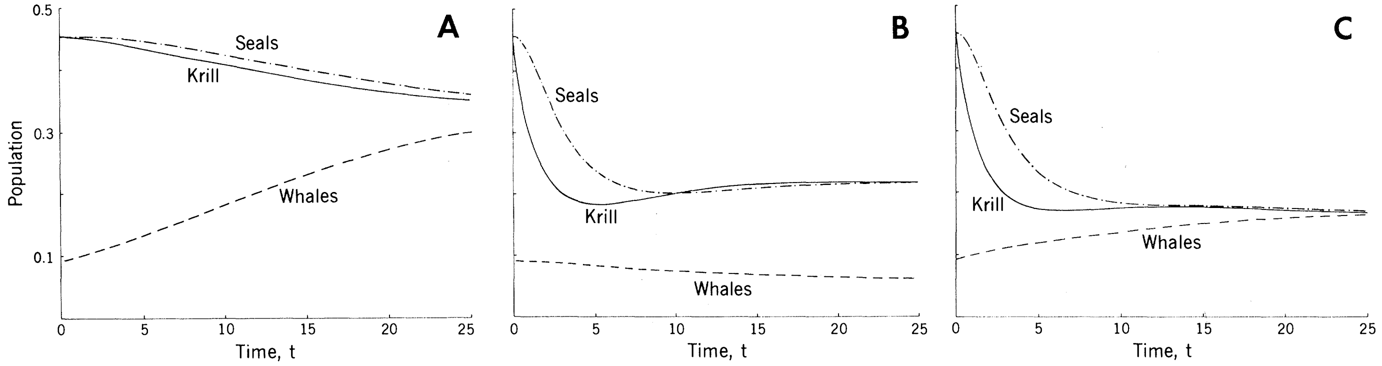


Fig. 5. The behavior of krill (X_1; solid curve), whale (X_2; dashed), and seal (X_3; dot-dash) populations under three different harvesting regimes. (A) After cessation of whaling in our model (*51*) where specifically the parameter values are $r_1 = 1$; $r_2 = 0.1$; $r_3 = 0.3$; $\nu = 1$; $\eta = 1$; and $F_1 = 0$. Initially, the system is at equilibrium under relatively heavy harvesting of whales ($F_2 = 0.8$); for $t > 0$, $F_2 = 0$. The general character of the dynamic response is as discussed in the text. (B) As for (A) but here the change in harvesting regime consists of initiating exploitation of krill, while maintaining the heavy harvesting of whales. That is, the parameter values are as in (A) except that F_2 remains steady at $F_2 = 0.8$, while $F_1 = 0.5$ for $t > 0$. The differing time scales for various responses to be manifested are as noted in the text. (C) This figure combines the harvesting regimes of (A) and (B). Here krill harvesting is begun, and simultaneously whale exploitation is stopped. That is, $F_1 = 0.5$ and $F_2 = 0$ for $t > 0$; all other parameter values are as in (A) and (B).

ten to have slower growth rates (and longer time scales for population change) than other competing predators (*46*). This is certainly the case in the Southern Ocean. Thus, for the illustrative examples in Fig. 5, we choose the intrinsic growth rate of the "seal" population, r_3, to be intermediate between that for the fast-growing krill, r_1, and the slow-growing whales, r_2 (specifically, for illustrative purposes we put $r_1 = 1$, $r_3 = 0.3$, and $r_2 = 0.1$). As a result, the changes depicted in Fig. 5A take place roughly on the whale time scale, $T_2 \sim 1/r_2$.

A more intricate dynamical response is exhibited if we initiate harvesting of krill, maintaining the existing exploitation levels for whales. The result is shown in Fig. 5B, which is to be compared with Fig. 4. Here the krill fishing effort is $F_1 = 0.5$, so that krill, seal, and whale populations are all eventually halved: the krill responds rapidly, on its time scale $T_1 \sim 1/r_1$; next the seal population adjusts, somewhat more slowly, to the diminished krill abundance (and the krill population itself increases slightly as seal predation diminishes); finally the whale population declines on its long time scale $T_2 \sim 1/r_2$ (with the krill concomitantly showing a further slow increase). Similarly, if the harvesting regimes of parts A and B of Fig. 5 are combined, to initiate krill exploitation and simultaneously to abandon harvesting whales ($F_1 = 0.5$ and $F_2 = 0$ for $t > 0$), we get the outcome shown in Fig. 5C. For this particular change in fishing efforts we see a fast decline in the krill population, followed more slowly by a decrease in the seal population (and an accompanying slight increase in krill abundance), and a final slow rise in the whale population (accompanied by slight declines in krill and seal populations). In short, the equilibrium population levels in systems of this kind change in complicated ways, and on a variety of time scales, in response to changes in harvesting regimes. Note that the metabolic rates of the various species [which are associated with physical size and growth rates (*46*)] are relevant to the rate at which populations respond to such changes. The ultimate equilibrium levels do not, however, depend directly on these rate processes in our models (although they do enter indirectly by way of the predation and consumption efficiencies a and α that go toward determining ν).

Our very simple model only hints at some of the complexities that competition can introduce into real ecosystems. For example, there may be direct or "interference" competition, whereby one predator species actively excludes another from a resource; if there is a high degree of intrinsic niche overlap between the two species, removal of one may result in its being effectively replaced by the other, with the consumption of the resource remaining essentially unchanged (*8, 52, 53*); that is, no increase in krill abundance. Baleen whales tend to gather krill in somewhat different locations from most seals and penguins, yet diffusion is likely to link krill abundance in different places, which suggests the need for a spatially dynamic model (*54*). Finally, there are behavioral complications. The large baleen whales tend to feed on large swarms of krill, which are also likely to be the focus of a krill fishery. Exploitation of these large swarms could thus have a disproportionate effect on baleen whales, shifting competitive equilibria in ways that would not be guessed from simple estimates of changing krill abundance.

This last point touches on a more general issue (*30, 55*). Fishermen will be motivated always to search for the highest concentration of fish. If the target species are prey to other species, it is likely that the predators also take advantage of the prey concentration. There are two consequences: the assumption that catch-per-unit-effort (CPUE) is linearly proportional to prey abundance will lead to a biased estimate of stock density (*56*); and fishing of the prey species will have a greater effect on the predator species than if prey abundance were uniformly affected. In some cases, the nonlinearities introduced by schooling or aggregation of harvested populations can have the effect that a gradual and continuous increase in harvesting rates may precipitate a sudden and discontinuous collapse of the stock. The implications of these concentration effects for optimal harvesting require further analysis, but the general trend would seem to call for a more conservative catch policy than otherwise.

Three Trophic Levels: Krill, Cephalopods, and Sperm Whales

Another complication arises in many fisheries where the top and bottom species in a three-level trophic ladder are harvested. An important example in the Southern Ocean is male sperm whales which eat cephalopods (squid), which in turn are significant consumers of krill (*57*).

A simple caricature of this circumstance may be obtained by extending the prey-predator model of Eqs. 3 and 4 into

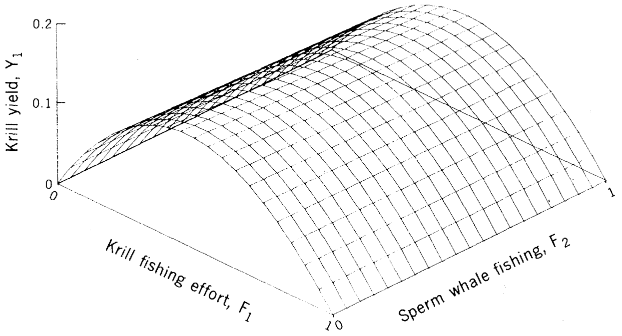


Fig. 6. For the krill-cephalopod-sperm whale model (*58*), the krill yield, Y_1, is shown as a function of fishing effort on krill, F_1, and on sperm whales, F_2. (Here $\nu = 1$, $\zeta = 1$, and the scaling constant of Eq. 8 is $r_1K = 1$). The trends illustrated here, especially the contrast with Fig. 2, are discussed in the text.

prey-predator-top predator form. Predation of sperm whales upon cephalopods is characterized by a dimensionless combination of parameters ν, akin to that of Eq. 5, and the prey-predator relation between krill and cephalopods is similarly characterized by a parameter ζ (*58*).

As in Fig. 1, the yield-effort curve for exploitation of sperm whales will again be peaked backward from the logistic pattern it would have if treated on a single-species basis. For a specified value of ν, this backward-peaking is, however, less pronounced in the three-level model than in the earlier two-level system. The reason is that, although a decrease in the sperm whale population implies a partially offsetting increase in their cephalopod prey, this increase in turn tends to diminish the krill population, thus decreasing all three populations to some extent. Thus tight coupling to a third level tends to weaken the backward-peaking of the yield-effort curve for the top predator, with the backward-peaking being most conspicuously manifested for large ν and small ζ.

The krill yield as a function of harvesting effort on krill and on sperm whales is illustrated in Fig. 6. The relation between krill yield and exploitation of sperm whales is the opposite of that between krill and baleen whales (Fig. 2), with the highest krill yield obtained when sperm whales are not exploited. The explanation is that high sperm whale abundance implies relatively low cephalopod abundance, and thence relatively low levels of predation upon krill; this is plainly in contrast to the direct interaction between krill and baleen whales. Note, however, that the coupling between krill yields and levels of sperm whale exploitation is typically weaker than for the corresponding two-species system, because of the attenuations implicit in the three-level structure.

A figure analogous to that in Fig. 3 can be drawn for the combinations of krill and sperm whale yields that are compatible with equilibrium. This figure looks like Fig. 3, and similarly demonstrates that multispecies systems cannot be managed by piecemeal application of single-species MSY concepts (*59*). It differs in details, most conspicuously in that the largest sustainable krill yield is attained when sperm whales are not exploited (whereas in Fig. 3 the largest yield is attained by extinction of baleen whales).

Other More Complicated Ecosystems

Considerably greater complications can arise in the complex ecosystems that have been studied in detail, as models for fisheries in the North Sea and elsewhere, by Anderson and Ursin (*7*), Jones (*8*), Steele (*9*), Laevastu and Favorite (*12*), Parrish (*26*), and others.

As one example of what can happen, let us consider the situation depicted schematically in Fig. 7 (*60*). Here the predator species A takes both prey species C and D, while the predator species B specializes on the prey D. The prey species C and D compete for resources E and F. Suppose that species C is competitively superior to species D, and in the absence of predation would displace it from the system, but that the predator species A has the effect of curbing this competitive superiority and enabling C and D to coexist (*50*). If species A is subjected to significant harvesting, the prey species C may escape control and assert its competitive superiority over species D, driving it to low population densities. As a consequence, the predator B that preys on D will also decline. Thus, far from exploitation of the predator species A benefiting the competing predator species B that occupies the same trophic level, species B will decrease as A is harvested. As Steele (*9, 61*) has emphasized, not only can this phenomenon occur, but it can easily be that the population B suddenly collapses in a discontinuous or catastrophic manner as the fishing effort on species A increases smoothly (*62*).

Steele (*9, 61*) and others have also demonstrated that changes in harvesting regimes can interact with structural aspects of the web of relationship among species, to produce great alterations in the way a complex system responds to disturbance. Thus changes in harvesting regimes can lead not only to dramatic shifts in the average values of stock densities and yields, but also to large changes in the variance of stock densities and yields.

Krill in the Southern Ocean

Laws (*2*) has recently drawn together much of the available information pertaining to the population dynamics of krill-eating animals in the Southern Ocean. Estimates of the magnitude of past and present populations of baleen whales suggest that the annual krill consumption of the present, depleted stocks is roughly 150 million metric tons less than it was around 1900.

In the Southern Ocean, humpback, blue, fin, sei, and, most recently, minke have successively been the preferred target for exploitation. All except minke currently have the status of protected stock and are believed to be well below pristine population levels. A variety of evidence points to shifts in the competitive equilibria, and enhanced population growth rates, as the remaining whales benefit from reduced competition within and between species (*2, 63*). For fin (*64*), sei (*65*), and minke (*20, 66*) there is direct evidence for an increase in reproductive capacity, with pregnancy rates increasing and age at sexual maturity decreasing; for sei and minke these trends were manifested before the species were themselves significantly exploited. There is also evidence of increased reproductive capacity for blue whales (*67*). In particular, the minke whale population (with a drop in the age of sexual maturity from around 14 to around 6 years) appears to have expanded into the ecological vacuum created by the removal of its competitors, especially the blue whale. Although the current level of exploitation of minke whales may be close to the replacement level (*68*), it is likely that their present population levels are well in excess of (possibly even double) those in the prewhaling era. These considerations play little part in the reckoning of the 150 million tons "surplus" of krill. If we start to harvest krill in substantial quantities, we can expect the growth rates of baleen whale populations to decline back toward the lower levels characteristic of the pristine system, as competition effectively becomes more severe.

There is also evidence that populations of many other krill-eating animals are increasing in the Antarctic, some of them at rates too fast to be explained as simple recovery from past exploitation (*2*). This is true for the southern fur seal (*69*) (where the fastest increases have occurred in the Scotia Arc, where its distribution overlaps that of baleen whales), of macaroni, chinstrap, Adélie, and rockhopper penguins (*2, 70*), and of some seabirds (*71*). The most significant of the seal and bird populations in the Southern Ocean is the crabeater seal. Of the world's seals, 80 percent (by biomass) dwell in the Antarctic, and to a good first approximation they are all crabeaters, consuming krill at an annual rate roughly equal to 1.5 that of current stocks of baleen whales. Various lines of evidence show that the reproductive capacity of crabeater seals has increased in recent years (*2*); in particular, in the Antarctic Peninsula, their mean age at sexual maturity was 4 years until the whaling zone known as the "Sanctuary" was reopened, since when the age has steadily fallen to 2.5 years.

Cephalopods are the least well understood of the major krill-consuming populations (*57*). They must have benefited from whaling in two ways. First, like many other species, cephalopods will have enjoyed the greater krill abundance attendant upon the depletion of their competitors, the baleen whales. Second, and less commonly appreciated, heavy exploitation of large male sperm whales in the Southern Ocean (*72*) (to the extent that sperm whales are now protected stock in some zones) will have resulted in increased abundance of their cephalopod prey, in the manner discussed above.

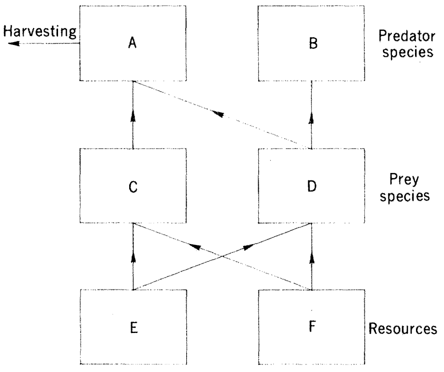


Fig. 7. A schematic illustration of a food web. As discussed in the text, in such a system harvesting of the predator species *A* can have the effect of *decreasing*, rather than increasing, the population of the other predator species, *B*. Furthermore, such indirectly produced population crashes can happen discontinuously; this is only one of a variety of counterintuitive things that can happen under harvesting in a complex ecosystem.

In brief, the Southern Ocean ecosystem is adjusting to new equilibria, following the depletion of baleen whale stocks. Because the quantitative data about population densities come mainly from harvested populations, it is not possible to say exactly how the "surplus" krill have been shared among relatively unexploited baleen whales (particularly minke), crabeater and other seals, birds, fish, and cephalopods (themselves increased by virtue of sperm whale harvesting), or have contributed to an increased standing crop of krill. Only one thing is certain: The system has not remained unaltered save only for the appearance of 150 million tons of "surplus" krill each year. We cannot even substitute krill-fishing boats for all the "missing" baleen whales (*73*), and hope to let other populations decline back to their original levels. Things are not that simple. Under such heavy exploitation of krill, the system will lurch toward some new equilibrium, in which baleen whale populations may well lie below their current low levels.

North Sea and Other Fisheries

In the past decade or so, increasingly intense levels of exploitation have created situations where many commercial fisheries have to be reappraised from a multispecies viewpoint (*7-19, 50*).

In the North Sea (*7-10*), the total fish catch rose from around 1.5 to 3 million tons per year in the period 1960 to 1967. It has remained steady at about 3 million tons since then, with a marked decline in the stock and catch of the heavily exploited herring and mackerel being compensated by increased yields of other species. In particular, over the span 1947 to 1974 there is an essentially linear correlation between the decline in the herring and mackerel catch and the increase in the catch of Norway pout, sand eels, and sprat (*74*). We cannot be certain of the extent to which these changes are due to compensatory shifts in population densities, to changes in patterns of harvesting, or even to coincidental environmental effects (*9*). It has been suggested, however, that the steady annual catch of 3 million tons has been drawn from a total stock that has remained approximately constant at around 9 million tons, but whose composition has shifted from roughly 6 million tons of herring and mackerel and 3 million tons of other fish in 1964 to around 2 million tons of herring and mackerel and 7 million tons of others in 1976. The estimates of individual populations are uncertain (some of them by factors as large as 2), and furthermore the overall totals do not include some species that may be significant in the ecosystem even though they are not subject to much commercial exploitation. Nevertheless, the figures do indicate broad trends that are not in dispute.

Building on the model constructed by Riffenburgh (*17*) for investigating the interplay between Pacific anchovy, sardine, and hake fisheries, Anderson and Ursin have developed a very elaborate system of equations (*75*) to describe the interactions among species in the North Sea under various harvesting assumptions. Although the details of this model are disputable, some qualitative features are illuminating. For example, the increase in stocks of the larger gadoids and other smaller fish is explicitly attributable to diminished predation on their larval and juvenile stages, as herring and mackerel are harvested more intensely. Without considering exploitation of unconventional species, the multispecies analysis by Anderson and Ursin suggests the sustainable yield for fish stocks in the North Sea might conceivably be increased to around 5 to 6 million tons per year. This would be achieved by systematic depletion of the stocks (and yields) of the larger predatory fish (cod, saithe, haddock), and by concentrating attention upon the younger age classes and smaller species that would then come to predominate in the North Sea. The basic process is strongly reminiscent of that illustrated in Figs. 1, 2, and 3; relatively large yields of stocks low on the trophic ladder usually require that their predators be driven to low levels.

Clearly, such an increase in the total catch implies concomitant shifts in patterns of consumption. The issue becomes "whether the marine resources should be put on the dining table in the form of cod fed with living fish or in the form of chicken fed with fish meal" (*10*). Thus biological considerations shade into economic and social questions. This leads into the next section.

Economic Considerations

The preceding discussion has focused on biological yields. But economic aspects of harvesting can be important for a variety of reasons (*76*). Proposed regulations that fly in the face of economic interests will not be acceptable to the fishing industry. Furthermore, unless economic aspects are taken into consideration, regulations that are actually imposed may lead to unexpected consequences.

The basic patterns that arise in the exploitation of living resources stem from two related causes, each of which involves certain conflicts of interest. First, since property rights are often lacking for these resources (this is particularly true for pelagic fish stocks), competition exists among various exploiters. There is an overwhelming incentive for each exploiter to "get there first" before the resource stock is captured by some competitor. Second, even if current exploiters of the resource are able to agree on a division of the catch (and this is itself quite unusual), the current generations of exploiters may have very little incentive to conserve the stock for the benefit of future generations; it may be better, in purely financial terms, to liquidate the stock as quickly as possible and to invest the proceeds elsewhere at a higher "interest rate." This last phenomenon (essentially the "time discounting" phenomenon) can have serious implications for conservation even under the "ideal" conditions of guaranteed sole property rights to the resource stock (*76*). More generally, we see that the less secure are property rights, the greater will be the preference for short-term benefits.

Notice that both the above phenomena tend to distort the time-path of harvesting of the resource toward the present, and are thus anticonservationist in their effects. Both phenomena also tend to result in overexpansion of the harvesting industry, relative to the minimum capacity that would be needed for sustained harvesting (*77*). This last problem, which has been largely ignored until recently, has severe implications for regulation and management of renewable resources (*78*).

Specifically, let us see how these two anticonservationist forces of competition and time-discounting can be expected to influence the harvesting of a prey-predator system of the type discussed above. Assume that predators (for example, whales) are more valuable than prey (krill), in the sense that they provide greater economic returns per unit of expenditure on capture. Then whales will certainly be preferred over the short run. Furthermore, maximum economic yield will probably imply the exclusive harvest of whales, at least under the assumptions outlined above. But, under competition or a high rate of time-discounting, the long-run equilibrium may be almost exclusively directed toward krill harvesting!

It is easy to see how this situation could arise. Whales, being preferred, are initially heavily exploited and whale stocks depleted. The industry then faces the option of switching to krill, or of abstaining from harvesting both krill and whales until the whale population has recovered. Even though revenues from krill harvesting may be much lower than potential revenues from whaling, the distortion in time profiles favors the immediate exploitation of krill. Indeed, if whale stocks are protected [as under current International Whaling Commission (IWC) regulations], it appears that the incentive for harvesting krill could be further increased, since the industry now has no short-term alternative. In addition, existing whaling vessels have few alternative uses, but may make useful krill processing factories, and there will be pressure so to utilize them.

Considerations of this type clearly lead to very difficult questions concerning the choice of appropriate principles and techniques for practical management of such resource systems. Regulations that control the worst consequences of competition should be generally acceptable to the industry, but regulations that significantly reduce economic benefits (discounted at a reasonable rate) will not be acceptable. For example, whaling nations agreed among themselves—and outside the IWC—to an allocated quota system for Antarctic whales, but refused for many years to eliminate the economically convenient "blue-whale-unit" (BWU) system of measuring catches. The allocated quota system was economically attractive, as it eliminated the motive for competitive overcapitalization, and the BWU system was attractive because it allowed for great freedom in harvesting whales. From the biological viewpoint, however, these regulations were not a success.

Uncertainty is another aspect of biological systems that has extremely important economic implications (*79*). In most instances exploiters will be fairly certain of short-term profitability of a resource system, but will be highly uncertain about long-term biological (or economic) effects. The omnipresent bias toward early benefits will therefore mitigate against conservative regulations whose future benefits are uncertain. Thus, while the biologist may feel that uncertainty should warrant greater caution and reduced harvest, the industry's viewpoint may well be the opposite.

These problems are especially severe for internationally exploited resource stocks, since in this case there is no central government that can act as a risk taker and regulate catches accordingly. The best that can be hoped for is that the international community will accept scientific recommendations for caution in the face of uncertainties.

Indeed, a positive approach toward uncertainty would go further than merely adopting a "safety factor" in allowable catch quotas. Contingency plans would be formulated to deal with unexpected situations, such as poor recruitment due to environmental fluctuations, or to miscalculation of sustainable harvest rates. Such contingency plans are normal, for example, in agriculture, but again depend on the existence of a central authority with full regulatory powers. The current IWC regulations, whereby quotas are coupled to estimated abundance levels of the stocks, are at least a move in the right direction for international resources. Similar rules seem appropriate for multispecies systems, although the proper target levels for various species may be very hard to determine.

Another situation, with somewhat different economic implications, arises where different species in a multispecies system are exploited by separate groups of people. For example, the California anchovy population supports a commercial fishery, but allowed catches are severely limited as a result of political pressure from sports fishermen who see the anchovies as a major food source for sport fishes. The system is further complicated by a competitive relation between the anchovy population and the formerly abundant California sardine (*17, 18*). Heavy fishing of the anchovies has been recommended by some biologists, in the hope that this would precipitate a revival of the sardine population that crashed in the 1950's; but sports fishermen have remained unconvinced. This is a particularly clear example of a complex situation where biology, economics, and politics roil together, and it is doubtful whether any "scientific" principles of management are particularly relevant.

The anchovy-sardine example harks back to an important aspect of harvesting in multispecies systems that was mentioned earlier. Namely, such systems will often manifest complex "catastrophic" behavior (*30, 62*), whereby the system is discontinuously transformed to a different equilibrium state as harvesting rates increase, or as environmental circumstances alter. This transformation will not usually be continuously reversible, with the result that significant reductions in harvesting rates may become necessary, or (as in the anchovy-sardine system) entirely new harvesting strategies may be required. Since these catastrophic changes are seldom, if ever, predictable in a quantitative sense, and since they can be expected to occur in almost any severely exploited ecosystem, the need for conservatism and contingency planning is emphasized.

Conclusion

For all its acknowledged shortcomings, MSY is at least a useful point of departure in discussion of management principles for single species. But it is clear from the foregoing discussion that simple considerations of MSY, species by species, are insufficient for enunciating management principles in multispecies situations, such as pertain in the Southern Ocean.

Some tentative findings that may serve as a basis for further discussion of management principles in multispecies systems are as follows.

1) For populations at the top of the trophic ladder, themselves not subject to significant natural predation, MSY will often remain useful. Such stocks should be kept at or above the level at which they provide the greatest net annual increment. [Given the difficulties in deducing yield-effort curves from noisy data, it is useful to keep in mind that these yield-effort curves are likely to be displaced backward from those that would be expected on a single-species basis, if the population is fairly tightly coupled to its sustaining prey population, as most baleen whales are (*41*).]

2) For populations other than these, preservation of the ecosystem would seem to require that stocks not be depleted to a level such that the population's productivity, or that of other populations dependent on it, be significantly reduced. An appropriate criterion of "significant reduction" of dependent stocks is not easily given (particularly when it is kept in mind that any stock subject to predation may well be below MSY in its natural state). One possibility, which is fairly clear in the krill-whale metaphorical model above, is to forbid any harvesting that has the effect of depressing top-trophic-level stocks below some specified fraction of their pristine levels.

3) In the management of multispecies ecosystems, it is very important that the different time scales for different population processes be kept in mind. It is the slowest time scales (often set by the top predators) that should be used in monitoring a harvesting regime.

4) All estimates of population parameters are liable to fluctuate in response to environmental stochasticity, and harvested populations may be typically less able to recover from external disturbances than are virgin stocks. If sustainable yields are the goal, harvesting levels should be set conservatively, allowing for safety factors to guard against accidental overexploitation.

5) In actuality, all these biological considerations about sustained yields intersect with a variety of economic and political factors, many of which do not arise in single-species systems. The consequences and management implications defy crisp summary.

References and Notes

1. S. J. Holt, *The Man/Food Equation*, F. Sleete and A. Bourne, Eds. (Academic Press, London, 1975), pp. 77–96; J. A. Gulland, Ed., *The Food Resources of the Ocean* [Fishing News (Books), London, 1971], p. 255; FAO, *FAO Fish. Rep. No. 175* (1975).
2. R. M. Laws, *Phil. Trans. R. Soc. London Ser. B*, **279,** 81 (1977); in *Adaptations Within Antarctic Ecosystems*, G. A. Llano, Ed. (Smithsonian Institution, Washington, D.C., 1977), pp. 411–438.
3. This figure rests on estimates for the energy budgets of baleen whales that have been reviewed by P. F. Brodie [in *Functional Anatomy of Marine Mammals*, R. J. Harrison, Ed. (Academic Press, London, 1977), pp. 45–57]. Brodie notes that the metabolic rates attributed to large cetaceans are sometimes "quite inconsistent with the available food resources and burden the animal with a specific rate so high it would appear that their greatest source of natural mortality is spontaneous combustion" (p. 45). Obviously, any overestimate of the energy budgets of baleen whales in the pristine Antarctic ecosystem will lead to an overestimate of the present "krill surplus."
4. I. Everson, *FAO Rep. GLO/SO/77/1* (1977).
5. J. L. Bengtson, *Review of Information Regarding the Conservation of Living Resources of the Antarctic Marine Ecosystem* (U.S. Marine Mammal Commission, Washington D.C., 1978), and references therein.
6. J. R. Beddington and J. H. Lawton, *Comments on the Draft Environmental Impact Statement for a Proposed Regime for Conservation of Antarctic Living Marine Resources* (U.S. State Department, Washington D.C., June 1978), pp. J37–J39. See also Bengtson (*5*).
7. K. P. Anderson and E. Ursin, *Meddr. Danm. Fisk.-og Havunders*. **7**, 319 (1977).
8. R. Jones, *ICES Document CM 1976/F:36* (1976).
9. J. H. Steele, *Appl. Biol.* **4**, 103 (1979).
10. E. Ursin, *Proceedings of the 16th Nordic Fisheries Conference, Mariehamn, Finland* (manuscript, 1978).
11. J. Harwood, *J. Appl. Ecol.* **15**, 413 (1978).
12. T. Laevastu and F. Favorite, *ICES Symposium on the Biological Basis of Pelagic Fish Stock Management* (1978), document 31, and references therein.
13. P. F. Lett and T. Benjaminsen, *J. Fish. Res. Board Can.* **34**, 1155 (1977).
14. W. Zalazhowski, J. Szypula, I. Krzykawski, *ICES Document CM 1976/P:23* (1976).
15. P. K. Dayton, *Fish. Bull.* **73**, 230 (1975); R. M. May, *Nature (London)* **260**, 284 (1976).
16. P. F. Lett and A. C. Kohler, *J. Fish. Res. Board Can.* **33**, 1353 (1976).
17. R. H. Riffenburgh, *ibid.* **26**, 2843 (1969).
18. G. I. Murphy, *Proc. Calif. Acad. Sci. Ser. 4* **34**, 1 (1966).
19. J. G. Pope, *Int. Comm. Northwest Atl. Fish. Selected Pap.* **1**, 163 (1976).
20. Among the acknowledged shortcomings and difficulties in MSY as a management goal are: uncertainties in the parameter estimates [S. J. Holt, *FAO Scientific Consultation on Marine Mammals, ACMRR/MM/SC/29* (1976); *Int. Comm. Whaling Rep.* **27**, 230 (1977); D. H. Cushing, *ICES Document CM 1973/F:29* (1973)]; the implicit assumption that the world is deterministic [see May *et al.* (*21*)]; arguments about whether catches should be maximized by numbers or by weight [S. J. Holt, *FAO Scientific Consultation on Marine Mammals, ACMRR/MM/SC/99* (1976)]; and the neglect of many economic factors [Clark (*22*), and references therein], including sustained harvesting costs (which should be incorporated to give a maximum sustainable net yield) [S. J. Holt, *Int. Comm. Whaling Rep.* **28**, 191 (1978)], and the propensity to discount future yields. For a general review of MSY in relation to management principles, see: S. J. Holt and L. M. Talbot, *Wildlife Monogr.* No. 59 (1978); FAO, *FAO Fish. Rep. No. 194* (1977); M. P. Sissenwine, *Fisheries* **3**, 22 (1978); J. R. Beddington, in *Population Dynamics*, R. M. Anderson, B. D. Turner, R. L. Taylor, Eds. (Blackwell, Oxford, 1979). There are, of course, practical difficulties in ensuring that agreed MSY or other levels are adhered to by fishermen.
21. R. M. May, J. R. Beddington, J. W. Horwood, J. G. Shepherd, *Math. Biosci.* **42**, 219 (1978), and references therein.
22. C. W. Clark, *Mathematical Bioeconomics* (Wiley, New York, 1976).
23. The IWC acknowledges both uses of the MSY concept. For a good account of current IWC management principles, see S. G. Brown, *Polar Rec.* **18**, 85 (1976); *ibid.* **19**, 59 (1978); see also R. M. May, *Nature (London)* **276**, 319 (1978).
24. This phrase occurs in the U.S. Marine Mammal Protection Act of 1972.
25. Scientific problems arising in the management of multispecies fisheries have also been considered recently by the FAO [*FAO Fish. Tech. Pap. No. 181* (1978), p. 42]. The FAO review uses models similar to ours to explore biological and technological aspects of the simultaneous harvesting of two species interacting as competitors or as prey and predator. The FAO paper gives relatively more attention to the details of some actual multispecies fisheries (on Georges Bank and in the Gulf of Thailand) and relatively less attention to general patterns and trends.
26. J. D. Parrish, *U.S. Fish Wildl. Serv. Fish. Bull.* **73**, 695 (1975).
27. Several refinements can be incorporated in the description of the prey-predator interactions; most of them buy greater reality, at the cost of more parameters. Thus the logistic form for the single-species growth of the krill population (without predators) can be generalized to the Pella-Tomlinson (*28*) form $r_1N_1[1-(N_1/K)^z]$, where z is a phenomenological parameter which gives a growth curve peaked backward from the logistic if $z > 1$, and peaked to lower population densities than the logistic if $z < 1$. Other modifications could include saturation of the predators' attack rate at high prey densities, time delays in the recruitment terms for prey and predator populations, and some population growth term other than the simple logistic for the predator. For further discussion of Eqs. 1 and 2, and other alternative forms, see R. M. May (*29*).
28. J. J. Pella and P. K. Tomlinson, *Inter-Am. Trop. Tuna Comm. Bull.* **13**, 421 (1969).
29. R. M. May, in *Theoretical Ecology: Principles and Applications*, R. M. May, Ed. (Blackwell, Oxford, 1976). chap. 4.
30. For example, see Clark (*22*). More generally, if the harvested stock is distributed in an uneven, patchy fashion and if fishing is concentrated in regions of maximum stock density, the yield will tend to have the form $Y = GN/(D + N)$; here D is related to the dispersal of the stock. If D is effectively large, this expression reduces essentially to the "constant effort" one used in the main text; if D is effectively small, the harvesting is essentially as for a "constant quota" strategy, until stock densities fall very low. The former is arguably the case for ground fish such as haddock, cod, or whiting (where there is normally no predictable dense concentration at scales relating to fishing methods), while the latter arguably pertains to whales or herring shoals (where the organic matter is "packaged" in large and conveniently catchable units). Restated in more intuitive terms, the catch of a highly aggregated species, that occurs in relatively predictable locations, may remain roughly constant as the stock declines, because the effort required to remove the last 100 herring shoals is not significantly greater than that required to catch the first 100. As discussed by J. R. Beddington and R. M. May [*Science* **197**, 463 (1977)] and Clark and Mangel (*31*), such stocks

for which D is effectively small are likely to possess two alternative equilibrium states for moderate levels of harvesting effort and are liable to collapse in a catastrophic or discontinuous way. In short, highly aggregated stocks are significantly more susceptible to extinction. This point was emphasized by J. H. Steele.

31. C. W. Clark and M. Mangel, *Fish. Bull.*, in press.
32. Equations essentially the same as these have been studied by J. W. Horwood [in *Dynamics in Large Mammals*, C. W. Fowler and T. Smith, Eds. (Wiley, New York, 1979)], who gives interesting numerical simulations of the joint yields obtained under various harvesting strategies.
33. For a more general discussion of rescaling in population equations and its use in disentangling parameters that influence the statics from those that influence the dynamics, see R. M. May (*29*), p. 6.
34. L. B. Slobodkin, *Am. Nat.* **108**, 665 (1974); M. E. Gilpin, *Group Selection in Predator-Prey Communities* (Princeton Univ. Press, Princeton, N.J., 1975); V. C. Maiorana, *Am. Nat.* **110**, 486 (1976); D. B. Mertz and M. J. Wade, *ibid.*, p. 489, W. M. Schaffer and M. L. Rosenzweig, *Theor. Pop. Biol.* **14**, 135 (1978); *ibid.*, p. 158.
35. If the logistic growth form for the krill is replaced by the more general expression given in (*27*), the backward-peaking of the yield-effort curve for whales will be more pronounced (for given ν) if $z < 1$, and less pronounced if $z > 1$.
36. For given ν and arbitrary $F_1 (F_1 < 1)$, the MSY effort is

$$F_2(MSY) = [1 + \nu - (1 + \nu)^{1/2}]/\nu$$

The corresponding whale population, relative to its unharvested level, is also

$$N_2^*(MSY)/N_2^*(F_2 = 0) = [1 + \nu - (1 + \nu)^{1/2}]/\nu$$

The MSY itself follows from Eq. 9, and is

$$Y_2(MSY) = (\alpha r_2 K)\ (1 - F_1)\{[(1 + \nu)^{1/2} - 1]/\nu\}^2$$

By eliminating F_2 between Eqs. 7 and 9, we can express the yield in terms of x, the equilibrium stock level referred to its unharvested value: $x = N_2^*(F_2)/N_2^*(0)$. The result is

$$Y_2 = (\alpha r_2 K)(1 - F_1)x(1 - x)/[1 + \nu(1 - x)]$$

That is, Y_2 here has the same functional dependence on x as it does on F_2.

37. A single-species treatment of the whale population corresponds formally to putting $\nu = 0$ in Egs. 6 to 9.
38. The models used by the IWC in setting levels of exploitation for whale stocks are more complicated than ours (embodying age structure and time lags), but, essentially, the population growth rates are modeled by backward-peaked Pella-Tomlinson curves (*28*). Specifically, the IWC currently uses $z = 2.4$ for both baleen whales and sperm whales; this corresponds to the MSY stock level being 60 percent of the unexploited density.
39. P. F. Lett and W. G. Doubleday [*Int. Comm. Northwest. Atl. Fish. Selected Pap.* **1**, 117 (1976)] have found the backward-peaked Pella-Tomlinson curve (with $z \sim 2$) fits the data on Gulf of St. Lawrence cod.
40. C. W. Fowler, W. T. Bunderson, R. J. Ryel, and B. B. Steele (report in preparation for the U.S. Marine Mammal Commission) have drawn together many data on density-dependent reproduction and survival in large mammals. On the basis of these data, and of general evolutionary considerations, C. W. Fowler (personal communication) has argued that populations of large mammals, both marine and terrestrial, tend to exhibit "backward-peaked" growth curves.
41. It can be justly argued that the logistic gives a very crude characterization of population growth processes, and in particular that it is unsatisfactory to combine recruitment and mortality in the two "lumped" parameters r and K. Various other models [R. J. Beverton and S. J. Holt, *Fish. Invest. London*, Ser. 2, (1957); J. G. Shepherd and J. W. Horwood, *J. Conseil. Perm. Int. Explor. Mer*, in press] accept the complications of a third parameter in order to disentangle recruitment and mortality processes; such models have a per capita recruitment rate ρ at low densities, and a mortality rate μ, along with some effective carrying capacity set by resource availability. For many commercial fisheries, it has been suggested that the density-dependent effects of resource limitation enter mainly in the larval stage of development (J. G. Shepherd and D. H. Cushing, *J. Conseil. Perm. Int. Explor. Mer*, in press), and that the abundance of plankton or other resources is itself little affected by this predation. In such fisheries, it is also typically true that $\rho >> \mu$. The upshot of these two effects is a propensity for yield-effort curves to be peaked significantly *forward* from the symmetrical logistic shape (that is, the opposite of the effects illustrated in Fig. 1). Conversely, for whales and other marine mammals, ρ and μ are usually of the same order of magnitude, and these predators often exert a strong influence on the population density of their prey. In these circumstances, the yield-effort curve tends to be "backward-peaked," and the essentials of the process are captured by Egs. 3 and 4 and Fig. 1. These ideas will be developed more fully elsewhere, and they go some way toward explaining why yield-effort curves for most fisheries have a forward-peaked (Beverton-Holt) shape, while those used in the management of baleen and sperm whale populations are backward-peaked [see (*38*)].
42. The full analysis is in (*43*). The boundary curve in Fig. 3. always gives the maximum yield of one species, subject to a prescribed yield for the other. The two interior curves describe other extremal solutions. The curve *AB* corresponds to the maximum krill yield when the specified whale yield is obtained by underexploitation rather than overexploitation; thus the point A corresponds to no harvest of whales ($Y_2 = 0$ because $F_2 = 0$), in contrast to the maximum possible krill yield (when $Y_2 = 0$ because $F_2 = 1$ and $N_2 \rightarrow 0$). Conversely, *AB* represents a locally minimum Y_2, for fixed Y_1. The curve *BC* corresponds to overfishing of krill: it gives a locally maximum Y_2 for a given Y_1 realized by overexploitation of krill; alternatively, it gives a locally minimum Y_1 for fixed Y_2. Figure 3 can be further illuminated by showing how Y_1 (or Y_2) depends in general on the stock levels N_1 and N_2, for fixed Y_2 (or Y_1). The broad features of Fig. 3 remain true for other prey-predator equations that retain the essential biological elements of Eqs. 3 and 4.
43. J. R. Beddington and R. M. May, in preparation.
44. Whether the ecological transfer efficiency, α, and the relative value, γ, are expressed in terms of numbers of animals or of biomass, the combination $\alpha\gamma$ in Eq. 11 remains the same. It is nonetheless easier to think in terms of biomass.
45. It can be shown that the global maximum of the expression for Y, Eq. 10, is obtained as follows. Define $g(\nu) = \nu^2/[(2 + \nu)(1 + \nu)^{1/2} - 2(1 + \nu)]$. If $\beta > g(\nu)$, Y is maximized by harvesting only whales ($F_1 = 0$). If $\beta < {}^1/_2\nu$, the solution is to extinguish whales ($F_2 = 1$) and harvest only krill. For ${}^1/_2\nu < \beta < g(\nu)$, which is possible if $\nu < 11.7$, the maximization of Y involves a mixed harvesting of whales and krill.
46. The general reason is that, particularly in marine systems, predators tend to be significantly larger than their prey. But there are positive correlations between body size and generation time, and negative correlations between size and metabolic rates, and between size and intrinsic growth rate, r. These conclusions are discussed by T. R. E. Southwood, in *Theoretical Ecology: Principles and Applications*, R. M. May, Ed. (Blackwell, Oxford, 1976), chap. 3.
47. R. M. May, G. R. Conway, M. P. Hassell, T. R. E. Southwood, *J. Anim. Ecol.* **43**, 747 (1974); J. R. Beddington, C. A. Free, J. H. Lawton, *ibid.* **45**, 791 (1976); J. R. Beddington, *Int. Comm. Whaling Rep.* **28**, 165 (1978); F. Brauer, *Math. Biosci.*, in press.
48. Specifically, for this system T_R is given by $T_R = 1/[\text{Real}\ (\lambda)]$, where λ follows from

$$2\lambda = (r_1' + r_2') - [(r_1' + r_2')^2 - 4(1 + \nu)r_1' r_2']^{1/2}$$

Here $r_1' = r_1(1 - F_1)/(1 + \nu)$ and $r_2' = r_2(1 - F_2)$.

49. See the discussion by May *et al.* (*21*).
50. R. T. Paine [*Am. Nat.* **100**, 65 (1966)], J. L. Harper [*Brookhaven Symp. Biol.* **22**, 48 (1969)], J. Roughgarden and M. Feldman [*Ecology* **56**, 489 (1975)], P. Yodzis [*Bull. Math. Biol.* **38**, 97 (1976)], R. R. Vance [*Am. Nat.* **112**, 797 (1978)] and others [for a brief review, see R. M. May, *Nature (London)* **269**, 103 (1977)] have considered general ecological questions concerning the way harvesting or predation can influence coexistence among competitors. The simultaneous exploitation of two or more competing fish populations has been considered by P. A. Larkin [*J. Fish. Res. Board Can.* **20**, 647 (1963); *ibid.* **23**, 349 (1966)], J. G. Pope [*Int. Comm. Northwest. Atl. Fish. Selected Pap.* **1**, 157 (1976)], J. W. Horwood [*ibid.*, p. 151], R. Hilborn [*J. Fish. Res. Board Can.* **33**, 1 (1976)], W. M. Getz (S.A. National Research Institute for Mathematical Sciences, *Tech. Rep. TWISK* **7**, (1977)], K. Shirakihara and S. Tanaka [*Res. Pop. Ecol.* **20**, 123 (1978)] and others. For a review that includes economic aspects of these problems see (*22*), chap. 9. Here we are concerned with the way yields alter, and the time scales of so doing, when one of two competing species is harvested along with their shared prey.
51. The "krill-seal-whale" model has the form

$$dX_1/dt = r_1X_1(1 - F_1 - X_1 - \nu X_2 - \eta X_3)$$

$$dX_2/dt = r_2X_2(1 - F_2 - X_2/X_1)$$

$$dX_3/dt = r_3X_3(1 - X_3/X_1)$$

Here, as before, X_1, X_2, and X_3 are the (dimensionless) populations of prey, harvested predator, and unharvested predator (krill, whales, and seals), respectively; r_1, r_2, and r_3 are the intrinsic growth rates of the three populations. This model, wherein competition stems indirectly from exploitation of a shared resource, has similarities to that introduced more generally by MacArthur (*52*). See also F. Stewart and B. R. Levin, *Am. Nat.* **107**, 171 (1973); D. L. DeAngelis, R. A. Goldstein, R. V. O'Neill, *Ecology* **56**, 881 (1975); D. Tilman, *ibid.* **58**, 338 (1977).

52. R. H. MacArthur, *Geographical Ecology* (Harper & Row, New York, 1972), pp. 33–40.
53. R. M. May, in *Progress in Theoretical Biology*, R. Rosen and F. Snell, Eds. (Academic Press, New York, 1974), vol. 2, pp. 1–50.
54. This question is discussed more fully in Clark (*22*), chap. 9.
55. R. J. Beverton and S. J. Holt, *Fish. Invest. London*, Ser. 2, sect. 10 (1957).
56. J. A. Gulland, *Rapp. Proc.-Verb. Reun. Cons. Int. Explor. Mer* **140** (No. 1), 21 (1956); and *Manual of Methods for Fish-Stock Assessment* (Food and Agricultural Organization, Rome, 1969).
57. The trophic relations among sperm whales, cephalopods, and krill are made more complicated by predation and cannibalism within the cephalopod community itself, and by our lack of knowledge about which krill-eating cephalopods are actually eaten by sperm whales [M. R. Clark *Adv. Mar. Biol.* **4**, 91 (1966); *Discover Rep.*, in press].
58. The krill–cephalopod–sperm whale model is

$$dX_1/dt = r_1X_1(1 - F_1 - X_1 - \zeta X_3)$$

$$dX_3/dt = r_3X_3(1 - X_3/X_1 - \nu X_2)$$

$$dX_2/dt = r_2X_2(1 - F_2 - X_2/X_3)$$

Here X_1, X_3, and X_2 are the (dimensionless) populations of prey, predator, and top predator (krill, cephalopods, and sperm whales), respectively; r_1, r_3, and r_2 are the intrinsic growth rates of these three populations. The equilibrium population values, and hence the possible equilibrium yields of krill and sperm whales, are obtained in the usual way by setting the right-hand sides of these equations equal to zero.

59. For the krill–cephalopod–sperm whale system, the relation between the maximum sustainable value of Y_1 (or, conversely, Y_2) for a given value of Y_2 (or, conversely, Y_1) is derived and discussed by Beddington and May (*43*).
60. J. H. Steele, private communication.
61. ———, *The Structure of Marine Ecosystems* (Harvard Univ. Press, Cambridge, 1974).
62. Various mechanisms whereby fish stocks can collapse in "catastrophic" fashion are discussed by C. W. Clark and M. Mangel (*31*); Y. Paloheimo and L. M. Dickie, *Rapp. Proc.-Verb. Reun. Cons. Int. Explor. Mer* **155**, 152 (1964); R. M. Peterman, *J. Fish. Res. Board Can.* **34**, 1130 (1977); R. M. May, *Nature (London)* **269**, 471 (1977); F. Brauer, A. C. Soudack, H. S. Jarosch, *Int. J. Control* **23**, 553 (1976); F. Brauer and A. C. Soudack, *J. Math. Biol.* in press; B. S. Goh, *Math. Biosci.* **33**, 359 (1977); P. K. Dayton, *Ecol. Monogr.* **45**, 137 (1975); and others. In particular, L. W. Botsford and D. E. Wickham [*J. Fish. Res. Board Can.* **35**, 833 (1978)] and L. W. Botsford (private communication) have offered a detailed explanation of the decline in the California Dungeness crab catch since 1960, in terms of a discontinuous shift to a new equilibrium state.
63. R. Gambell, *J. Reprod. Fert. Suppl.* **19**, 531 (1973); *FAO Scientific Consultation on Marine Mammals, ACMRR/MM/SC/37* (1976); A. Kawamura, *Int. Comm. Whaling Rep.* **28**, 411 (1978).
64. R. M. Laws, *Discovery Rep.* **31**, 327 (1961); C.

H. Lockyer, *J. Conseil. Perm. Int. Explor. Mer* **34**, 276 (1972).

65. C. H. Lockyer, *J. Conseil. Perm. Int. Explor. Mer* **36**, 71 (1974); Y. Masaki, *Int. Comm. Whaling Rep.* **28**, 421 (1978); S. J. Holt, *ibid.*, p. 389.
66. S. Ohsumi and Y. Masaki, *J. Fish. Res. Board Can.* **32**, 995 (1975); Y. Masaki, *Int. Comm. Whaling Rep.*, in press.
67. J. A. Gulland, *FAO Scientific Consultation on Marine Mammals ACMRR/MM/SC/76* (1976).
68. Anonymous, "Report of the IWC Special Scientific Meeting on Minke Whales", *Int. Comm. Whaling Rep.* in press.
69. W. N. Bonner, *FAO Scientific Consultation on Marine Mammals, ACMRR/MM/SC/50* (1976); M. R. Payne, *Phil. Trans. R. Soc. London. Ser. B* **279**, 67 (1977).
70. N. Rankin, *Antarctic Isle* (Collins, London, 1951); B. Stonehouse, *Ibis* **109**, 176 (1967); W. B. Emison, in *Antarctic Bird Studies*, O. L. Austin, Ed. (American Geophysical Union, Washington, D.C., 1968); M. G. White and J. W. H. Conroy, *Ibis* **118**, 371 (1975); J. Croxhall, in preparation.
71. R. Carrick and S. E. Ingham, *Jpn. Antarctic Res. Exped. Sci. Rep.*, Spec. Issue No. 1 (1967), p. 151.
72. Anonymous, "Report of the Sperm Whale Subcommittee," *Int. Comm. Whaling Rep.*, in press.
73. The currently used ships harvest krill in a fashion that is similar to the large baleen whales in their seasonal patterns of exploitation and their tendency to concentrate on krill swarms. We estimate very roughly that one fishing ship is the equivalent of 100 blue whales. (Blue whales are estimated to eat about 3.5 percent of their approximately 84-ton body weight daily during a 120-day feeding season; this amounts to a consumption rate around 3 tons per day. Current factory ships can handle about 300 tons per day over the same season.)
74. See figures 1 and 2 and table 14 in Anderson and Ursin (*7*).
75. The model of Anderson and Ursin (*7*) involves from 14 to 81 kinds of animals, plants, and nutrients, whose dynamics are described by 42 to 308 coupled differential equations. The model of Laevastu and Favorite (*12*) is of similar complexity.
76. H. S. Gordon, *J. Pol. Econ.* **82**, 1035 (1954); C. W. Clark, *Science* **181**, 630 (1973). For a formal discussion of maximizing the discounted "present value" of a multispecies fishery, see W. Silvert and W. R. Smith, *Math Biosci.* **33**, 121 (1977).
77. C. W. Clark and G. R. Munro, *J. Environ. Econ. Mgmt.* **2**, 92 (1975).
78. J. A. Gulland, *The Management of Marine Fisheries* (Univ. of Washington Press, Seattle, 1974); C. W. Clark *et al.*, *Econometrica*, in press.
79. K. H. Borch, *The Economics of Uncertainty* (Princeton Univ. Press, Princeton, N.J., 1968).
80. This article developed from a meeting of a working group of the IUCN Interim Committee on Marine Mammals, held at Grottaferrata, Italy, in July 1978. The work was supported in part by grants from the IUCN and the World Wildlife Fund (J.R.B.), by NSF grant DEB77-01565 (R.M.M.), and by NSERC grant 3990 (C.W.C.). We thank J. A. Gulland, J. G. Shepherd, and J. H. Steele for helpful discussions.

Risk and Responsibility

David L. Bazelon

Risk Regulation: A Problem for Democracy in the Technological Age

In 1906, Congress enacted the Pure Food and Drug Act, the first general food and drug safety law for the United States. Commenting on the provisions of the act, the House committee observed: "The question whether certain substances are poisonous or deleterious to health the bill does not undertake to determine, but leaves that to the determination of the Secretary . . . under the guidance of proper disinterested scientific authorities, after most careful study, examination, experiment and thorough research."

This statement reflected a deep faith in the ability of "disinterested" scientists to determine for society what substances posed an unacceptable risk. More than 70 years of regulation have called into question that naïve faith. We are no longer content to delegate the assessment of and response to risk to so-called disinterested scientists. Indeed, the very concept of objectivity embodied in the word disinterested is now discredited. The astounding explosion of scientific knowledge and the increasing sophistication of the public have radically transformed our attitude toward risk regulation. As governmental health and safety regulation has become pervasive, there is a pressing need to redefine the relation between science and law. This is one of the greatest challenges now facing government and, indeed, society as a whole.

Risk regulation poses a peculiar problem for government. Few favor risk for its own sake. But new risks are the inevitable price of the benefits of progress in an advanced industrial society. In order to have the energy necessary to run our homes and our factories, we incur risks of energy production, whether they be the risks of coal mining, nuclear reactor accidents, or the chance that a tree will fall on a man felling it to produce firewood. In order to have mobility, we risk auto accidents and illness from air pollution. In order to have variety and convenience in our food supply, we risk cancer or other toxic reactions to additives.

Ironically, scientific progress not only creates new risks but also uncovers previously unknown risks. As our understanding of the world grows exponentially, we are constantly learning that old activities, once thought safe, in fact pose substantial risks. The question then is not whether we will have risk at all, but how much risk, and from what source. Perhaps even more important, the question is who shall decide.

In our daily lives we do not confront the trade-off between dollars and lives very directly or self-consciously. But when we make societal policy decisions, such as how much to spend to eliminate disease-producing pollutants, we are painfully aware that we must make what Guido Calabresi has called "tragic choices."

In primitive societies these choices were often made by the tribal witch doctor. When the need to choose between cherished but conflicting values threatened to disrupt the society, the simplest path was decision by a shaman, or wizard, who claimed special and miraculous insight. In our time shamans carry the title doctor instead of wizard, and wear lab coats and black robes instead of religious garb.

But ours is an age of doubt and skepticism. The realist movement in law effectively stripped the judiciary of its Solomonic cloak. So, too, the public has come to realize the inherent limitations of scientific wisdom and knowledge. We have been cast from Eden, and must find ways to cope with our intellectual nakedness. To the basic question of how much risk is acceptable—a choice of values—we have learned that there is no one answer. To the problem of how much risk a given activity poses, we have learned that even our experts often lack the certain knowledge that would ease our decision-making tasks. Often the best we can say is that a product or an activity poses a "risk of risk."

The author is a Senior Circuit Judge, United States Court of Appeals for the District of Columbia Circuit, Washington, D.C. 20001. This article is based on a talk given at the American Bar Association National Institute on Law, Science, and Technology in Health Risk Regulations, Washington, D.C., 20 April 1979.

0036-8075/79/0720-0277$01.00/0