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METHODS FOR INCREASING THE LIKELIHOOD OF RESTORING AND MAINTAINING PRODUCTIVE FISHERIES

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ABSTRACT

Years of scientific inquiry have developed sophisticated methods for setting fishing quotas. Unfortunately, these methods tend to be information intensive and can lead to population crashes if information is wrong. Previous work has illustrated that highly responsive quota systems, which curb fishing decisively when stocks drop below target abundance levels, promote optimum average yields in varying environments and when parameters are uncertain. These policies have generally been rejected, though, because they make fishing yields uncertain and create the potential for temporary closures. They have also been criticized because the managed population can crash if abundance is overestimated. We performed analyses to reexamine the performance of highly responsive management systems. Our analyses show that these systems outperform less-responsive alternatives at maintaining healthy stocks and productive fish catches when managers misestimate parameters. Although these systems can cause populations to crash under the circumstances previously identified, we were able to show that they are less prone to do so under all circumstances than less-responsive constant-fishing-mortality systems. We discuss the implications of this work for fisheries management and highlight methods for achieving highly responsive management systems that are both precautionary and ecosystem-oriented.

"Science is being asked to deliver far more than it can produce"
(Peter Leipzig, Fisherman's Marketing Group,
Environmental News Network, 2000).

"We need a better way of... managing with gaps in scientific information"
(Lisa Speer, Natural Resources Defense Council,
H. John Heinz III Center for Science, 2000).

Scientists and managers have struggled for decades with how to set appropriate fishing quotas—the amount of fish that can be caught without jeopardizing the future productivity of the population. By the 1950s, sophisticated mathematical models were developed to aid managers with setting quotas. Despite these models, fisheries have not fared well. Nearly half of the known fish stocks in the U.S. are considered overfished, experiencing overfishing, or both (Fig. 1), and nearly 70% of fish stocks worldwide are estimated to be fished to or beyond their maximum capacity (FAO, 1998; NMFS, 2001).

One of the biggest problems with using the sophisticated models as tools has been that they require a substantial amount of information. Applying these models to reality breaks down because most fish stocks have never been studied to the extent required for accurate use. In the U.S. for example, which has better resources for studying fish populations than most other countries, scientists have fully assessed the status of less than one-quarter of the fish stocks under federal management (NMFS, 2001; Fig. 1).

These problems with quota setting raise three important areas of concern. First, what do we know about fish stocks, what do we need to know under conventional management, and can we do better? Second, are there less information-intensive quota systems,

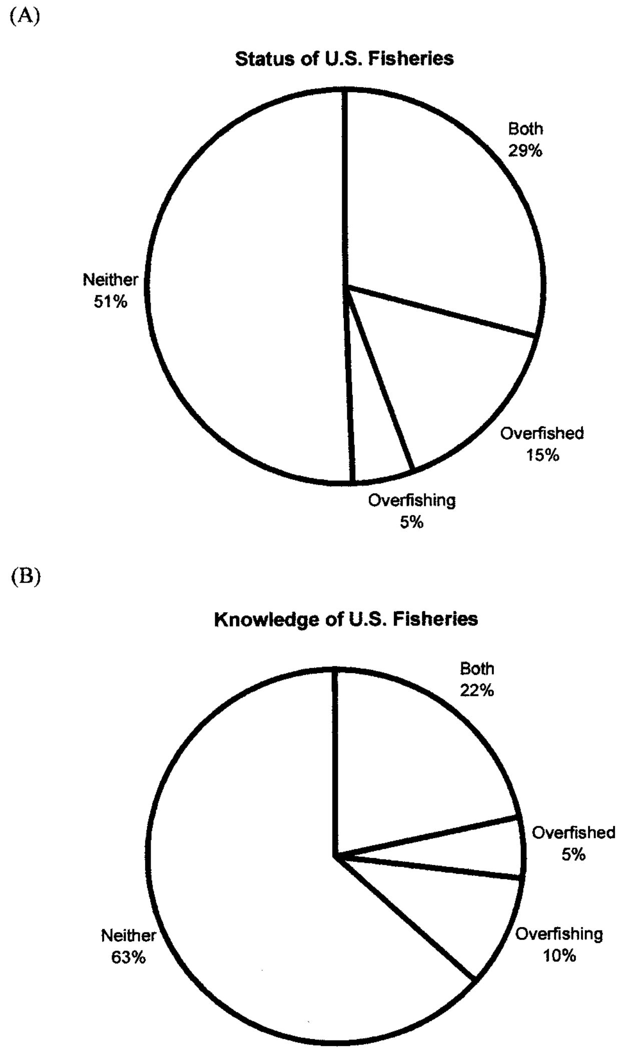


Figure 1. The status of federally managed fish stocks in the United States. (A) Known fish stocks were categorized as overfished, experiencing overfishing, both, or neither on the basis of criteria that vary somewhat across stocks. Generally speaking, a stock was declared overfished only if it had dropped below one-half of the target MSY level and experiencing overfishing only if it was experiencing fishing mortality rates in excess of the best available estimate or proxy for the rates associated with MSY. (B) Most stocks are categorized as unknown with respect to one or both of these characteristics because they have not been assessed. Data from National Marine Fisheries Service (NMFS, 2001).

and how do these perform relative to conventional methods? Finally, how do we manage stocks for which we lack the most basic information?

INFORMATION NEEDS AND STATUS UNDER CONVENTIONAL MANAGEMENT.—Conventional management is information intensive. Historically, fisheries mangers set quotas using a constant fishing mortality rate—a fixed proportion of the population removed by fishing each year or season. Proper use of a constant-fishing-mortality system requires a thor-

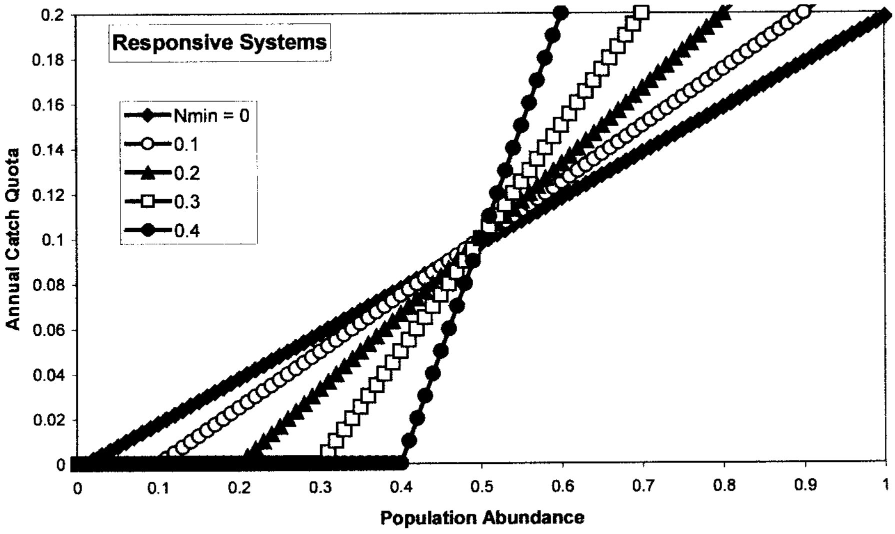


Figure 2. Quota policies. This graph shows a series of lines representing different management systems. The line nearest horizontal (N_{min} = 0) represents a constant-fishing-mortality-rate policy; steeper lines are more responsive. All policies were engineered to pass through one common point—the maximum sustainable yield of the fishery. As a result, if managers made no mistakes, each of these policies would achieve the maximum sustainable yield.

ough understanding of the biology and ecology of the stock in the form of productivity values, current abundance, and actual catches (Fig. 2). Each of these information needs has its pitfalls, which is one of the reasons so many stocks remain categorized as unknown with respect to their overfished status.

Productivity estimates are generally created in the context of maximum sustainable yields (MSY). The MSY is defined as the maximum rate of exploitation a population can sustain and is associated with a fishing mortality rate F_{MSY} and an abundance level N_{MSY}, also sometimes called B_{MSY}. It is determined through a stock assessment, in which one or more scientists develop a complex computer simulation using detailed information about the history of abundance and fishing pressure experienced by the stock in question. This assessment also incorporates basic biological characteristics, such as the growth rate of individuals. Because these biological characteristics are generally poorly understood, most stocks remain unassessed. Even the best stock assessments must make educated guesses when it comes to certain factors, in particular the natural mortality rate and the stock-recruitment relationship. Both of these factors help to define the ecology of the stock in question and are typically unknown or at best poorly understood. The uncertainty surrounding them adds a great deal of uncertainty for management of stocks that are assessed.

Stock abundance also plays a key role in conventional management. The assessment and determination of MSY define the appropriate fishing mortality rate F_{MSY}—the fraction of the stock that, if removed on a continuing basis, will ultimately produce the MSY. An estimate of absolute stock abundance is required to calculate quotas because the total allowable catch will be the fraction F_{MSY} of the total. Counting fish is not easy. The ocean is large and complex, and some of the many difficulties in estimating stock abundance include the limits of making direct underwater observations at depth due to human limitations (SCUBA) or expense (submersible), the impracticality of mechanically sampling many habitats due to their structural complexity, changes in fish behavior in response to counting efforts, and many other challenges. Consequently, fish abundance is sampled infrequently, if at all. Even the data for sampled stocks may not be analyzed. Only recently, the barndoor skate (*Raja laevis*), a large elasmobranch caught incidentally in northwest Atlantic bottom-trawl fisheries, was found to be severely depleted when decades of information were finally examined (Casey and Myers, 1998).

Although catches seem easy to measure by comparison, they are typically poorly tracked at best. Commercial catches brought into port are fairly easy to count, but it is much more difficult to account for fish discarded at sea. They may be discarded because they are too small, exceed the legal quota, or are of an unmarketable or prohibited species. These fish are typically only counted if the government or industry pays an independent observer to do so, although fishing log books can also be of use. Recreational catches are equally challenging to document because recreationally fishing men and women are so spread out in space and time.

THE QUOTA DEBATE—Fishery managers arrived at the current convention for setting quotas after a robust scientific debate spanning several decades (see Thompson, 1999, for review). Scientists examined constant catch, under which fishers are permitted to catch an invariant number of fish each year (Russell, 1931; Hjort et al., 1933); constant-escapement policies, where maximum fishing is allowed if a population is above a threshold abundance but prohibited if it is below that abundance (Ricker, 1958); and constant-fishing-mortality-rate policies, under which fishers are permitted to catch an invariant fraction of the population each year (Thompson and Bell, 1934; Graham, 1935).

These techniques have been compared and contrasted extensively (e.g., by Reed, 1978), and many additional complexities have been examined, including policies defined by multiple parameters allowing changes in policy in relation to changes in stock size (e.g., by Ricker, 1958). Ricker's work helped to establish some basic principles in comparing the performance of policies in a varying environment. He showed that more responsive policies provided higher average catches but introduced higher rates of variability from year to year in catch levels and could lead to temporary fishery closures. These findings have been confirmed in a number of studies (see Thompson, 1999, for review). Scientists have also used highly complex dynamic programming exercises to identify detailed quota-setting rules (e.g., Walters, 1975; Hilborn, 1976). These complex models allow managers to fine tune an optimal policy but at the expense of accessibility (Thompson, 1999). They also often derive policies similar to those derived by simple rules (see, e.g., Walters, 1975; Hilborn, 1976). A third alternative was proposed by Walters and Hilborn (1978), that of the fixed form optimization. In this technique, one conjures up an appropriate functional form for the quota-setting process based on intuition and experience and then optimizes its parameters on the basis of the balance a manager wants between high average catches and low catch variance (see, e.g., Quinn et al., 1990).

Scientists and managers have generally not adopted highly responsive management systems because of high variability in catches, frequent fishery closures, and potential for population crashes if abundance is overestimated (Engen et al., 1997). Instead, they tend to rely on constant fishing-mortality rates but with a few promising signs of changing to policies with constant rates at higher abundance that are tapered down if abundance drops to low levels (Thompson, 1999).

We set up a framework to revisit responsive systems over a broad range of management error and environmental variability. The most responsive system resembled constant-escapement policies, and the least responsive used constant-fishing-mortality-rate policies. We compared the performance of these systems across a wide range of errors in estimation of parameters related to production, abundance, and catches in a stable environment and compared their performance with specified errors in two different variable environments.

Derivation of a Framework

We built and analyzed a series of mathematical models, starting with general forms and becoming more specific as necessary to address particular questions of interest. Generally, we wanted to examine a population of size N governed by the dynamic.

$$\frac{dN}{dt} = p(N)N - h(N) \qquad \text{Eq. 1}$$

where N is some measure of population abundance, $p(N)$ is the per capita growth function, and $h(N)$ is the catch function. For simplicity we assumed a linear-control feedback loop for the catch function,

$$h(N) = f\left(N - N_{\min}\right) \qquad \text{Eq. 2}$$

based on intuition gained from designing rocket guidance systems. We defined per capita production deterministically with steady state $r_{ss} = p(N_{ss})$. Note that this catch function sets aside a reserve population N_{min} and exploits only the population abundance above the reserve at a rate f, similar to models examined previously by Ricker (1958), Engen et al. (1997), and others (reviewed by Thompson, 1999).

Deterministic Logistic Example

To illustrate this framework, we assumed a simple logistic production function

$$p(N)N = r(1 - N)N \qquad \text{Eq. 3}$$

Note that this production function peaks at N_{MSY} = 1/2 with a productivity of r/4. Any quota-setting policy will hit this peak if

$$f_{MSY} = \frac{r}{2 - 4N_{\min}} \qquad \text{Eq. 4}$$

and N_{min} falls in the range $N_{MSY} > N_{min} \geq 0$. To illustrate the effects of management errors, we can introduce error terms representing the three types of information necessary under conventional fisheries management: production-estimation error, ε_r; abundance-estimation error, ε_n; and catch-estimation error, ε_h. A positive production-estimate error would occur if a manager overestimated production and consequently set quotas higher than intended. A positive abundance-estimation error would indicate that managers overestimated the actual abundance, and therefore probably set higher quotas than intended. A positive catch-estimation error would occur if catches exceeded quotas. All three errors range from −1 to infinity; negative values represent lower catches than intended.

With errors, catches indicated in equation Eq. 2 differed from quotas by a factor of $(1 + \varepsilon_h)$.

$$h(N) = (1+\varepsilon_h) f_{est}(N_{est} - N_{\min}) \qquad \text{Eq. 5}$$

where f_{est} represents the estimated optimum fishing mortality rate and N_{est} represents the estimated population abundance. We can obtain an MSY-intended policy by combining Eqs. 4 and 5. Adding errors in the estimation of the MSY fishing mortality rate and of population abundance yields

$$h(N) = \frac{(1+\varepsilon_h)(1+\varepsilon_r)r\left[(1+\varepsilon_n)N - N_{\min}\right]}{2-4N_{\min}} \qquad \text{Eq. 6}$$

With this formulation, errors in the estimation of production, ε_r, and actual catches, ε_h, are functionally equivalent (i.e., $\varepsilon_{h/r}$) and were so treated in analyses of the system equation:

$$\frac{dN}{dt} = r(1-N)N - \frac{(1+\varepsilon_{h/r})r\left[(1+\varepsilon_n)N - N_{\min}\right]}{2-4N_{\min}} \qquad \text{Eq. 7}$$

Note that errors are not introduced into the production function $r\,(1-N)N$ because it is beyond the control of managers. We consider the effects of a variable environment below by making the production parameter r stochastic.

We found stable abundances and catches by solving this equation for conditions where change in abundance $dN/dt = 0$ (see Appendix for derivation). In general, the stable population abundance and catch levels in this system were given by:

$$N_{ss} = \frac{2-4N_{\min} - (1+\varepsilon_{h/r})(1+\varepsilon_n) + \sqrt{(1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n)^2 + 16\varepsilon_{h/r}N_{\min}(1-N_{\min}) + 8\varepsilon_n N_{\min}(1+\varepsilon_{h/r})}}{4-8N_{\min}} \qquad \text{Eq. 8}$$

$$h_{ss} = \frac{(1+\varepsilon_{h/r})r\left[(1+\varepsilon_n)N_{ss} - N_{\min}\right]}{2-4N_{\min}} \qquad \text{Eq. 9}$$

but only when N_{SS}, as defined by Eq. 8, multiplied by $(1 + \varepsilon_n)$ is greater than N_{min}. Otherwise, no fishing would be allowed, and the population would remain at its unfished abundance of 1. Although the quadratic solution provides two potential solutions, one adding the square root and the other subtracting, only negative abundances are achieved if the square root is subtracted.

If we set the abundance estimation error $\varepsilon_n = 0$, Eqs. 8 and 9 become

$$N_{ss} = \frac{2 - 4N_{\min} - \left(1 + \varepsilon_{h/r}\right) + \sqrt{\left(1 - \varepsilon_{h/r}\right)^2 + 16\varepsilon_{h/r} N_{\min}\left(1 - N_{\min}\right)}}{4 - 8N_{\min}} \qquad \text{Eq. 10}$$

$$h_{ss} = \frac{\left(1 + \varepsilon_{h/r}\right) r \left(N_{ss} - N_{\min}\right)}{2 - 4N_{\min}} \qquad \text{Eq. 11}$$

Or, if we set the production and catch estimation error $e_{h/r} = 0$, Eqs. 8 and 9 become

$$N_{ss} = \frac{2 - 4N_{\min} - \left(1 + \varepsilon_n\right) + \sqrt{\left(1 - \varepsilon_n\right)^2 + 8\varepsilon_n N_{\min}}}{4 - 8N_{\min}} \qquad \text{Eq. 12}$$

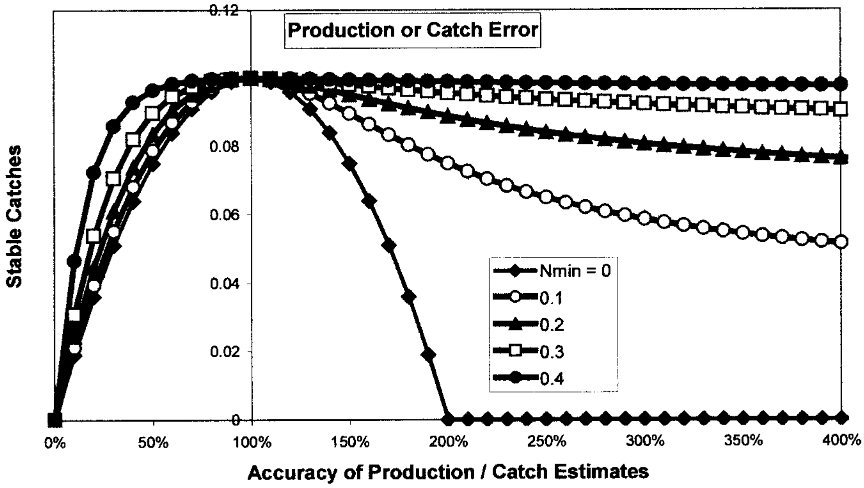
$$h_{ss} = \frac{r\left[\left(1 + \varepsilon_n\right)\right] N_{ss} - N_{\min}}{2 - 4N_{\min}} \qquad \text{Eq. 13}$$

or $h_{ss} = 0$ and $N_{ss} = 1$ if N_{SS}, as defined by Eq. 12, multiplied by $(1 + \varepsilon_n)$ is less than N_{min}.

These results provide several important insights (Fig. 3). First, catches were equivalent under all policies if management estimates were correct. Consequently, no long-term costs were associated with using responsive management systems when information was good, at least in the stable environments represented by these equations. Second, catches were most affected by management error when management systems were least responsive. Under a constant-fishing-mortality system (i.e., $N_{min} = 0$), the fishery was reduced to commercial extinction when any combination of production, catch, or abundance estimates was off by a factor of two. More responsive management systems fared better in the face of abundance overestimates, but catches still did decline as a result of these errors. Responsive management systems fared exceptionally well in the face of production or catch overestimates. Highly responsive systems (e.g., $N_{min} = 0.4$) maintained almost optimum catch levels even when production or catch estimates were off by a factor of four. Only when abundance was underestimated did responsive systems yield smaller catches than less-responsive systems. In some of these cases, fishing was not allowed even though fish populations were at peak abundance because abundance was estimated to be below N_{min}, the threshold at which fishing was prohibited. These cases present only a minor management challenge because fish are still plentiful and capable of providing fishing opportunities once the management error is rectified, without any long-term loss of fish productivity or ecosystem function.

Bigger problems arose when responsive systems were examined in a fluctuating environment. We simulated a discrete version of Eq. 7 in two different environments over a period of 500 yrs (Fig. 4). In both cases, we sampled from distributions of production constants (r) with a mean of 0.4 and used the same production history for each run in a given environment. Our moderately variable environment was normally distributed and

(A)



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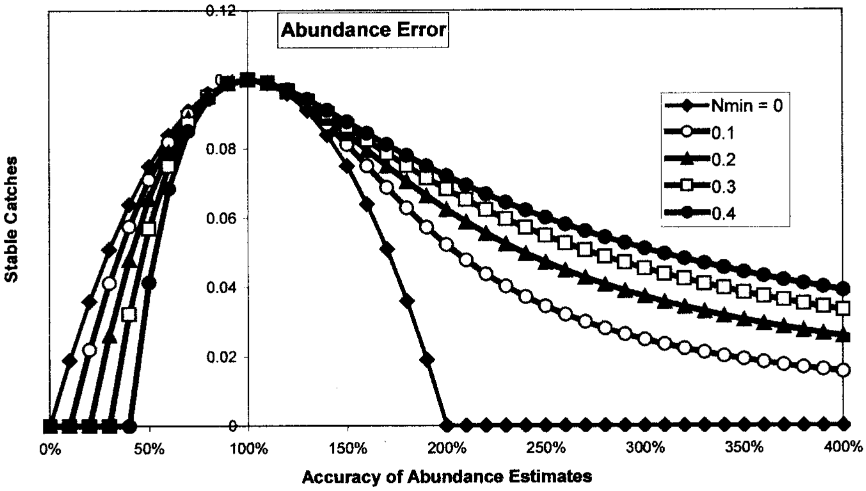
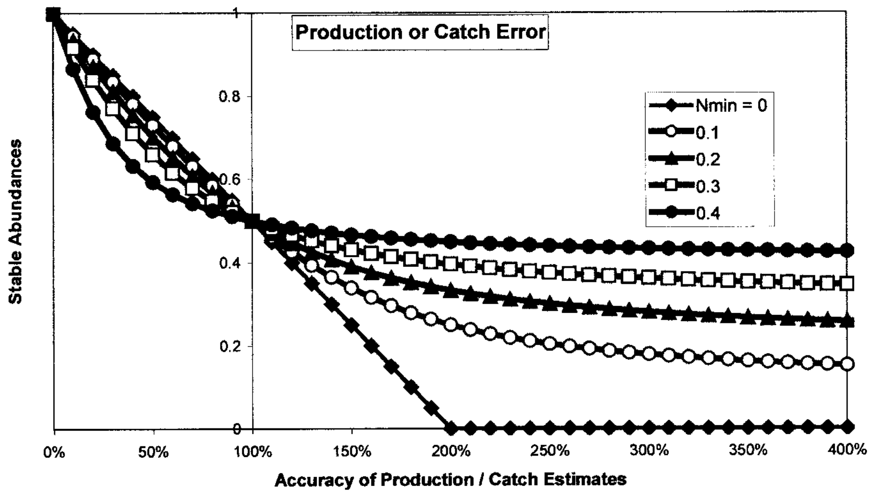


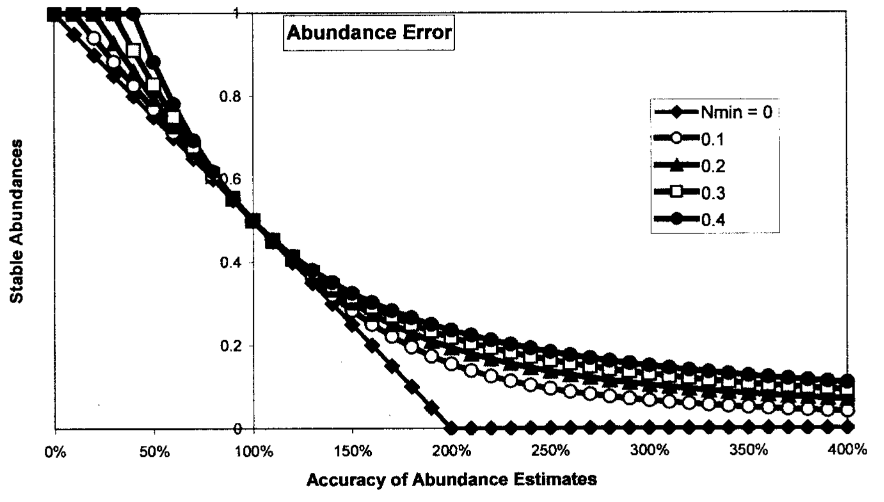
Figure 3. Resiliency in a stable environment. Stable catches (A, B) and abundance levels (C, D) *(opposite page)* were influenced by errors in estimates of production or actual catch (A, C) and of abundance (B, D). Results were obtained by means of a mathematical analysis of a logistic production fishery model and quota-setting systems as defined in Fig. 2. In all cases r = 0.4, so MSY = 0.1.

had a standard deviation of 0.12, or 30% of the mean value. Our highly variable environment was chi-square distributed, providing a greater frequency of bad years and a greater magnitude of good years. This distribution had a standard deviation of 0.6, or 150% of the mean value. Each simulation started with the population at 50% of its unfished abundance, and we assumed positive errors of 50% in production/catch estimates and 50% in abundance, leading to inadvertent overfishing. These values were intended to reflect realistic challenges managers regularly face. We should therefore expect acceptable performance from potential management systems under these circumstances.

(C)

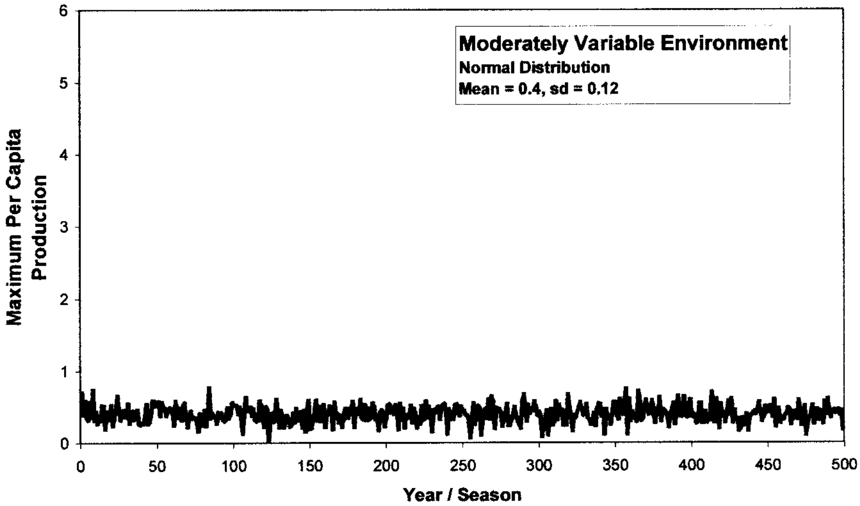


(D)



In the moderately variable environment, average catches and abundance did in fact increase with responsiveness (Fig. 5A). The population under least-responsive management crashed to levels that were barely able to maintain fish or fishery, whereas the most highly responsive system maintained a population at 60% of desired (MSY) levels and catches near the MSY value of 0.1 despite the management errors. With increased responsiveness, catches did become more variable, and fisheries were closed more frequently. These results were more dramatic in the highly variable environment (Fig. 5B). Highly responsive systems were characterized by highly variable catches and frequent closures. Moreover, the population under most highly responsive management crashed, contradicting the pattern of higher abundance and catches with greater responsiveness. In

(A)



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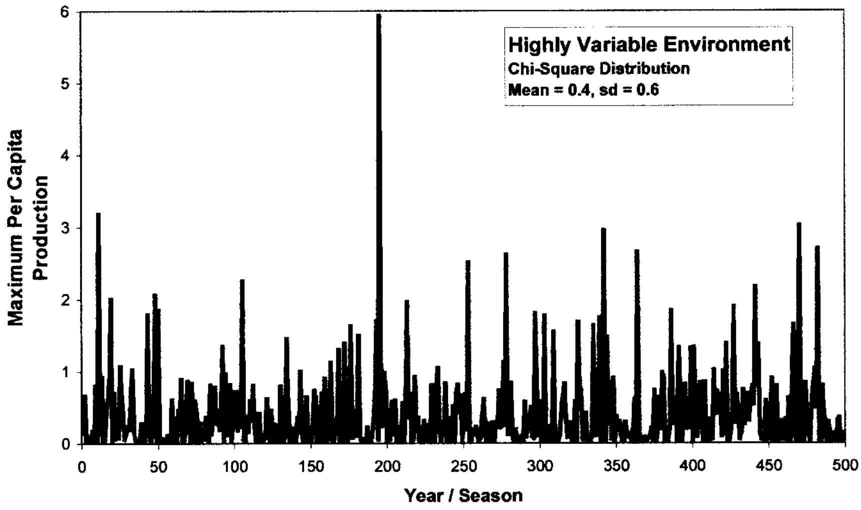

Figure 4. Simulated environments. This figure shows the two simulation environments we used. (A) The moderately variable environment was characterized by a normally distributed production constant distribution with an average of 0.4 and a standard deviation of 0.12. (B) The highly variable environment was characterized by a chi-square-distributed production constant distribution with an average of 0.4 and a standard deviation of 0.6.

this case, the overestimate of abundance after a really productive year led to a quota so high as to provoke extinction. Note, though, that this level of error caused population crashes under the least responsive system in both environments, but did so only under the most responsive management system in a highly variable environment.

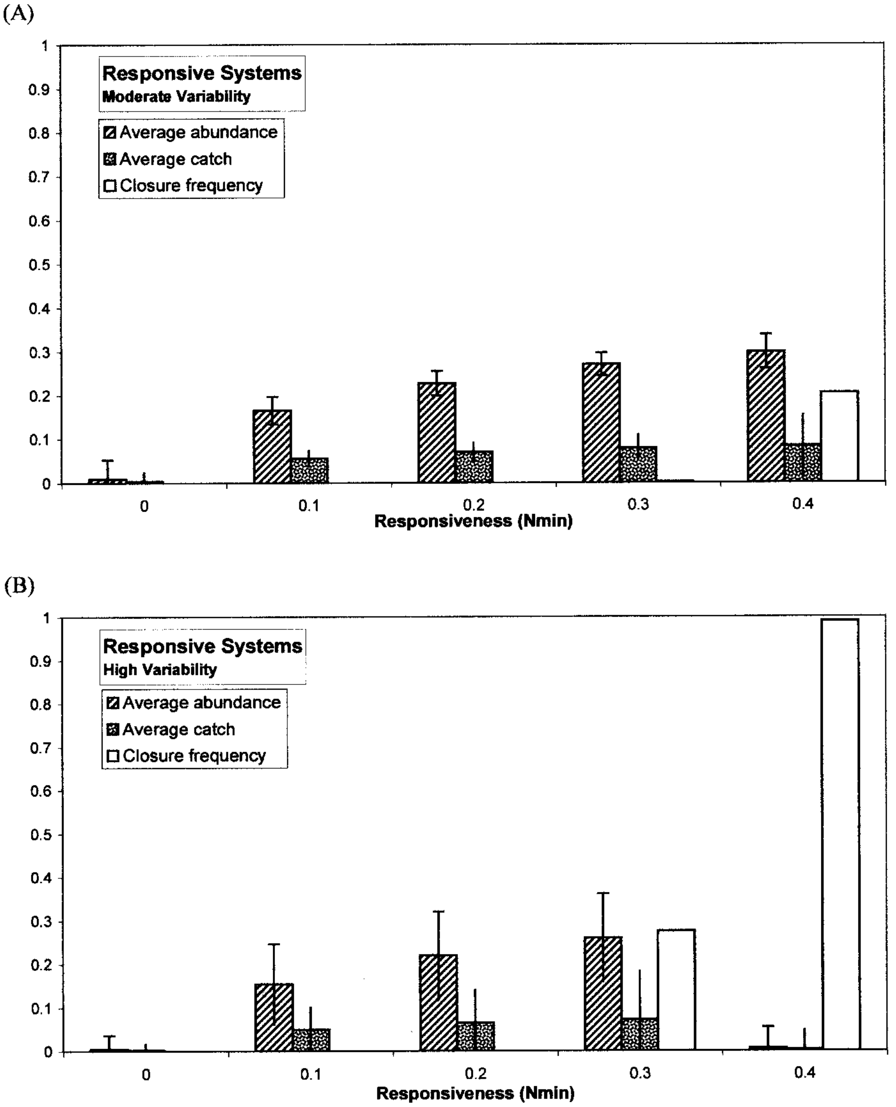

Figure 5. Resiliency in a variable environment. Performances of various management systems were compared under two variable environments and with positive management errors of 50% in catch/production and abundance estimates. Averages over 500-yr model runs are presented, and error bars represent one standard deviation. Closure frequencies are the proportion of years of the 500 during which the fishery was closed either for rebuilding or because the target species went extinct. Results are presented for the moderately variable (A) and highly variable (B) environments pictured in Fig. 4.

Conclusions

We examined the performance of management systems that ranged from constant fishing mortality to constant escapement policies. Our results showed that the more responsive policies provided higher catches in varying environments and in the face of even very large management errors. In contrast, constant-fishing-mortality policies led to population crashes with modest errors even in stable environments. Our results provide perspective on the sensitivity of responsive systems to errors in abundance estimation. Although these errors can reduce the effectiveness of highly responsive systems and even lead to population crashes, they cause even greater problems under less-responsive systems. These results contradict prior concern about the potential for crashes under highly responsive management systems and leave one major problem associated with responsive systems—variability in catches and resulting temporary fishery closures.

We are currently studying systems that are highly responsive when stocks drop below target levels but cap quotas at constant catch levels above. Preliminary results suggest these policies virtually eliminate the chance of fishery crashes and provide managers with a range of options from near-maximum catches with high variability to lower catches with virtually no variance.

Given the apparent success of these systems, it is surprising they are not used more widely or aggressively. In the United States, a few fish stocks are managed with responsive policies. The best-studied North Pacific groundfish stocks are managed according to a policy that reduces fishing mortality rates if stocks are below target levels. These reductions are modest, though, and prohibit fishing only when stocks drop to 2% of their historic abundance (NMFS, 2001). Pacific groundfish are managed according to a similar policy. Their fishing mortality rates are reduced more slowly initially but prohibit fishing when stocks drop to 10% of their historic abundance. This policy is optional, however, and fishing has not been eliminated even on stocks that have dropped to 2 to 4% of their historic abundance (Pacific Fishery Management Council, 1998). The National Marine Fisheries Service has recommended a departure from constant-fishing-mortality systems as well, but their recommendation does not begin to reduce fishing mortality rates until stocks have dropped to a threshold below the target abundance and then only recommends reducing fishing mortality to zero when a stock is extinct (Restrepo et al., 1998). Consequently, these policies are generally less responsive than the $N_{min} = 0.1$ system considered above. Many less-well-studied fish stocks are fished under constant-catch policies (Pacific Fishery Management Council, 1998; NMFS, 2001) even though these policies are substantially less responsive than constant-fishing-mortality policies and thus highly likely to lead to crashes.

Although highly responsive systems carry a cost in the form of unpredictable catches and occasional temporary closures, our results raise the question of whether these costs are not but a small price to pay for the long-term stability these systems provide to fish stocks and the ecosystems and fishing communities they support.

New Insight into Science Needs.—Using these buffered policies would reduce our reliance on good information about productivity and actual catches, as long as catches are really reduced to zero when populations fall below the threshold population size (N_{min}). To make these buffered policies work, we would rely more heavily on two types of data—the target abundance and the current abundance. The target abundance should ideally be based on historical information about the population before fishing or a clear understanding of the biology and ecology of the stock projected through modeling, but the target can be estimated without this information. If it is the sense of managers, fishers, and others that fish are fairly abundant and catches reasonable, current abundance may serve as a reasonable target. In many cases, some rebuilding may be required, because historical analyses suggest that many stocks have been reduced dramatically over hundreds or thousands of years (Jackson et al., 2001). When we have no information about historical abundance, marine reserves can help (see Implementation, below).

Measuring current abundance also poses challenges, but there are encouraging developments on this front. Cooperative efforts between the fishing industry and scientists are providing much more timely and geographically representative data. Costs of running smaller boats part-time are lower than those of maintaining and running a large government research vessel. These costs may also be offset at least in part if boat and crew are paid for with a cut of the quota. With lower costs, much more frequent sampling is possible. Assessments are also time consuming and a bottleneck in the management process. Assessments are used primarily to estimate productivity and appropriate fishing rates. Therefore, they would become less crucial under highly responsive management systems where these pieces of information are less critical. Although assessments also provide estimates of abundance over time, abundance can also be estimated directly from fishery-independent surveys and fishery-dependent data without the long process of a full stock assessment.

Precautionary and Adaptive Management.—Highly responsive systems, where a reserve population is protected from fishing, are highly effective ways to manage in a precautionary manner. Alternatively, overall fishing mortality rates could be reduced to provide adequate precaution, but this technique has some major disadvantages. If we have little information about the fish population, even a reduced fishing mortality rate could be excessive. Moreover, if we do reduce the fishing mortality rate below the optimal level, we do so at the expense of overall catch levels. In contrast, responsive systems provide the opportunity to maintain optimal catch levels over the long term while providing substantial protection against fishery collapses.

Responsive systems also provide an opportunity to learn. With experience, responsive systems allow us to discover appropriate fishing rates. Doing so requires some tracking of catches, not just abundance, although this information can be estimated with existing techniques. With this information, we can gain a thorough understanding of the productivity of a stock at and near its target level and therefore a fishing mortality rate that is appropriate. It does not provide us with an understanding of how productivity varies with stock abundance but does provide perhaps more valuable information about how much fishing is appropriate.

Implementing Responsive Systems.—Management systems with the characteristics of the highly responsive systems we tested can be designed in several ways. The responsiveness can be engineered into the quota-setting process directly. This approach may be the best for some species but faces two challenges. First, many fisheries catch multiple species simultaneously, intentionally or otherwise. The species will almost certainly differ in their productivity, and the least productive species are likely to reach no-fishing levels before more productive species. Ricker (1958) showed that the best catch rates in a multispecies fishery were obtained when each stock was caught independently. He recommended that managers explore ways to increase selectivity of multispecies fisheries. Highly responsive quota systems face a second challenge in that they still require a fair amount of information, albeit less than conventional systems. This information includes target abundance, actual abundance, and a rough estimate of productivity, all of which may not be available for many species.

Size limits are an alternative to quotas and can contribute to a highly responsive management system. If regulations prohibit fishers from killing fish until the fish are large enough to have reproduced one or more times, the fishery is much less prone to collapse (Myers et al., 1997; Myers and Mertz, 1998; Sladek Nowlis, 2000). This approach at minimum requires information on the size at maturity of fish, and more detailed growth and fecundity information can help to ensure that a reasonable total fraction of reproductive output is assured through the size limit. This information may not be available for some species, and the approach has two additional problems. First, many types of fishing gear, from trawls to individually held hook and line in deep water, often kill fish before they are brought on board, so size limits do not prevent their death. Second, size limits are likely to cause conflict in a multispecies fishery. Gear that allows large-maturing fish to escape is likely to substantially reduce catches of smaller species.

Marine reserves, areas closed to fishing and protected from other major human impacts, are another method for creating highly responsive management policies. Reserves maintain a proportion of a species' range off-limits to fishing in much the same way that a highly responsive quota system protects a proportion of the population (N_{min}). Reserves may be a particularly useful technique when even basic information on target and current abundance are lacking. Ideally, to use reserves as a buffer against management mistakes, we should know the habitat requirements of the fish population as well as its movement tendencies. Habitat requirements may become less important when large-scale marine reserve networks are created. Under this scenario, a representative proportion of each marine habitat is included in the reserve network, so many species are likely to find suitable refuge inside the reserve network. Movement tendencies can be more troublesome. Mobile species are more likely to cross reserve boundaries and become vulnerable to fishing, so smaller effective population sizes of these species will be protected in reserves. Consequently, for these species either individual reserves will need to be large enough to incorporate the home ranges of widely migrating fish, or smaller reserves will have to be supplemented with quotas, size limits, and possibly gear restrictions.

Reserves also provide the opportunity to minimize the impacts of by-catch (Ricker, 1958; Sladek Nowlis, 2000). Even our approach used without reserves could malfunction if fisheries with multiple target species cannot avoid depleted populations while harvesting abundant ones. By protecting a core number of all fish species, reserves can lessen the chance that fishing outside the reserve will drive less-productive species to problematically low levels. Mobile species will still be of concern but to a lesser extent than under conventional management.

Ecosystem-based Management.—Highly responsive management policies have several useful implications for ecosystem-based management. By virtually guaranteeing that no population will drop to low levels, responsive policies ensure that all species will perform their ecosystem functions, at least to some degree. The use of marine reserves to protect relatively unknown species can also protect habitat features and functioning ecosystems within their borders. Finally, our framework can be modified to make it even more ecosystem-based through setting of ecosystem-informed targets.

So far, we have only discussed cases where targets are set at MSY, and where N_{min} thresholds are used to help obtain the target, but abundance targets can be set with consideration of roles that species play in their ecosystems. Hard corals, for example, provide hiding places and substrate for numerous species in the coral reef ecosystem, and squid are a key prey species for numerous species in their pelagic ecosystem. In both of these cases, abundance targets should be set higher than those associated with maximum yields. In fact, for many species lower on the food web, fishing to achieve maximum yields can have widespread negative ecosystem-level effects (May et al., 1979).

Through ecosystem-based target setting, appropriately responsive quota systems, and a network of marine reserves, fisheries managers can achieve precautionary and ecosystem-based management. Given the poor state of fishery resources in the U.S. and elsewhere, though, these changes will require substantial economic costs in the short run. We propose that managers commit themselves to adopting better management systems immediately, using a phased approach to minimize the costs during the time of transition. The end result will be more productive ocean ecosystems and more stable fisheries.

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APPENDIX

Equation 8 was derived as follows. We set the change in abundance $dN/dt = 0$ so that

$$0 = r(1 - N_{ss})N_{ss} - \frac{(1+\varepsilon_{h/r})r[(1+\varepsilon_n)N_{ss} - N_{\min}}{2-4N_{\min}}$$
$$= (2-4N_{\min})(1-N_{ss})N_{ss} - (1+\varepsilon_{h/r})[(1+\varepsilon_n)N_{ss} - N_{\min}]$$
$$= (2-4N_{\min})(N_{ss}-1)N_{ss} + (1+\varepsilon_{h/r})[(1+\varepsilon_n)N_{ss} - N_{\min}]$$
$$= (2-4N_{\min})N_{ss}^2 - (2-4N_{\min})N_{ss} + (1+\varepsilon_{h/r})(1+\varepsilon_n)N_{ss} - (1+\varepsilon_{h/r})N_{\min}$$
$$= (2-4N_{\min})N_{ss}^2 - [2-4N_{\min} - (1+\varepsilon_{h/r})(1+\varepsilon_n)]N_{ss} - (1+\varepsilon_{h/r})N_{\min}$$

Solving according to the quadratic formula yields

$$N_{ss} = \frac{2-4N_{\min} - (1+\varepsilon_{h/r})(1+\varepsilon_n) \pm \sqrt{[2-4N_{\min} - (1+\varepsilon_{h/r})(1+\varepsilon_n)]^2 + 4(2-4N_{\min})(1+\varepsilon_{h/r})N_{\min}}}{4-8N_{\min}}$$

Separating the square root and solving yields

$$\sqrt{} = (2-4N_{\min} - 1 - \varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n)^2 + (8-16N_{\min})(1+\varepsilon_{h/r})N_{\min}$$
$$= (1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n - 4N_{\min})^2 + (8N_{\min} - 16N_{\min}{}^2)(1+\varepsilon_{h/r})$$
$$= (1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n)^2 - 8N_{\min}(1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n) + 16N_{\min}{}^2 + (8N_{\min} - 16N_{\min}{}^2)$$
$$(1+\varepsilon_{h/r})$$
$$= (1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n)^2 - 8N_{\min} + 8\varepsilon_{h/r}N_{\min} + 8\varepsilon_n N_{\min} + 8\varepsilon_{h/r}\varepsilon_n N_{\min} + 16N_{\min}{}^2$$
$$= (1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n)^2 + 16\varepsilon_{h/r}N_{\min} + 8\varepsilon_n N_{\min} + 8\varepsilon_{h/r}\varepsilon_n N_{\min} - 16\varepsilon_{h/r}N_{\min}{}^2 + 8N_{\min}$$
$$-16N_{\min}{}^2 + 8\varepsilon_{h/r}N_{\min} - 16\varepsilon_{h/r}N_{\min}{}^2$$
$$\sqrt{} = (1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n)^2 + 16\varepsilon_{h/r}N_{\min}(1-N_{\min}) + 8\varepsilon_n N_{\min}(1+\varepsilon_{h/r})$$

Substituting back into the full equation yields

$$N_{ss} = \frac{2-4N_{\min} - (1+\varepsilon_{h/r})(1+\varepsilon_n) \pm \sqrt{(1-\varepsilon_{h/r} - \varepsilon_n - \varepsilon_{h/r}\varepsilon_n)^2 + 16\varepsilon_{h/r}N_{\min}(1-N_{\min}) + 8\varepsilon_n N_{\min}(1+\varepsilon_{h/r})}}{4-8N_{\min}}$$