

Delay in fishery management: diminished yield, longer rebuilding, and increased probability of stock collapse¹

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When a stock is depleted, catch reductions are in order, but typically they are implemented only after considerable delay. Delay occurs because fishery management is political, and stricter management, which involves short-term economic loss, is unpopular. Informed of stock decline, managers often hesitate, perhaps pondering the uncertainty of scientific advice, perhaps hoping that a good year class will render action moot. However, management delay itself can have significant costs, when it exacerbates stock decline. To examine the biological consequences of delay, we simulated a spectrum of fisheries under various degrees of delay in management. Increased delay required larger catch reductions, for more years, to recover benchmark stock status (here, spawning-stock biomass at maximum sustainable yield). Management delay caused stock collapse most often under two conditions: (1) when the stock–recruitment relationship was depensatory, or (2) when catchability, unknown to the assessment, was density-dependent and fishing took juveniles. In contrast, prompt management resulted in quicker recoveries and higher cumulative yields from simulated fisheries. Benefits to stock biomass and fishery yield can be high from implementing management promptly.

Keywords: catchability, depensation, fishery management, precautionary approach, reference points, REPAST, stock assessment.

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Introduction

Management of a declining fish stock is typically a delay-ridden process. Because catch reductions impose short-term losses on fishers, merchants, and processors, managers face political opposition—and even legal challenges—and they may hesitate to change the *status quo* (Rosenberg, 2003).

Besides the underlying economic issue, several features of fishery management can spark significant delay. (We write from a US perspective, but the problems seem worldwide.) Uncertainty in scientific advice is often used to delay management, although adoption of the precautionary approach (FAO, 1995; Rosenberg, 2002) has weakened that rationale. Nonetheless, distrust or dislike of assessment results can spark extended debate and delay.

Composition of management panels can influence the extent of delay, which tends to increase when members have strong economic interests. In the United States, where membership in regional Fishery Management Councils is heavily weighted towards fishing interests (Okey, 2003), protracted debate has often delayed introduction of lower catch limits.

A related cause of delay is the practice in many jurisdictions of providing repeated opportunities for public comment, with the attendant need to ensure that procedures are followed correctly. Powers (2004) demonstrated that, given the current balance of interests on US Fishery Management Councils, litigation (and by inference, delay) is to be expected.

Again in the US, the National Research Council (1994, p. 22) stated: “The process for developing, approving, and implementing a fishery management plan needs to be improved. The speed of the implementation process is important because . . . lack of a plan can allow over-capitalization and over-harvest”. That comment notably links two important problems: overcapitalization of fisheries and management delay.

The prevalence of delay has been recognized for some time. Gulland (1974) wrote: “The Californian sardine fishery is a monument to the failure to act in time, and to the insistence of having conclusive scientific evidence before acting”. That fishery collapsed in the early 1950s (MacCall, 1979). Weber (2002) described monkfish (*Lophius americanus*) management in New England. As the population dropped to its lowest recorded levels, “managers adapted slowly to the growing threat of overfishing . . .” Only after seven years of debate was a fishery management plan approved. Weber (2002) described similar delays in management of haddock (*Melanogrammus aeglefinus*), cod (*Gadus morhua*), and yellowtail flounder (*Pleuronectes ferrugineus*).

The precautionary approach has been widely discussed and praised, yet fisheries rarely are restricted during the often lengthy debate that precedes catch reductions. A declining stock thus continues to decline. Since delay in accepting scientific advice carries risks of reduced yield or even stock collapse, it seems important to quantify those effects systematically.

We used simulation to examine consequences of delayed management on stocks already in decline. Simulations were intended to be general, rather than representative of specific stocks. Our goal was to discover situations in which delay may

¹Opinions expressed are those of the authors and do not necessarily reflect the policies or findings of NMFS, NOAA, or any other government agency.

have particularly negative effects on stock size and long-term yield.

Methods

Simulations were conducted with an age-structured population model, described briefly here and fully in the appendix. The model includes submodels of survival, growth, maturity, recruitment, fishing, assessment, and management. We attempted to represent an average fished population by using life-history invariants to set biological parameter values.

In each simulation, initial conditions were determined as the stable age distribution in the absence of fishing. From that condition, the population was simulated for 50 years, at first under substantial overfishing (depletion period), then under various lengths of management delay (delay period), and finally under reduced fishing (regulated period). The delay period represents a period of absent or insufficient regulation.

To provide more general results, simulations examined eight different stock types. These were defined by binary levels of three factors known to affect stock dynamics: selectivity (before or at maturity), catchability (constant or density-dependent), and stock–recruit relationship (depensatory or non-depensatory). Simulation results were tabulated from years following the depletion period; i.e. during the delay and regulated periods, by which time the initial population declines were in the past. Thus, results should be more representative of established, depleted fisheries than of new fisheries in the fishing-down stage.

General simulation properties

In the simulated stocks, the total instantaneous mortality rate Z was the sum of fishing mortality rate F and natural mortality rate M . The latter was set at $M = 0.3 \text{ y}^{-1}$, a compromise between values typical of short-lived and long-lived species.

Other biological parameter values (Table A1) were estimated from the theory of life-history invariants (Charnov, 1993), which provides typical growth and maturity parameters corresponding to the given M . This procedure was chosen to describe a typical stock and thus to provide more general results.

Simulated length- and weight-at-age followed the von Bertalanffy (1938) growth model. Proportion mature and selectivity-at-age were modelled with logistic (sigmoid) functions. Each stock type’s MSY-based benchmarks, e.g. F_{MSY} , were estimated from an age-structured, stochastic simulation conducted for that purpose.

Factors varied by stock type

We now describe the three factors (Figure 1) that, in combination, determined each of the eight stock types simulated (Table 1).

Factor 1: Selectivity relative to maturity

In an age-structured population, the amount of reproduction before harvest helps determine potential yield, equilibrium yield per recruit, and whether a given fishing mortality rate is sustainable (Williams and Shertzer, 2003). We modelled that factor by relating the age of 50% selectivity A_s to the age of 50% maturity A_m . Simulations included four stock types in which $A_s = A_m$ and four in which $A_s < A_m$ (Figure 1a).

Factor 2: Density-dependent catchability

A fishing gear is characterized in part by its catchability coefficient q , which scales the fishing effort rate f_t to the fishing mortality rate

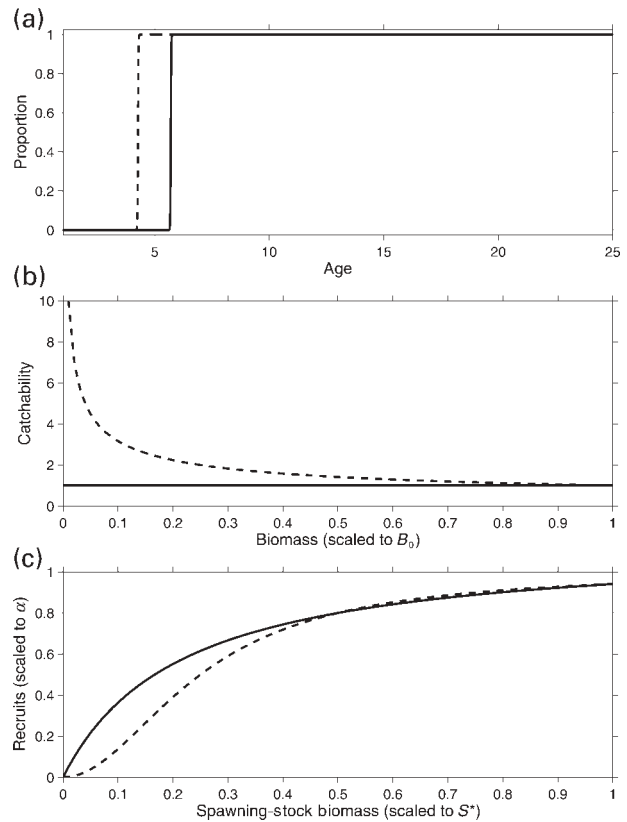


Figure 1. Characteristics of eight stock types simulated. All combinations of three binary factors were used: (a) 50% selectivity, before maturity (dashed line) or at maturity (solid line); (b) catchability, density-dependent (dashed) or constant (solid); and (c) stock–recruit relationship, depensatory (dashed) or non-depensatory (solid). In (b), biomass is scaled to the virgin level (B_0); in (c), spawning-stock biomass and recruits are scaled to their maximum levels (S^* and α , respectively).

by $F_t = qf_t$ (t is time in years). Typically, catchability is assumed constant across years. This can be a poor assumption: increased catchability at low stock sizes has been observed in many fisheries (Harley *et al.*, 2001), especially those on schooling stocks (e.g. Clark and Mangel, 1979; Ahrenholz *et al.*, 1987; Mackinson *et al.*, 1997; Rose and Kulka, 1999). Such density-dependent catchability

Table 1. Stock types considered through simulation.

Scenario	Acronym	Depensatory recruitment	Density-dependent catchability	Selection before maturation
a	NDR/CC/SAM	–	–	–
b	NDR/CC/SBM	–	–	+
c	NDR/DDC/SAM	–	+	–
d	NDR/DDC/SBM	–	+	+
e	DR/CC/SAM	+	–	–
f	DR/CC/SBM	+	–	+
g	DR/DDC/SAM	+	+	–
h	DR/DDC/SBM	+	+	+

can substantially affect the dynamics of an exploited population (Clark and Mangel, 1979; Mackinson *et al.*, 1997; Katsukawa and Matsuda, 2003).

To allow for density-dependent catchability, we followed MacCall (1976) and Csirke (1989) in modelling catchability as a decreasing power function of stock biomass B . In our simulations, four stock types were subject to constant catchability and four to density-dependent catchability (Figure 1b).

Factor 3: Depensatory recruitment

For stocks in decline, the possibility of depensation (Allee effect) is important. Depensation, a reduction in per capita population growth rate at low population size, is a form of positive feedback and thus leads to population instability. Although depensation is difficult to detect in typically noisy stock–recruitment data (Liermann and Hilborn, 1997; Shelton and Healey, 1999), mechanisms that would cause it (e. g. reduced probability of fertilization, impaired group dynamics, niche loss) have been well-documented (Courchamp *et al.*, 1999; Liermann and Hilborn, 2001). Depensation would prevent or delay recovery of a depleted stock.

We modelled expected recruitment with a modified Beverton–Holt spawner–recruit function (Thompson, 1993; Liermann and Hilborn, 1997), using different parameter values to specify presence or absence of depensation (Figure 1c). Realized recruitment was made stochastic through multiplicative lognormal process error.

Simulated fishing and management

Fishing

During the depletion and delay periods, annual F was drawn from a truncated (at zero) normal distribution with mean $\mu = cF_{\text{MSY}}$ and $\text{CV} = 10\%$, where c is a constant and F_{MSY} is the fishing mortality rate providing maximum sustainable yield. Any value $c > 1$ leads, on average, to overfishing. We used $c = 3$, a value similar to estimates from some depleted stocks (Edwards and Murawski, 1993; Vaughan and Prager, 2002).

Because of overfishing in the depletion period, spawning-stock biomass (S_t) declined below that at maximum sustainable yield (S_{MSY}) by about year five. The resulting continuous decline is a pattern that has been observed in fisheries worldwide (Mullon *et al.*, 2005).

Stock assessment

Beginning in year six, assessment results were generated every second year. We did not simulate specific assessment methods, but rather assumed that results were available from an unspecified method. The primary assessment result ($\hat{\lambda}$) was an estimate of a dimensionless reference point λ , defined as the ratio of the limit reference point F_{MSY} to current F ; i.e. $\lambda = F_{\text{MSY}}/F_{\text{now}}$. An estimate $\hat{\lambda} < 1$ implies overfishing, both under US guidelines and in this simulation study. (Thus $1/\hat{\lambda} = F_{\text{now}}/F_{\text{MSY}}$ is a typical fishery-status indicator.) When examined by Prager *et al.* (2003), bootstrap distributions of $\hat{\lambda}$ from several stocks appeared normally distributed.

We simulated assessment uncertainty by drawing $\hat{\lambda}$ from a normal distribution with CV of 10%. In stock types with constant catchability, the mean of the distribution was $\mu(\hat{\lambda}) = \lambda$. Under density-dependent catchability, the mean was a function of total-stock biomass (see appendix), with $\mu(\hat{\lambda}) > \lambda$ when $B_t < B_{\text{MSY}}$ and $\mu(\hat{\lambda}) < \lambda$ when $B_t > B_{\text{MSY}}$. (Here, B_{MSY} is the expected biomass level from fishing at F_{MSY} indefinitely.) That is, under density-dependent catchability the estimate of F relative to F_{MSY}

was too small when the stock biomass was below B_{MSY} , too large when the stock biomass was above B_{MSY} .

Management control rule

Simulated management was accomplished by regulating future F relative to present F through a control rule based on fishery reference points. In each simulation, the limit reference point was set to $\text{LRP} = F_{\text{MSY}}$; a corresponding target reference point (TRP) was provided by the control rule “ratio-extended probability approach to setting targets” (REPAST) (Prager *et al.*, 2003). This rule computes a TRP from an estimate of the LRP and its probability distribution, the estimated or assumed probability distribution of management implementation (i.e. distribution of realized F_t when aiming at the TRP), and a predetermined allowable probability p that $F_t > \text{LRP}$ in any year. In a real fishery, the value of p , which quantifies the level of risk acceptable to managers, would be based mainly on political considerations.

The purpose of the REPAST control rule is to set the distance between the TRP and LRP based on three things: precision of the assessment, ability of management to control F in the fishery, and risk tolerance of managers. Thus, under the REPAST control rule, the TRP is set closer to the LRP as assessment precision increases or as the estimated or assumed control of F by management becomes more precise. Additionally, the TRP is moved closer to the LRP when managers are more risk prone (larger p), but further from the LRP when they are more risk averse (smaller p). By requiring p to be specified *a priori*, the REPAST control rule formally incorporates the non-scientific aspects of fishery management. Here, we fixed $p = 0.25$ and updated the TRP at each assessment. Because of the structure of this study, using the REPAST control rule here was roughly equivalent to using $\text{TRP} = 0.9 F_{\text{MSY}}$.

Management implementation

To study the relationship of management delay to stock rebuilding, we varied the length of the delay period by adjusting the number ($D = 1, 2, \dots, 10, \infty$) of consecutive assessments indicating overfishing before new management was enacted. ($D = \infty$ represents perpetual insufficient or no management.) As noted, assessments occurred every two years. Once management was enacted, it was put into place the following year. Thus, after the depletion period of six years, the delay period lasted for $2(D - 1) + 1$ years.

Management was implemented as imprecise changes to the observed (via stock assessment) fishing mortality rate \bar{F}_t of the simulated population. The value of \bar{F}_t applied in the next period was drawn from a normal distribution with mean $\mu(\bar{F}_t) = \text{TRP}$ (where the TRP was calculated with the REPAST control rule) and $\text{CV} = 10\%$. In all stock types, $F_t = q\bar{F}_t$. In stock types with density-independent catchability, $q = 1$ for all stock levels; thus, management of \bar{F}_t in effect controlled the actual fishing mortality rate. In stock types with density-dependent catchability, $q > 1$ for all B_t less than the virgin level (Figure 1b), and therefore $F_t > \bar{F}_t$. Thus, when management controlled \bar{F}_t , the actual fishing mortality rate was mediated by density-dependent catchability. This corresponds to an assessment based mainly on fishery-dependent data, where catchability changes are not observed directly.

Outcomes

We generated 1000 stochastic simulations of each stock type at each length of delay. From results, we examined annual median values of yield (Y_t), spawning-stock biomass (S_t), and related

quantities. Medians were used to represent central tendencies; other quantiles generally provided similar results. One such quantity was the number of years in which median S_t was below its limit reference point in biomass, defined to be the so-called minimum stock-size threshold (MSST) of US fishery management. The MSST of each stock type was computed from the natural mortality rate by $(1 - M)S_{MSY}$, as suggested in Restrepo *et al.* (1998). Also examined were the probability of stock collapse and the number of years to recover under management. A stock was considered collapsed if S_t fell below 1% of virgin level during the 50-year simulation, and was considered recovered when median S_t reached S_{MSY} . Computation of recovery times, in some cases, required extending simulations beyond 50 years.

Results

Stock dynamics

As expected, each simulated stock declined during the initial period of overfishing. When management was implemented with the shortest delay considered—one year after the first assessment—each stock recovered during the simulation period, some quite rapidly (bold solid lines in Figure 2). Under longer-delayed management, the stocks reached lower median levels of abundance and remained below the limit reference point (MSST) longer (Table 2). Consequently, recovery was slower, was incomplete, or the stock collapsed (Figure 2, Table 2).

Depensatory recruitment (stock types e–h in Table 1) and density-dependent catchability (stock types c, d, g, h) were

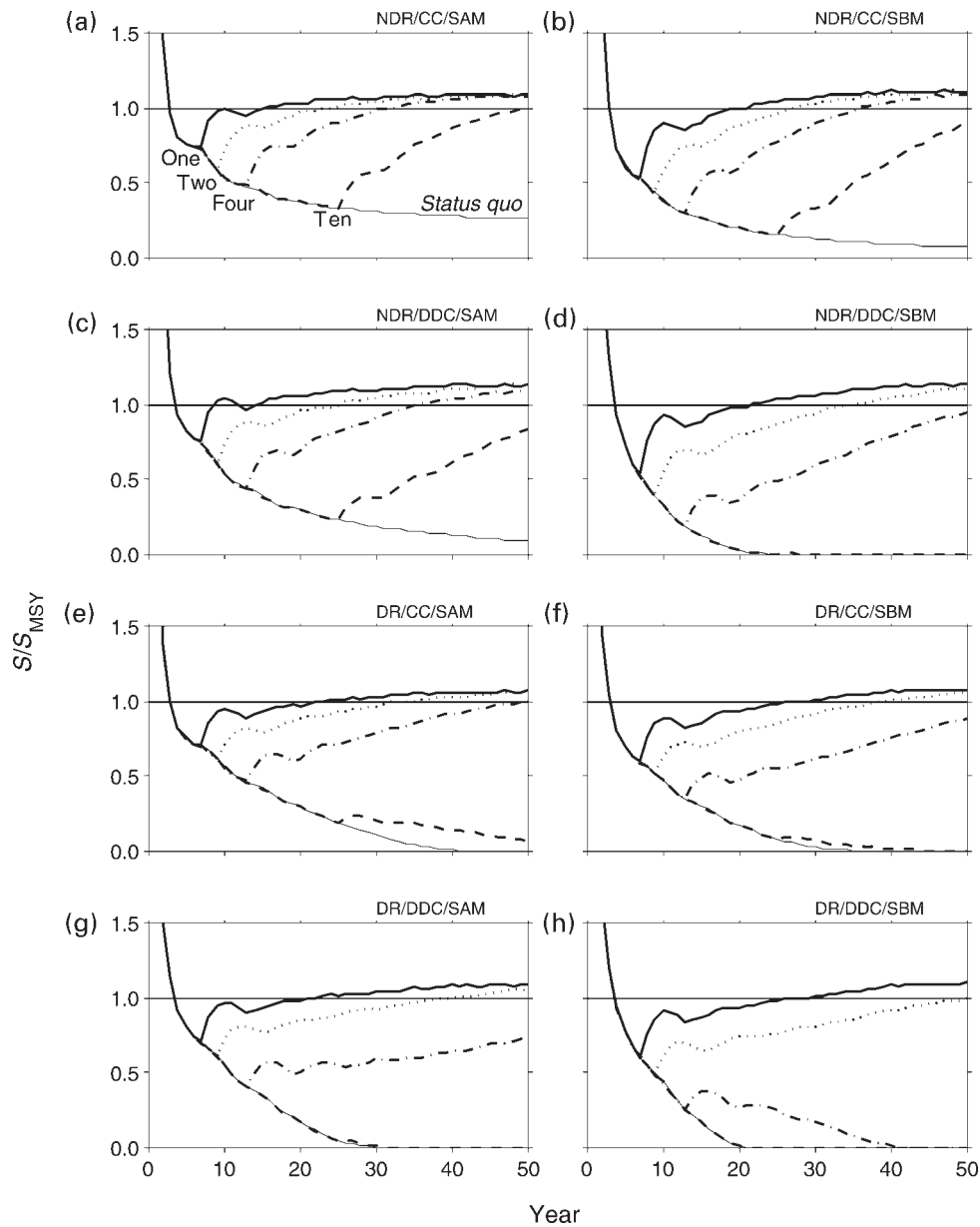


Figure 2. Simulated time trajectories of spawning-stock biomass S_t relative to S_{MSY} . Line types depict effects of delaying management. Thick solid line, management implemented after one assessment; dotted line, after two; dash-dotted line, four; dashed line, ten; thin solid line, *status quo*. Horizontal line at unity is $S_t = S_{MSY}$. Panel labels (a–h) represent stock types; acronyms on panels relate each stock type to its characteristics (Table 1). Medians of 1000 trials are shown.

Table 2. Effects of delaying management by *D* assessment cycles of two years each.

Scenario and acronym	Delay length, <i>D</i>	Probability of stock collapse	Minimum S_t/S_{MSY}	Number of years $S_t < MSST$	Recovery duration [y]	Lowest Y_t/MSY	Number of years $Y_t > Y_{t, D=\infty}$	Total yield (scaled)
a NDR/CC/SAM	1	0.00	0.74	0	9	0.68	34	1.00
	2	0.00	0.59	2	16	0.53	31	0.99
	4	0.00	0.49	7	20	0.44	27	0.97
	6	0.00	0.40	16	20	0.36	23	0.95
	8	0.00	0.37	21	21	0.34	20	0.92
	10	0.00	0.34	26	22	0.31	16	0.89
	∞	0.00	0.26	43	—	0.60	—	0.87
b NDR/CC/SBM	1	0.00	0.53	3	14	0.64	35	1.00
	2	0.00	0.43	7	19	0.49	33	0.98
	4	0.00	0.30	18	24	0.36	29	0.93
	6	0.00	0.23	25	25	0.28	25	0.88
	8	0.00	0.19	31	28	0.23	22	0.81
	10	0.00	0.16	37	30	0.19	18	0.75
	∞	0.00	0.07	46	—	0.25	—	0.65
c NDR/DDC/ SAM	1	0.00	0.75	0	5	0.71	33	1.00
	2	0.00	0.61	2	16	0.61	31	0.99
	4	0.00	0.45	13	24	0.50	28	0.97
	6	0.00	0.34	21	27	0.41	25	0.93
	8	0.00	0.29	29	32	0.37	21	0.89
	10	0.00	0.23	36	35	0.32	17	0.85
	∞	0.01	0.09	43	—	0.32	—	0.77
d NDR/DDC/ SBM	1	0.00	0.53	2	16	0.72	35	1.00
	2	0.00	0.39	11	26	0.61	34	0.97
	4	0.00	0.19	30	42	0.43	32	0.88
	6	0.05	0.08	45	65	0.29	29	0.68
	8	0.81	0.00	45	∞	0.01	27	0.45
	10	1.00	0.00	45	∞	0.00	14	0.40
	∞	1.00	0.00	45	—	0.00	—	0.40
e DR/CC/SAM	1	0.00	0.71	0	16	0.66	33	1.00
	2	0.00	0.62	2	25	0.56	32	0.98
	4	0.00	0.47	15	39	0.43	28	0.91
	6	0.00	0.36	35	54	0.33	25	0.79
	8	0.01	0.28	43	∞	0.26	22	0.65
	10	0.22	0.07	43	∞	0.06	18	0.57
	∞	1.00	0.00	43	—	0.00	—	0.56
f DR/CC/SBM	1	0.00	0.60	3	22	0.66	34	1.00
	2	0.00	0.52	8	30	0.55	33	0.96
	4	0.00	0.36	32	52	0.38	30	0.81
	6	0.03	0.25	46	∞	0.23	26	0.56
	8	0.60	0.01	46	∞	0.01	22	0.46
	10	0.98	0.00	46	∞	0.00	19	0.46
	∞	1.00	0.00	46	—	0.00	—	0.47
g DR/DDC/SAM	1	0.00	0.71	0	16	0.70	33	1.00
	2	0.00	0.61	2	31	0.64	32	0.98
	4	0.08	0.42	38	110	0.50	29	0.87
	6	0.71	0.00	43	∞	0.00	27	0.59
	8	0.98	0.00	43	∞	0.00	19	0.52
	10	1.00	0.00	43	∞	0.00	13	0.51
	∞	1.00	0.00	43	—	0.00	—	0.52

Continued

Table 2. Continued

Scenario and acronym	Delay length, D	Probability of stock collapse	Minimum S_t/S_{MSY}	Number of years $S_t < MSST$	Recovery duration [y]	Lowest Y_t/MSY	Number of years $Y_t > Y_{t, D=\infty}$	Total yield (scaled)
h	1	0.00	0.61	2	23	0.74	34	1.00
DR/DDC/SBM	2	0.00	0.50	10	46	0.66	34	0.96
	4	0.73	0.00	45	∞	0.00	29	0.54
	6	1.00	0.00	45	∞	0.00	14	0.44
	8	1.00	0.00	45	∞	0.00	8	0.44
	10	1.00	0.00	45	∞	0.00	0	0.44
	∞	1.00	0.00	45	—	0.00	—	0.44

S_{MSY} defined as spawning-stock biomass (S) at maximum sustainable yield (MSY); Y_t defined as annual yield; total yield scaled to that with least delay in management ($D = 1$). Probability of collapse computed as proportion of 1000 replicates; other values based on annual medians.

associated with possible stock collapse, particularly when combined with each other or with selectivity before maturation (stock types d, f, h). All stock types with depensatory recruitment collapsed or nearly collapsed under the longest management delays. The two stock types that combined depensatory recruitment and density-dependent catchability (g and h) collapsed under management delayed by ten years or more (Figure 2, Table 2).

Yield dynamics

Each simulated stock started at high abundance, and its yields in the depletion period and early years of the delay period were well above MSY (Figure 3). By definition, though, any yield greater than MSY is unsustainable. As abundance declined because of overfishing, median yield declined as well. When management was delayed sufficiently, stock and yield collapsed together (Figure 3d–h).

In most cases, though, the stock did not collapse, and the yield trajectories illustrate the usual contrast between short-term and longer-term results. Yield from a managed stock initially lagged that of the corresponding unmanaged stock, but increased as the stock recovered. Yield under management usually exceeded that from the unmanaged stock within about 10 years (Figure 3). In general, shorter delay resulted in higher minimum annual yield, by either preventing stock collapse or by requiring less drastic initial reductions in yield (Table 2). It also resulted in more years during which yield exceeded that from maintaining *status quo* (Table 2).

Increases in annual yield under management correspond to long-term gains. Like annual yield, cumulative yield of the managed stock initially fell below, but later surpassed, that of the corresponding unmanaged stock. Long-term total yield was highest when management was delayed least; total yield diminished with each increment of delay (Table 2).

Discussion

Delay can cause markedly more severe management measures to be needed for rebuilding a stock. For example, in US federal fishery management, if the stock size falls below its limit reference point in biomass (the minimum stock-size threshold, or $MSST$), a formal rebuilding plan is required. Such plans usually require drastic reductions in catches; thus, initiation of a rebuilding plan is particularly unfavourable to the fishing industry. In our simulations, increasing delay in management increased the number of years a stock was below its $MSST$ (Table 2). Conversely, prompt

management decreased the likelihood that a rebuilding plan would become necessary.

Related to rebuilding plans is the recovery time frame. As shown by our simulations, the required time frame increases with delay in management. Consequently, delay may lead not only to more severe regulations, it also lengthens their duration, in some cases by decades.

Our simulations indicate that delay in management can lead to stock collapse. That result is in agreement with a recent report (Suckling *et al.*, 2004) that examined US plant and animal extinctions between December 1973 and December 1994. Those authors found that, under the Endangered Species Act, the listing process for 77% of species that became extinct was marked by “lengthy delays”. In fisheries, economic collapse may occur prior to stock collapse.

In our simulations, depensation was associated with stock collapse when management was delayed for longer periods. Myers *et al.* (1995), in a meta-analysis of stock–recruitment relationships, found evidence of depensation in few of the examined stocks. However, depensation may be difficult to detect using fishery data (Liermann and Hilborn, 1997; Shelton and Healey, 1999), and mechanisms that cause depensation appear to be widespread (Liermann and Hilborn, 2001).

Here, we have defined depensation (as did Myers *et al.*, 1995) as a single-species phenomenon, a property of the stock–recruitment relationship. Nevertheless, depensation may be indistinguishable from detrimental ecosystem or community events such as niche replacement, which cannot be ruled out in several known cases of population declines (Jackson *et al.*, 2001; Frank *et al.*, 2005). Lately, ecosystem management—a term with a seeming infinity of definitions—has received considerable support and discussion. Those discussions should include the possibility that prolonged overexploitation can lead to collapse whether from single-species or community effects.

Results presented here assume a natural mortality rate of $M = 0.3$, a compromise between values typical of short-lived and long-lived species. Further simulations were conducted to analyse the consequences of management delay under different values of M ; these analyses applied a natural mortality of $M = 0.5$ to represent short-lived species or $M = 0.1$ to represent long-lived species. In both cases, results were qualitatively the same as those presented, but occur over different time scales. In general, short-lived species respond more quickly to management, so the benefits of prompt management are realized sooner. Conversely, long-lived species respond more slowly, so the negative consequences of delay can be even more severe.

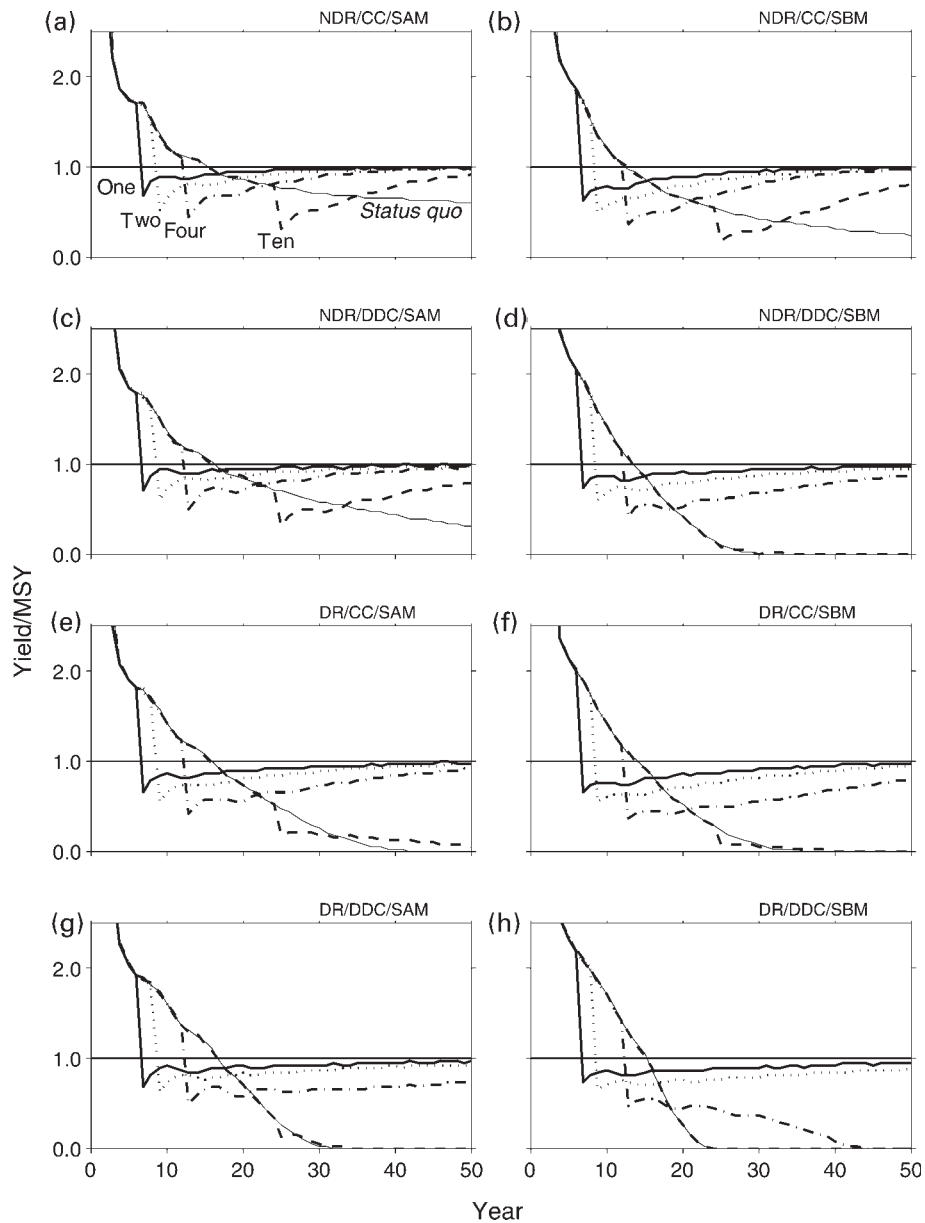


Figure 3. Simulated time trajectories of yield Y_t relative to MSY. Line types depict effects of delaying management. Thick solid line, management implemented after one assessment; dotted line, after two; dash-dotted line, four; dashed line, ten; thin solid line, *status quo*. Horizontal line at unity is $Y_t = MSY$. Panel labels (a–h) represent stock types; acronyms on panels relate each stock type to its characteristics (Table 1). Medians of 1000 trials are shown.

Imprecision simulated here in assessment and stock dynamics was lower than in most real situations. For example, the CV in simulated assessment results was set at 10%. We chose relatively low values so that variability in simulated dynamics and assessments would not obscure patterns related to delay length. To check this approach, we made additional simulations with assessment $CV = 25\%$ or with CV decreasing over time. Results in both cases were quite similar to those presented.

Several consequences of delay were not modelled here. As mentioned, delay increases the probability that a formal rebuilding plan will be required, at least in US federal fishery management. Although rebuilding plans typically reduce yield drastically, such reductions were not simulated. A compounding issue, also not

modelled here, is that when management is delayed, additional fishing vessels may join the fleet (Gulland, 1974). If that happens, eventual regulation can be more painful to each fisher.

For simplicity, our models also excluded some aspects of biology, such as maternal and genetic effects. Older mothers tend to produce offspring with greater growth and survival, so that age truncation—removal of older ages due to fishing—reduces the population’s potential for growth (Berkeley *et al.*, 2004). Likewise, loss of genetic diversity through fishing can reduce growth rate and adaptability of a population (Tittensor *et al.*, in press). These maternal and genetic effects would diminish the population’s response to management as overfishing is prolonged. Thus, our simulations likely underestimate the consequences of delayed management.

We assumed that stock status was described with uncertainty, including imprecision, inaccuracy, or both. In practice, uncertainty can be reduced by better sampling and appropriate models, which serve to improve scientific advice. At least in theory, effects of imprecision can be accounted for with control rules like REPAST (Prager *et al.*, 2003) or other applications of the precautionary principle. Inaccuracy can be assessed by such tools as retrospective analysis and simulation modelling, or more directly by examining the population's responses to management measures already applied.

In that connection, prompt management can improve the quality of subsequent scientific advice. When management is prompt, scientific advice is regularly tested against the population responses it predicts. When management is deferred, this feedback does not occur, and delay itself holds back the science from advancing (Walters, 1986).

One leading cause of management delay is lack of confidence in the scientific advice, especially when that advice contradicts an *a priori* assumption of a healthy stock not threatened by current fishing. Given scientific uncertainty, managers have tended to guard the fishing industry against the possibility of spurious detection of population declines. This approach favours avoidance of type-I statistical error, i.e. incorrectly concluding that the stock is declining. As discussed by Dayton (1998), a type-I error usually causes only short-term economic loss, whereas a type-II error—incorrectly concluding that the stock is healthy—can result in long-term ecological damage, such as collapse of the stock, and therefore long-term economic loss as well. In a study of natural resource management, Field *et al.* (2004) found that when a species' economic value substantially exceeds its recovery cost, a management policy based on avoiding type-I error is rarely optimal in an economic sense. More attention to type-II error (Peterman, 1990; Lindley *et al.*, 2000) might benefit both the resource and industry by reducing management delay.

From one perspective, waiting for more information is a rational response from managers who must choose between strict management (short-term pain for fishers and uncertain recovery) and *laissez-faire* management (short-term benefit for fishers and possible recovery under favourable environmental conditions) (Walters and Martell, 2004). What is known but often pushed aside is that during such a delay the stock continues to decline, and then increasingly harsh management measures are needed for recovery. The severity of proposed management fuels political resistance, which causes further delay, in a destructive positive-feedback cycle. For that reason, the practice of waiting for more information in the face of unpleasant scientific advice is considered by many a discredited paradigm. It has led to severe over-exploitation in fishery management and degradation in other ecological contexts.

Another fact often overlooked—or perhaps considered an acceptable risk—is that some stocks, after being fished to low levels, have failed to recover, even under stringent management (Caddy and Agnew, 2004). Thus, it seems entirely possible that “rational” delay can lead to the point of no return. Although one cannot ignore the influence of favourable stochastic events on population and fishery dynamics, it hardly seems prudent to bet on them.

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Appendix: Model description

Simulations were conducted with an age-structured population model that includes effects of survival, growth, maturity, fishing, recruitment, and management.

Survival

Let $N_{a,t}$ be the number of fish in age class a at the start of year t . The number of fish in that cohort one year later is

$$N_{a+1,t+1} = N_{a,t} \exp(-M - F_{a,t}), \quad (1)$$

where M is the instantaneous rate of natural mortality and $F_{a,t}$ is the year- and age-specific instantaneous rate of fishing mortality. The model used a maximum age of 25 years, with the terminal age being a plus group (accumulator).

Growth and maturity

Length- and weight-at-age

Length-at-age L_a was modelled with the von Bertalanffy (1938) growth model,

$$L_a = L_\infty [1 - \exp(-Ka)], \quad (2)$$

where K and L_∞ represent growth rate and asymptotic length, respectively. Length-at-age was converted to weight-at-age W_a by the allometric relationship

$$W_a = w_1 L_a^{w_2}, \quad (3)$$

with constants w_1 and w_2 . As weight scales with volume, typically $w_2 \approx 3$. Total-stock biomass (B_t) was computed as $B_t = \sum_a N_{a,t} W_a$.

Maturity

Maturity-at-age was modelled as a logistic function of age,

$$m_a = \frac{1}{1 + \exp[-\eta_m(a - A_m)]}, \quad (4)$$

where m_a is the proportion of fish at age a that are mature. Parameter η_m controls the slope and was set to a large value to provide a knife-edge maturity curve. Parameter A_m is the age at which 50% of fish are mature (Table A1).

Table A1. Model parameters.

Parameter	Value [alternative]	Description [units]	Source
M	0.3	Natural mortality rate [y^{-1}]	Assumed
L_{∞}	1 000	Asymptotic length [len]	Assumed
K	0.18	Growth rate [y^{-1}]	Charnov (1993)
w_1	1×10^{-8}	Length-weight coefficient [wgt len $^{-3}$]	Assumed
w_2	3	Length-weight exponent	Assumed
η_m	100	Steepness of maturity curve [y^{-1}]	Assumed knife-edge
A_m	5.7	Age at 50% maturity [y]	Beverton (1992)
η_s	100	Steepness of selectivity curve [y^{-1}]	Assumed knife-edge
D	{1, 2, ..., 10, ∞ }	No. assessments before regulations	Independent variable
σ_R	0.25	Lognormal recruitment variation	Assumed
CV_{λ}	10%	Assessment uncertainty	Assumed
CV_{τ}	10%	Implementation uncertainty	Assumed
P	0.25	Probability of $F > F_{MSY}$	Assumed
Alternative stock types			
κ	1.0 [0.75]	Selectivity relative to A_m	Assumed
q'	1.0 [B_0^{ψ}]	Catchability coefficient [wgt $^{-1}$]	Katsukawa and Matsuda (2003)
ψ	0.0 [0.5]	Catchability exponent	Katsukawa and Matsuda (2003)
α	114 [100]	Asymptotic recruitment [no. fish]	Liermann and Hilborn (1997)
β	44 [52]	Recruitment half-saturation [wgt]	Liermann and Hilborn (1997)
γ	1 [2]	Depensatory exponent	Assumed

Values in brackets correspond to scenarios with depensatory recruitment, density-dependent catchability, or selection before maturation. Parameter units are year (y), length (len), weight (wgt), or number of fish (no. fish). No reported unit indicates a dimensionless parameter.

Use of life-history invariants

To maintain biological generality, we based values of K and A_m for our simulated stocks on life-history invariants. We set the value of K from the relationship $M/K = 1.65$ estimated by Charnov (1993), and the value of A_m from the relationship

$$A_m = \frac{1}{K} \log\left(\frac{3K + M}{M}\right) \quad (5)$$

estimated by Beverton (1992).

Fishing mortality rate

Simulated instantaneous rates of fishing mortality varied annually. They also varied by age, simulating selectivity of harvest. Finally, rates were modified in some cases to simulate density-dependent catchability.

Fishing at age

Year- and age-specific fishing mortality rates were computed as the product of a year-specific rate (F_t) and an age-specific selectivity (s_a); thus, $F_{a,t} = s_a F_t$. Selectivity was modelled as a logistic function of age,

$$s_a = \frac{1}{1 + \exp[-\eta_s(a - A_s)]}. \quad (6)$$

Here η_s controls the slope, and was set to a large value to provide a knife-edge selectivity curve. Parameter A_s is the age at which 50% of fish are subject to exploitation (Table A1).

Selectivity relative to maturity

We explicitly related selectivity and maturity by setting $A_s = \kappa A_m$, where $\kappa < 1.0$ describes a fishery that selects individuals before they mature. In our simulations, we considered stock types in which selectivity coincided with maturity ($\kappa = 1.0$) and stock types in which selectivity occurred before maturity ($\kappa = 0.75$) (Figure 1a).

Catchability

Along with selectivity and fishing mortality rate, a fishery is characterized by the catchability coefficient q , which scales the applied fishing effort rate f_t to the instantaneous rate of fishing mortality by $F_t = qf_t$. Catchability may be constant or density-dependent. To allow for density dependence, we modelled catchability as a power function of stock biomass B (MacCall, 1976; Csrirke, 1989):

$$q_B = q' B^{-\psi}. \quad (7)$$

Here, q' is the nominal catchability coefficient, and ψ sets the increase in catchability as biomass declines. We used differing values of $\{q', \psi\}$ for constant and density-dependent catchability. When simulating constant catchability, we defined $q' = 1$ and $\psi = 0$, so that $q_B = 1.0$ and thus $F_t = f_t$ for all B . When simulating density-dependent catchability, we set $\psi = 0.5$. Estimates of ψ from actual stocks range from about 0.5 to 1.0 (Katsukawa and Matsuda, 2003). Following Katsukawa and Matsuda (2003), we set $q' = B_0^{\psi}$, where B_0 is the stock's virgin biomass. Thus, realized catchability was $q_B = 1.0$ when $B = B_0$ and was $q_B > 1.0$ when $B < B_0$ (Figure 1b).

In this study, the quantity $\bar{F}_t = f_t$ represents the nominal "perceived" rate of fishing mortality, defined as the rate that would be

obtained under constant catchability. This nominal rate was “observed” by the simulated assessments and controlled by the simulated management; the rate actually applied to simulated populations was $F_t = q \bar{F}_t$. Thus, F_t equaled \bar{F}_t when catchability was constant, and F_t exceeded \bar{F}_t when catchability was density-dependent.

Removals by fishing

Annual catch-at-age ($C_{a,t}$) was computed using the Baranov (1918) catch equation,

$$C_{a,t} = \frac{F_{a,t}}{M + F_{a,t}} N_{a,t} [1 - \exp(-M - F_{a,t})]. \tag{8}$$

The corresponding yield in weight (Y_t) was computed from catch-at-age and weight-at-age as,

$$Y_t = \sum_a C_{a,t} W_a. \tag{9}$$

Recruitment

To compute the number of recruits (R_t), we used a Beverton–Holt spawner–recruit function, modified to allow for depensation (Thompson, 1993; Liermann and Hilborn, 1997),

$$R_{t+1} = \frac{\alpha S_t^\gamma}{\beta^\gamma + S_t^\gamma}. \tag{10}$$

Here, α is the asymptotic level of recruitment, β the half-saturation coefficient, γ a parameter controlling degree of depensation, and S_t the female spawning-stock biomass assuming a 50:50 sex ratio, computed each year as

$$S_t = \sum_a 0.5 N_{a,t} m_a W_a. \tag{11}$$

When $\gamma = 1$, Equation (10) is the usual Beverton–Holt function

with no depensation, and when $\gamma > 1$, the function includes depensation.

Simulations used two different sets of parameter values for Equation (10), one with depensation ($\gamma = 2$) and one without ($\gamma = 1$). The two were made comparable via the parameterization of Liermann and Hilborn (1997), which solves for the usual Beverton–Holt parameters (α' , β'), given a set of depensatory Beverton–Holt parameters (α , β , γ). The parameterization scales the two stock–recruit curves for similarity by equating them at the maximum observed spawner level S^* and also at $S^*/2$. Using the Liermann and Hilborn (1997) parameterization,

$$\alpha' = \frac{0.5zR^*}{z - 0.5}, \tag{12a}$$

$$\beta' = \frac{0.5(1 - z)S^*}{z - 0.5}, \tag{12b}$$

where R^* is the recruitment level at S^* and z is defined by

$$z = \frac{1}{R^*} \frac{\alpha(0.5S^*)^\gamma}{\beta^\gamma + (0.5S^*)^\gamma}. \tag{13}$$

We assumed S^* to be the product of asymptotic recruitment (α) and spawners per recruit at $F = 0$. We arbitrarily let $\alpha = 100$, and we assumed that half the asymptotic recruitment (0.5α) would be produced by 25% S^* , equivalent to assuming $\beta = 0.25 S^*$ (Figure 1c).

Equation (10) describes deterministic recruitment. To include stochasticity, we applied lognormal process error, $N_{1,t+1} = R_{t+1} \cdot \exp(\nu)$. The random variable ν was drawn from a normal distribution with $\mu = 0$ and $\sigma_R = 0.25$, which led to a coefficient of variation (CV) in recruits of approximately $CV_R = 25\%$.