

How long can fisheries management delay action in response to ecosystem and climate change?

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Abstract. Sustainable management of fisheries is often compromised by management delaying implementation of regulations that reduce harvest, in order to maintain higher catches in the short term. Decreases or increases in fish population growth rate driven by environmental change, including ecosystem and climate change, affect the harvest that can be taken sustainably. If not acted on rapidly, environmental change could result in unsustainable fishing or missed opportunity for higher catches. Using simulation models of harvested fish populations influenced by environmental change, we explore how long fisheries managers can afford to wait before changing harvest regulations in response to changes in population growth. If environmental change causes population declines, delays greater than five years increase the probability of population collapse. Species with fast and highly variable population growth rates are more susceptible to collapse under delays and should be a priority for revised management where delays occur. Generally, the long-term cost of delay, in terms of lost fishing opportunity, exceeds the short-term benefits of overfishing. Lowering harvest limits and monitoring for environmental change can alleviate the impact of delays; however, these measures may be more costly than reducing delays. We recommend that management systems that allow rapid responses to population growth changes be enacted for fisheries management to adapt to ecosystem and climate change.

Key words: adaptive management; climate change impact; fishery management; population dynamics.

INTRODUCTION

Fisheries management is plagued historically with failures to limit catches to sustainable levels and this continues in many areas of the world (Worm et al. 2009). Overfishing often occurs despite harvest restrictions recommended by fishery scientists and is driven by strong social and political pressure to maintain the employment and profitability of fisheries (Rosenberg 2003, Fulton et al. 2011). Many fisheries failures may also have coincided with periods of slow fish population growth, driven by changes in ecosystems or climate (Walters and Kitchell 2001, Planque et al. 2010, Eero et al. 2011). In the future human impacts on global climate and marine ecosystems may mean that changes leading to fisheries failure are even more pervasive (Perry et al. 2010), however the interactive effects of climate change, trophic dynamics, and fishing pressure are not well understood. In many cases, climate and ecosystem change may greatly increase the probability of stock

collapse (Perry et al. 2010, Planque et al. 2010) and in other cases they may benefit fisheries productivity (Hamilton et al. 2004, Brown et al. 2010, Hare et al. 2010).

Environmental change affects population growth on short and long time scales. Year-to-year variation in population growth is common in wild fish populations (Spencer and Collie 1997). For instance, survival of larval fish, and their subsequent contribution to population growth, is strongly influenced by ocean climate through enrichment of nutrients, the concentration of plankton (food for fish), and the retention of larvae in areas with high food availability (Bakun 1996). The often highly variable relationship between spawning biomass and recruitment is a testament to the role year-to-year environmental variability plays in regulating population growth and abundance (Bakun 1996). Ecosystem changes, including predation mortality and prey availability, can also play a strong role in driving population growth variability (see Plate 1). Environmental change can also cause persistent trends in population growth and, therefore, productivity for fisheries. For instance, long-term changes in ocean currents and enrichment affect plankton growth that

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regulates food availability further up the food chain, resulting in changes in fish population growth (Beaugrand and Kirby 2010, Brown et al. 2010).

Adapting fishery management to environmental change in fish populations is critical for the sustainability of communities that depend on fisheries (Hamilton et al. 2004, Allison et al. 2009). Environmentally driven changes in population growth can be challenging to manage; they may be unexpected, and thus there would be insufficient time to implement appropriate management measures. Walters and Parma (1996) show that a constant exploitation-rate strategy (so that catch varies year to year depending on population size) is robust to climate-driven increases and decreases in stock productivity. However, social and political pressure can cause lengthy delays between when fisheries scientists advise that catches need to be reduced and when catch reductions are implemented by managers (Shertzer and Prager 2007). Delays may also result from the time taken to assess stock status, or undetected changes in stock status. Delays in reducing harvest limits in over-fished fisheries have negative consequences for long-term harvests and population persistence (Shertzer and Prager 2007). For instance, in the southeast Australian fishery for orange roughy (*Hoplostethus atlanticus*), it took at least five years to implement the catch limits recommended by scientists (Bax et al. 2003). By this time several stocks had already collapsed.

The example of orange roughy is extreme, because this slow-growing species is susceptible to overfishing. However, if delays were to occur during worsening environmental conditions, even species that are considered to be well managed and robust to overfishing could be susceptible to collapse. Here we explore how delays in management interact with environmentally driven changes in population growth to impact the sustainability and viability of fisheries. We begin with a review of the causes and lengths of delays in fisheries management. We then develop a simulation model and explore how delays in the decision to change catches in response to changes in population growth influence viability of fishing operations. We explore management approaches to both population-growth increases and decreases, because in many fisheries the impacts of climate and ecosystem change are uncertain. We show that the long-term cost of delay exceeds the short-term benefits of continued fishing.

METHODS

Initially, we searched the peer-reviewed literature and scientific reports for evidence of delays in setting harvest limits. Our review is not exhaustive but is provided to illustrate the lengths and causes of delays in management action. Based on the review, we devised a simple simulation model to illustrate consequences of management delays under environmental change. Our simulation model has three components. The first component uses the Schaefer model (Hilborn and Walters 1992) to represent a harvested population. The intrinsic popula-

tion growth rate was varied annually to represent changes in environmental conditions. The second component represents the standard monitoring of the population (using catch per unit effort) by fishery scientists and their recommendation of sustainable catch limits based on biomass reference points. The third component represents the management decisions on and delay in implementing the scientifically recommended harvest. Below we describe each component of our simulation model and detail different scenarios investigated using this model.

Population model

We use the difference equation formulation of the Schaefer model to simulate change in biomass over time:

$$B_t = B_{t-1} + B_{t-1}r_t \left(1 - \frac{B_{t-1}}{K}\right) - H_t \quad (1)$$

where B_t is the biomass at time t , K is the biomass at carrying capacity, r_t is the intrinsic population growth rate at time t (the population growth rate at small population sizes), and H_t is the harvest at time t (see *Population monitoring...*, below). We also tried other population models (Ricker, Beverton-Holt difference equation), however results were qualitatively similar. We consider the population to be collapsed if biomass falls below 5% of the carrying capacity and the simulation was ended for any collapsed population. The 5% threshold was chosen on the basis of Hutchings' (2001) meta-analysis that showed stocks that decline by 95% show little recovery even after 15 years of reduced fishing mortality. We investigated other collapse thresholds in a sensitivity analysis, where lower collapse thresholds represent species better able to recover from overfishing. However, we only present results for the 5% threshold in the main text because results were qualitatively similar for other thresholds (Appendix: Fig. A1).

We model the intrinsic population growth rate, r_t , dynamically to represent effects of environmental change on fish population dynamics. Changes in r_t represent variability in recruitment and mortality, and ultimately affect fishery productivity. This approach allows us to consider, in a general way, effects of environmental change, on any species (e.g., Spencer and Collie 1997), including recruitment variability caused by oceanographic variability and changes in predation of adults or larvae. Our model of changes in r_t through time captures two interrelated components of environmental variation of interest here: short-term year-to-year stochastic variation and persistent long-term trends.

To model environmental effects on population growth, r_t is selected from a normal distribution, which allows control of the year-to-year variability in r_t and the rate and direction of change in its long-term trend:

$$r_t = r_0 + vt + \omega_t \quad (2)$$

where r_0 is the initial mean of the intrinsic rate of natural

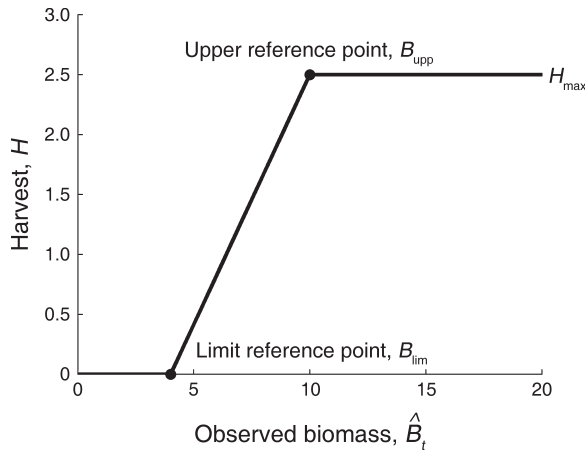


FIG. 1. Rule for scientifically recommended harvest. Reference points are indicated with solid circles. The limit reference point indicates the observed biomass below which harvesting is 0, and the upper reference point is the biomass above which harvest is constant at H_{\max} .

increase, v is the rate of change in r_t , and ω_t is a normally distributed random variable with mean of 0 and standard deviation ∂_r . Thus the mean r changes linearly through time. The rate of change in r_t was varied to illustrate different magnitudes and directions of long-term impacts. The intrinsic population growth rate could take negative values that would incorrectly result in population growth if $B_t > K$, however this situation never occurred due to harvesting. We also ran the model with autocorrelated noise in r_t (using equations from Walters and Parma 1996) superimposed on the long-term trend, rather than white noise.

Under the Schaefer model, per capita population growth increases linearly as population size decreases. In reality, population growth may be much less at small population sizes, due to depensation effects (Stephens and Sutherland 1999). For instance, breeding densities can be lower than a critical threshold required for successful fertilization or fishing to small population sizes can remove older more productive individuals from the population. To explore effects of depensation in our model in a general way, we added a single depensation parameter to the Schaefer model, which reduced per capita population growth when population size is below a threshold (Gregory et al. 2010). The Schaefer model with depensation was thus

$$B_t = B_{t-1} + B_{t-1}r_t \left(1 - \frac{B_{t-1}}{K}\right) \left(\frac{B_{t-1} - A}{B_{t-1}}\right) - H_t \quad (3)$$

where A is the depensation parameter.

Population monitoring and scientific recommendations of harvest

In the fisheries of many nations scientifically recommended harvest amounts are tied to biomass reference points. The scientifically recommended harvest in our

model was tied to a limit and upper reference point (Fig. 1), where recommended harvest each year is given by

$$H'_t = \begin{cases} 0 & \text{if } \hat{B}_t < B_{\text{lim}} \\ H_{\max} \left(\frac{\hat{B}_t - B_{\text{upp}}}{B_{\text{upp}} - B_{\text{lim}}} + 1 \right) & \text{if } B_{\text{lim}} \leq \hat{B}_t \leq B_{\text{upp}} \\ H_{\max} & \text{if } \hat{B}_t > B_{\text{upp}} \end{cases} \quad (4)$$

where \hat{B}_t is observed biomass, B_{lim} is the limit reference point, B_{upp} is the upper reference point, and H_{\max} is the maximum harvest. We used the harvest at maximum sustainable yield (MSY, which, despite criticism, remains a common target for harvest; Mackinson et al. 2009) for maximum harvest and varied this in sensitivity analyses. As maximum sustainable yield was calculated using the initial value of r , the harvest recommendations assumed constant environmental conditions, a common assumption in stock assessments (Brander 2010). Positive values of the depensation parameter, A , increase the biomass at maximum sustainable yield and reduce the MSY slightly. We adjusted the reference points and MSY to account for these shifts in simulations with non-zero values of A . We also conducted scenarios where the r used to calculate MSY was varied; they are described below.

Observed biomass was calculated assuming data on harvest, effort, and an estimate of catchability were available:

$$\hat{B}_t = (H_t/E_t\hat{q})e^{\varepsilon_t} \quad (5)$$

where E_t is effort, \hat{q} is the estimate of catchability, and ε_t is randomly distributed, normal observation error, with standard deviation ∂_{obs} . Estimated catchability took a fixed value of 1, but we allowed the true catchability, q_t , to vary in sensitivity analyses (Shertzer and Prager 2007), such that

$$q_t = B_t^{-\psi} K^{\psi} \quad (6)$$

where ψ determines the steepness of the increase in actual catchability as biomass declines. Increases in catchability as a population declines may occur in schooling species and may be a significant cause of stock collapse, because biomass is overestimated (Pitcher 1995). We assumed that effort was measured accurately; thus to ensure effort was consistent with harvest, biomass and the true catchability:

$$E_t = H_t/(B_t q_t). \quad (7)$$

Therefore, if $q_t > \hat{q}$ biomass will be overestimated.

Model of management-decision delays

To explore the impact of delays in management decisions on scientifically recommended harvest we prespecified the length of delays in each of our simulations. For our main analysis, delays were asymmetrical: action on recommended reductions in harvest was delayed, but immediate action was taken on recommended increases. This represents asymmetry in

TABLE 1. Parameter values for scenarios from a literature search, variables in the model, and relevant equations.

Parameter/variable	Values†	Units	Reference/equation
Parameters			
Carrying capacity, K	20	Biomass units	assumed, fixed
Threshold for population collapse	5 (1–20)	% of B_0	Hutchings (2001)
Initial intrinsic population growth rate, r_0	0.5 (0.05, 0.25, 0.5)	per year	Caddy (2004)
Mean change in r over 50 years (used to calculate v)	–50, 0, +50	% of r_0	assumed, varied
Standard deviation of intrinsic population growth rate, ∂_r	0.15 (0–0.7)	NA	Spencer and Collie (1997)
Autocorrelation coefficient	0 (0–1)	NA	assumed, varied
Depensation parameter, A	0 (0–5)	biomass	Gregory et al. (2010)
Maximum harvest, H_{\max}	H_{MSY} ($0.25H_{\text{MSY}} - 1.2H_{\text{MSY}}$)	biomass	assumed, varied
Upper reference point, B_{upp}	50 (30–130)	% of K	assumed, varied
Limit reference point, B_{lim}	20 (0–49)	% of K	assumed, varied
Observation error standard deviation, ∂_{obs}	0.2 (0–0.5)	NA	Punt et al. (2008)
Estimated catchability, \hat{q}	1	units effort per unit of biomass	assumed, fixed
Catchability steepness, Ψ	0 (0–0.3)	NA	Shertzer and Prager (2007)
Management delay, D	0 to 15	years	Table 1
Initial harvest, H_1	H_{MSY}	biomass	assumed, fixed
Initial biomass, B_1	B_{MSY}	biomass	assumed, fixed
Variables			
Biomass at time-step, B_t	NA	biomass	Eqs. 1 and 3
Observed biomass at time-step, \hat{B}_t	NA	biomass	Eq. 5
Intrinsic population growth rate at time step, r_t	NA	per year	Eq. 2
Harvest as time-step, H_t	NA	biomass	Eq. 8
Scientifically recommended harvest at time-step, H'_t	NA	biomass	Eq. 4
Effort at time-step, E_t	NA	units of effort	Eq. 7
True catchability at time step, q_t	NA	units of effort per unit of biomass	Eq. 6
Years since harvest was last changed, x_t	NA	years	Eq. 8
Observation error at time-step, ε_t	NA	NA	Eq. 5

Note: “NA” indicates not applicable.

† Parameter values for scenarios were assumed where no literature values were available, and key assumptions were tested by varying parameter values. Ranges in parentheses indicate values tested in sensitivity analyses.

management decisions towards favoring politically acceptable decisions (Botsford et al. 1997). For instance, in the past, management of the Atlantic Canadian ground-fish stocks worked on a rule of decreasing catches by 50% of the amount recommended by scientists, but always increasing catches by the full amount (Charles 1998). Delays may also occur because of lags in the stock-assessment process, in which case they would be symmetrical. Consequently, we also examined the effect of symmetrical delays on results.

A delay of 0 years meant that harvest each year was the same as the scientifically recommended harvest for that year. A delay of D years meant that harvest limits were reduced only if the scientifically recommended harvest remained below the current year’s harvest for D consecutive years. In the intervening years, the harvest limit was held constant. If the scientifically recommended harvest in a year was greater than last year’s harvest, harvest was increased and the count of years contributing to the delay was reset. Once the pre-specified delay period was reached, the observed biomass in the most recent year is used to calculate the harvest taken that year. In simulations with symmetrical delays, increases

were also delayed until recommended harvest was greater than current harvest for the pre-specified number of years. The algorithm for calculating yearly harvest in the case of asymmetrical delays is

$$\begin{aligned}
 H_t &= H_{t-1}, x_t = x_{t-1} + 1 && \text{if } x_{t-1} < D, H'_t < H_{t-1} \\
 H_t &= H'_t, x_t = 0 && \text{if } x_{t-1} < D, H'_t \geq H_{t-1} \\
 H_t &= H'_t, x_t = 0 && \text{if } x_{t-1} = D
 \end{aligned}
 \tag{8}$$

where D is the prespecified length of delay and x_t is the number of years since harvest was last changed.

Scenarios

Initially, we present results for a single simulation, to illustrate the model’s dynamic properties. We then present results for a representative set of parameter values (Table 1). Each model simulation is stochastic, so we calculate results across 5000 simulations. Simulations were initialized with biomass at the biomass of maximum sustainable yield (B_{MSY}) and a harvest of H_{MSY} , to represent a fish stock that is initially sustainably managed. We calculate the probability of collapse over 50-year simulations, because this represents an adequate time period to study

the effects of trends in population growth on fisheries collapses. Delays ranged from 0 to 15 years in each set of 5000 simulations. All results are presented for three environmental-change scenarios, a linear decrease in mean r , no change in mean r , and a linear increase in mean r . We also calculate the mean of summed harvest over 50 years and mean variability within 50-year simulations for each set of 5000 simulations.

We explore sensitivity of probability of collapse and summed harvest to key biological and management parameters. We only present sensitivities in situations where mean r declines, because results showed these conditions have the most severe implications for management. In initial sensitivity analyses we varied each parameter of interest between high and low values (Table 1) while keeping other parameter values fixed. Sensitivities to biological parameters were used to identify species life-history traits that may make a fishery more susceptible to collapse under delays. Analyses covered species that have slow or fast population growth rates, greater variability and autocorrelation in population growth rate, depensation effects and show increased susceptibility to fishing gear at low population sizes.

In the model, three key management parameters could be used to reduce the probability of collapse when delays are unavoidable: maximum harvest, the limit reference point, and the upper reference point (Fig. 1). Observation error is also partly under the control of managers who have the choice of investing more resources into fishery surveys. We conducted sensitivity analyses to identify which of these parameters is the most effective for control of both harvest and probability of collapse. We then conducted crossed sensitivity analyses, where we co-varied management parameters and biological parameters. These analyses were used to find management options that compensate for delays and are robust across different types of fish species.

Delays in management action in response to environmental change are expected to reduce long-term harvest and increase the risk of population collapse. We calculated the reduction in harvest required to achieve a target probability of population collapse under differing lengths of delays. Reductions in harvest were achieved by reducing H_{\max} . To calculate the harvest loss required to achieve a fixed probability of collapse under a delay, we varied H_{\max} between high and low values (Table 1) and then numerically found the value that gave the desired probability of collapse. We also compared the reductions in harvest required when the estimate of r used for calculating H_{\max} was monitored over time. Monitoring of r_t was modeled by updating the estimate of r each year as the mean of the previous five years. In reality, most fisheries scientists do not use an estimate of r for calculating harvest parameters, but rather use estimates of recruitment and mortality from stock assessments. However, our simple formulation represents these parameters without adding unnecessary complexity to the model.

RESULTS

Causes and lengths of delays

We found that management delays are pervasive and commonly recognized by fishery scientists, although their cause was rarely reported. Delays in acting on population declines may be caused by sociopolitical, institutional, and ecological factors (Table 2). Longer delays, of up to 25 years occurred when social pressure meant managers were reluctant to reduce harvest limits despite evidence of population declines. In some fisheries, stock assessments can take a considerable amount of time, resulting in delays between data collection and catch changes. These institutional factors could cause delays of up to 5 years. The final cause of delays we found in the review was related to scientific uncertainty. If the status or productivity of a fish population is uncertain, such as in the case of orange roughy, managers may be more reluctant to reduce catches.

Example simulation

Two simulations, one with no management delay and another with a 10-year delay, and both with a 50% decline in the mean intrinsic population growth rate, r , were conducted to illustrate model properties. Delays in management action resulted in collapse of the fish population. Catch was varied less often in the simulation with a 10-year delay resulting in more stable harvests in the short-term (compare the dashed line in Fig. 2B and C). However, with a 10-year delay larger changes are necessary in the long-term to account for overfishing. In situations where the intrinsic population growth rate decreases, delays tend to result in lower population biomasses over time and higher probabilities of population collapse. From the example simulations, the population with delayed management collapses after 31 years due to overfishing in a period of low population growth (Fig. 2C).

Impacts of delays

Overall, delays in acting on scientific advice to reduce harvest caused increases in the probability of collapse (Fig. 3). Increases in probability of collapse were more severe with long-term declines in mean r , while long-term increases in population growth compensated for delays in management action. When population growth declined, there was minimal effect on harvest over 50 years if delays were short (e.g., less than five years), but there was on average a 40% drop when delays reached 15 years (Fig. 4A). In contrast, when population growth increased, delays had much less of an effect, with long-term harvest only 5% lower even with 15-year delays (Fig. 4C). Lower harvests under delays were a consequence of the increased risk of collapse and overfishing during periods with poor environmental conditions. Delays also increased variability in harvest (Fig. 4D–F), indicating that in the long-term, greater numbers of small harvest adjustments result in more stable catches

TABLE 2. Examples of delays in implementing management action on harvest changes recommended by scientists.

Species/fishery	Delay†	Cause	Reference
Multispecies lake fishery of piscivores and benthivores; Lake IJsselmeer, the Netherlands	15–25 years, ongoing (as of 2008)	effort reductions delayed to reduce short-term losses in profit to fishers	de Leeuw et al. (2008)
Australian Commonwealth fisheries	3–5 years	policy requirement for turnover in strategic assessments	Smith et al. (2008)
North Pacific Minke whale (<i>Balaenoptera acutorostrata</i> , Balaenopteridae)	12 years	scientific uncertainty led to a long process to calculate catch limits	Punt and Donovan (2007)
Whales	5 years	time period required between reviews of management strategy by the International Whaling Commission	Punt and Donovan (2007)
Orange roughy (<i>Hoplostethus atlanticus</i> , Trachichthyidae); South-East Australia	5–7 years	biological uncertainty meant a lengthy debate over sustainable catch limits	Bax et al. (2003)
European eel (<i>Anguilla Anguilla</i> , Anguillidae); multiple river basins in Europe	not reported, but ICES has repeatedly recommended that a recovery plan is needed.	not clear from report	ICES (2005)
Herring (<i>Clupea harengus</i> , Clupeidae); North Sea and Skagerrak (ICES Subareas IV and IIIa)	5 years	not specified	ICES (2008)
Atlantic Cod (<i>Gadus morhua</i> , Gadidae); North Sea and Skagerrak (ICES Subareas IV and IIIa)	8 years, ongoing (as of 2009)	not specified	ICES (2008)
Elasmobranchs; North Sea (ICES Subarea IV)	2 years	stock assessments provided every two years	ICES (2008)

† Delays from the ICES (2008) report were calculated by comparing the timeline of ICES advice with the actual regulations set by managers.

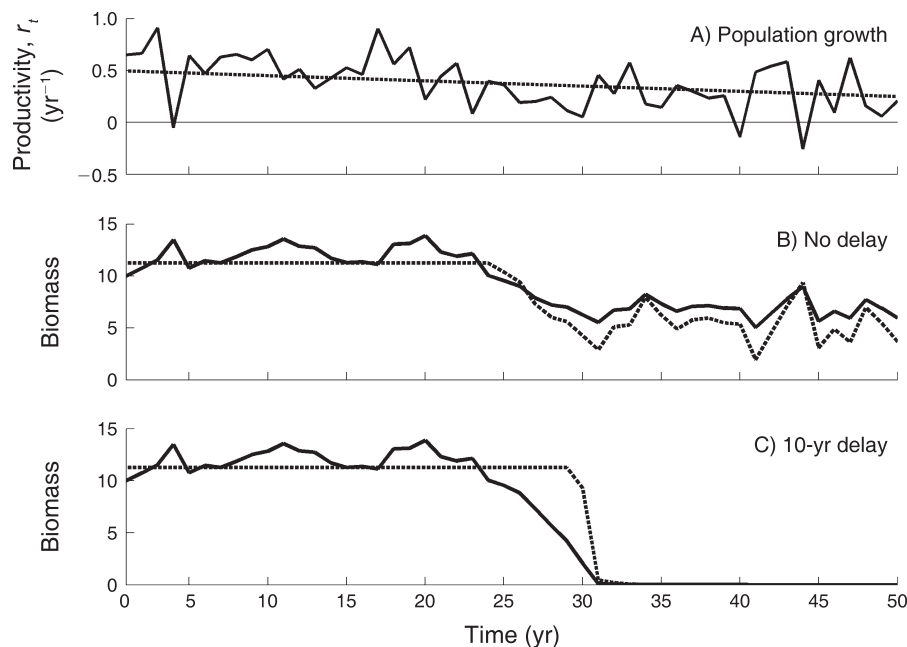


FIG. 2. Example of a fished population simulated with environmental effects on the intrinsic population growth rate at time t , r_t . (A) Productivity (r_t) over the simulation period (solid line); r_t was set for a mean decline of 50% over 50 years (dotted line). (B) A simulation with no management delay; catches (dotted line) closely follow biomass (solid line). (C) A 10-yr management delay means that catches are more stable in the short term, but overfishing requires larger changes in the medium term and eventually results in population collapse after 31 years. Catch biomass is multiplied by 4.5 for ease of viewing.

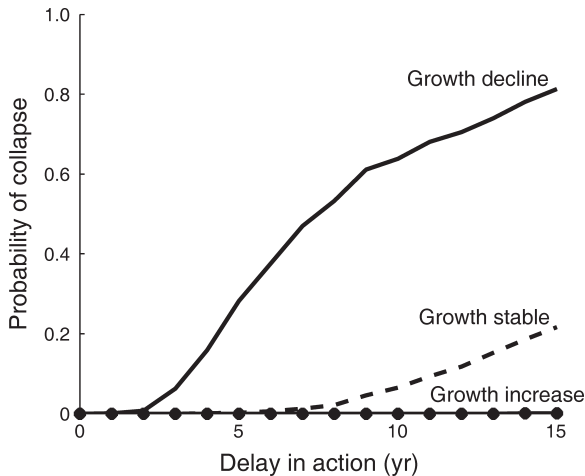


FIG. 3. Probability of collapse increases under longer management delays, with 50-year declines in mean r_t (-50% , solid line) causing higher probabilities of collapse than when mean r_t is stable (dashed line). When mean r_t increases ($+50\%$, solid line with points) the probability of collapse is close to 0.

than fewer harvest adjustments, which must be very large. Increases in harvest variability were particularly great when population growth declined (Fig. 4D).

For simulations with symmetrical delays (delays on harvest increases and decreases) and increasing or stable population growth, the probability of collapse is similar to simulations with asymmetrical delays, although the overall probabilities are lower (Appendix: Fig. A2). For declines in population growth, increases in delay cause a nonmonotonic pattern in probability of collapse. Delays of 8 to 11 years initially result in overfishing in the first decade of each simulation but are unlikely to cause collapse in this time frame. If action to increase harvests is delayed, the population has time to recover before fishing resumes. This causes the drop in probability of collapse across simulations with delays from 8 to 11 years. This situation is unlikely to occur in reality because symmetrical delays will tend to be caused by gaps in assessments and thus be less than 8 years. Total harvest losses with delays are similar for simulations with and without delays on increases (Appendix: Fig. A3). For very long delays and increases in population growth, variation in total harvest is very low because harvest can only be increased several times in the 50-year period of the simulations.

Comparison of simulations with slow-, medium-, and fast-growing species indicated that slower-growing species have lower rates of collapse when compared to

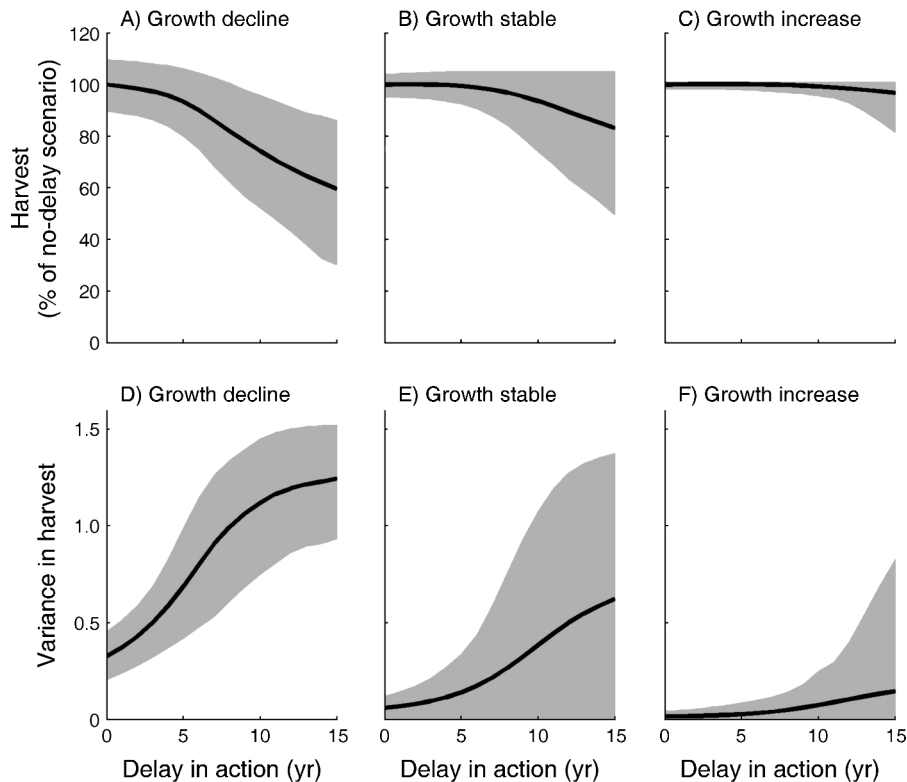


FIG. 4. Long-term cumulative harvest is generally lower under longer management delays, with (A) 50-year declines in mean r_t (-50%) resulting in lower harvests than when mean r_t is (B) stable or (C) increasing ($+50\%$). Variability in year-to-year harvest increases most when management delays are longer and when (D) mean r_t declines than when mean r_t is (E) stable or (F) increasing. Results for summed harvest are shown relative to the simulation with no delays. Black lines are means across simulations, and gray shaded bands represent the 10% and 90% quantiles.

TABLE 3. Qualitative sensitivity of long-term harvest and probability of collapse to key model parameters and their interactions with the length of delay.

Parameter	Qualitative sensitivity			
	Harvest		Pr(Collapse)	
	Short delay	Long delay	Short delay	Long delay
Fishery and biological				
Std. intrinsic population growth rate, ∂_r	↓	↓↓	↑	↑↑
Auto-correlation coefficient	0	0	0	0
Observation error, ∂_{obs}	↓	↓	↑	↑
Depensation, A	↓	↓↓	↑	↑↑
Catchability steepness, Ψ	↓	↓	↑	↑
Threshold for population collapse	0	0	↑	↑
Management				
Limit reference point, B_{lim}	0	0	0	↓
Upper reference point, B_{upp}	∩	↑	↓	↓↓
Maximum harvest, H_{max}	∩	∩	↑	↑↑

Notes: Key to symbols: “↓” indicates a decline in the property as the parameter increases, while “↑” indicates an increase; “0” indicates no change, “∩” indicates a nonlinear increase then decrease; “↓↓” and “↑↑” indicate strong interactive effects between the parameter and the length of delay, such that harvest or probability of collapse became more sensitive to the parameter when delays were longer. Parameter values for sensitivity analyses are given in Table 1.

faster-growing species over the same time period. If simulations were run for 50 generations (i.e., simulation length = $50/r_0$ [r_0 = initial mean intrinsic rate of natural increase]), then qualitatively similar results are found for fast- and slow-growing species, indicating the results presented here are general if considered in terms of number of generations.

Sensitivity analyses for key biological parameters indicated the potential for some non-linear and interactive changes in harvest and probabilities of collapse when biological parameters and lengths of delay were covaried (Table 3). The standard deviation of intrinsic population growth rate and the depensation parameter had interactive effects with the length of delay. Higher variance in the intrinsic population growth rate caused lower harvests and higher probabilities of collapse, because periods of low population growth were more likely to occur (Table 3; Appendix: Fig. A4). Stronger depensation reduces a population’s capacity to recover from overfishing, causing increased probabilities of collapse under long delays (Table 3; Appendix: Fig. A5).

Alternative management measures that accommodate delays

Below we explore the effects of changing the reference points and maximum harvest parameters in simulations with a decline in intrinsic population growth rate. Changing the limit reference point had little effect on probability of collapse and harvest, unless it was set to 0, at which point the probability of collapse increased and harvest decreased as a result (Table 3; Fig. 5A and D). Thus, this parameter is not useful for compensating for delays. Changing the upper reference point reduced the probability of collapse and had a nonlinear effect on harvest (Table 3, Fig. 5B and E). Harvest increased initially if the upper reference point was increased, reflecting the long-term benefits of more conservative

harvest limits. Increasing the upper limit reference point to very high values means harvests will be more conservative, and high values of this parameter caused lower harvests. However, under long delays, increasing the upper reference point had only positive effects on harvest, within the parameter range tested. The probability of collapse decreased as the maximum harvest limit was decreased and harvest peaked for intermediate values (Table 3; Fig. 5C and F). Changes to the maximum limit were an effective way to compensate for long delays, and the optimal harvest occurred at lower maximum harvest limits if delays were longer.

Increasing observation error reduced the effectiveness of the reference points as controls on harvest and probability of collapse (Fig. 5A, B, D, and E), because drops in population size below the reference points were unlikely to be detected. Limiting the maximum harvest was a much more effective control on harvest and probability of collapse, even for long delays (Fig. 5C and F).

Crossed sensitivity analyses between management parameters and key biological parameters also demonstrate that changing the maximum harvest is the most effective way to adjust management for different types of fisheries. For stronger depensation and higher year-to-year variation in population growth rate, changing the maximum harvest was the most effective way to compensate for long delays (Appendix: Figs. A6 and A7). The upper reference point was also effective but only in scenarios with low observation error (Appendix: Figs. A8 and A9).

We explored how reducing harvest, by varying the maximum allowed harvest, could be used to offset the impact of delays on the probability of collapse. If the long-term goal is to keep probability of collapse at 5% or less, required reductions in harvest are relatively small (<5% over 50 years) for delays <5 years under all

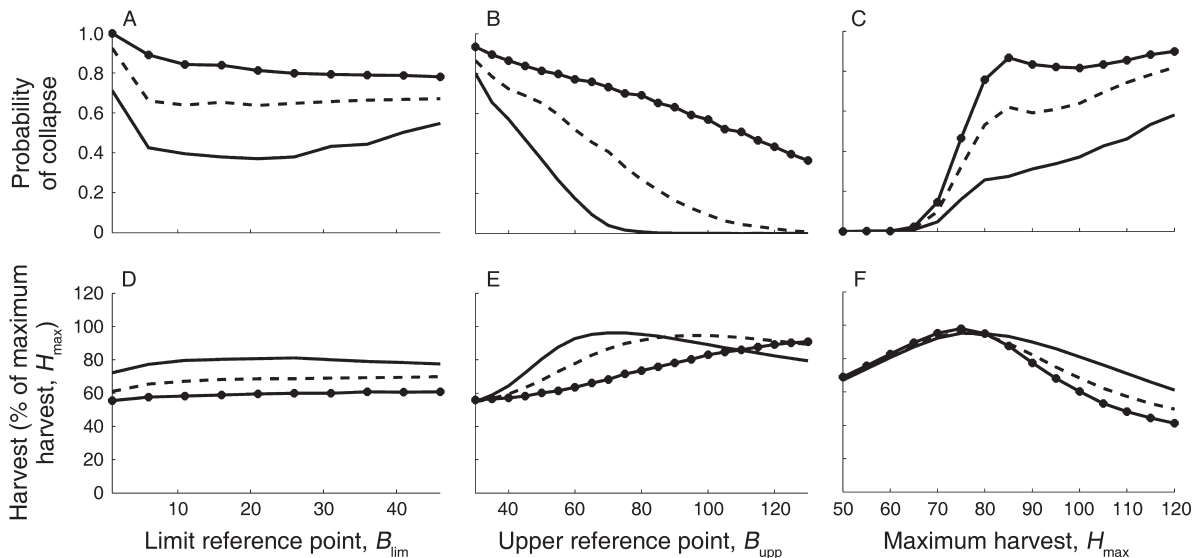


FIG. 5. The effect of varying (A, D) the limit reference point (B_{lim}), (B, E) the upper reference point (B_{upp}), and (C, F) maximum harvest (H_{max}) on (A, B, C) the probability of collapse and (E, F, G) the cumulative harvest for different levels of observation error with a 10-yr delay. Results for summed harvest are shown relative to the simulation with no delays. Shown are simulations with no observation error (solid line), intermediate observation error (dashed line, $\delta_{obs} = 0.2$), and high observation error (solid line with points, $\delta_{obs} = 0.5$).

scenarios for changes in population growth (Fig. 6A–C). For longer delays, 15% of harvest was lost to compensate for delays under population growth declines and 5–10% if population growth is constant or increasing.

Long-term monitoring of population growth and updating of harvest reference points to account for changes may mean fewer reductions in harvests to compensate for delays. Adjusting harvest limits under population growth declines reduced long-term harvest losses, particularly under long delays (Fig. 6D–F). However, additional reductions of 10% were still required to counteract for the effect of long delays (Fig. 6B). Monitoring and updating of harvest limits had much less effect when population growth did not change in the long term, although even then less long-term harvest was lost. When population growth increased, the updating of harvest limits actually led to greater lost harvest, as limits were less conservative and greater reductions in harvest are required to compensate for management delays. This result indicates that maintaining conservative harvest limits, even when evidence indicates population growth is increasing, results in higher longer-term catches.

DISCUSSION

Current fisheries management paradigms are based on equilibrium assumptions (Brander 2010). Climate change, environmental regime shifts, and changes in species interactions will cause long-term changes in fish population growth that, if not accounted for, may increase the chance of stock collapse. We have shown here that even in fisheries managed with a precautionary reference point system (Deroba and Bence 2008), delays

in acting on declines in population growth can significantly increase the risk of collapse. Further, harvests will be lower and more variable over the long term when managers delay action, defeating the common short-term goal of maintaining high catches in the face of population declines. These results suggest that even when little is known about long-term population growth changes for a particular fishery, avoiding management delays can greatly reduce the risk of collapse and improve long-term harvests.

Achieving reduced delays will be challenging, and requires greater understanding of the factors leading to delays in fisheries. Our review of the literature indicates that causes of delays vary greatly (Table 2), however, social pressures were often involved. For instance, delays may often stem from social pressure to maintain current harvest limits when scientific recommendations to reduce harvest are uncertain (Botsford et al. 1997).

We could find no clear examples of actions taken by managers specifically to reduce delays, however there are potentially two main strategies to overcome the social pressures that lead to delays. The first is to implement stronger top-down governance and enforcement of harvest changes. Past experience has shown that maintaining these structures is challenging, because strict enforcement can often create unexpected incentives, such as the race to fish in fisheries managed only on a total allowable catch quota system (Costello et al. 2008). The second is to create incentives for sustainable fishing practices. A recent review shows that globally those fisheries where fishers, managers, and scientists cooperate to manage harvest are less likely to be overexploited (Gutierrez et al. 2011). For instance,

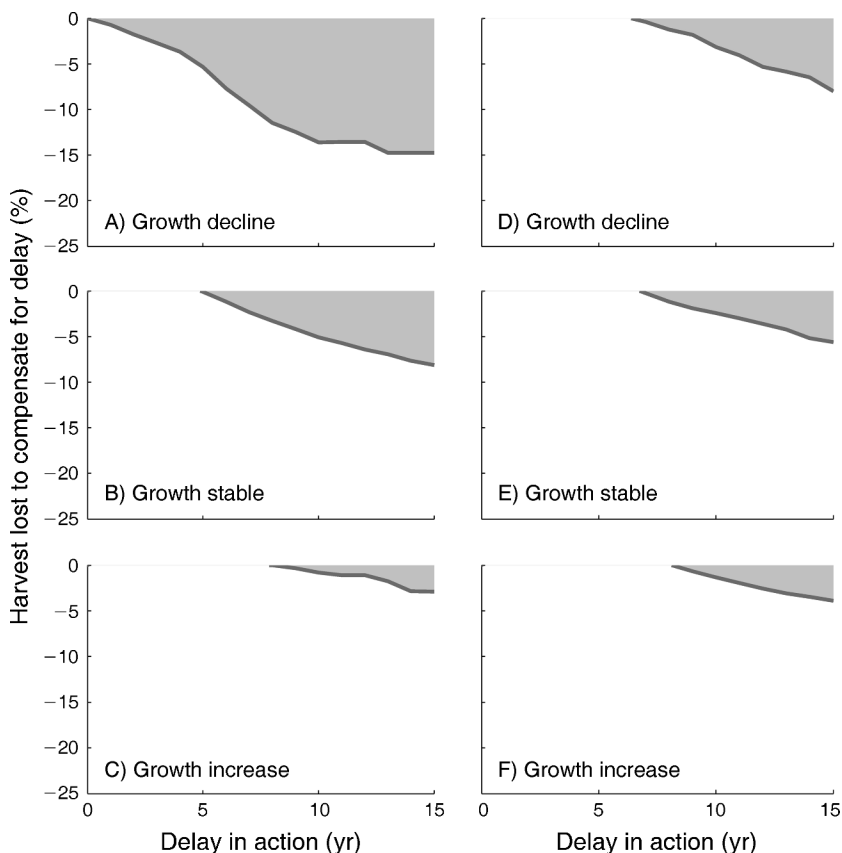


FIG. 6. Harvest reductions (%) required to maintain the probability of collapse at 5% (A, B, C) with and (E, F, G) without monitoring of r_t . (A) 50-yr declines in mean r_t (-50%) require greater reductions in harvest than when mean r_t is (B) stable or (C) increasing ($+50\%$). Monitoring r_t results in more accurate scientific recommendations, resulting in lower harvest losses when mean r_t (D) declines or (E) is stable. (F) Updating scientific recommendations causes greater harvest losses when mean r_t increases because harvest limits are less conservative as growth increases. Results are relative to the harvest in the simulation with no delays. The gray shaded area illustrates the difference from no harvest loss.

assigning territorial rights to fishing communities can remove incentives for racing to meet harvest quotas by creating ownership of fishing resources and encouraging self-enforcement among community members (White and Costello 2011). However, the effectiveness of these approaches also depends on fish life history (e.g., White and Costello 2011), so developing approaches effective for reducing delays requires greater collaboration between social and ecological scientists in the future (Fulton et al. 2011).

In many cases, reducing management delays in fisheries may come at a financial cost. For instance, stock assessments are often not annual, and increasing their frequency would require a greater investment in suitably qualified staff. Unobserved population declines would also cause delays that could be reduced by greater investments in monitoring. Therefore, an economic perspective will be valuable for weighing up the relative costs and benefits of reducing delays in management. For well-managed fisheries not at risk of depensation and with low variability in population growth, these

delays are unlikely to fall in the range that we identified as significantly increasing the probability of collapse. Further, in some cases these delays may reduce the probability of collapse because delays on increases in harvest result in more conservative management. Alternative management strategies may be a cost-effective solution in fisheries sensitive to delays in management. Martell and Walters (2002) demonstrate that for some fisheries, monitoring and regulating harvest rate can be more cost effective than monitoring stock size and regulating catch limits. Fisheries managed on a constant-harvest-rate basis will also be more robust to changes in population growth, because there will be no delays between fluctuations in population size and changes in harvest (Walters and Parma 1996).

Species life histories provide some clues for identifying fisheries most susceptible to collapse under management delays, and that are thus priorities for development of alternative management strategies that can reduce delays. Commonly, slow-growing species are more susceptible to overfishing than are fast-growing species



PLATE 1. Mangrove jack (*Lutjanus argentimaculatus*) school on the Great Barrier Reef, Australia. Photo credit: M. I. Saunders.

and will be more likely to collapse if efforts to curb fishing pressure are slow (Shertzer and Prager 2007). However, in our model, species with fast population growth were more susceptible to collapse than slow-growing species. For a fast-growing species that is initially well managed, greater and more rapid changes in harvest limits are required in response to fluctuations in biomass and so tend to result in greater overfishing than those of a slow-growing species, which is initially fished more conservatively (Pinsky et al. 2011). For example, build up of fishing fleets in highly productive fisheries, such as those for North Sea herring, contributes to fishery collapse when fishing effort cannot be significantly reduced in low-growth years (Gislason 1994). Thus, while managers may often consider fast-growing species as less prone to overfishing, our results show they may be more sensitive to delays in acting on population growth declines.

Traits that make a species susceptible to periods of slow population growth also increase the risk of collapse under delays. In our sensitivity analysis, such situations were produced by depensation, and higher variability in intrinsic population growth rate. High variability in population growth may be common in species with short life spans,

high growth rates, low trophic levels, and low ages at maturity—for instance, herring and sardine (Spencer and Collie 1997). Species with more stable abundances may be less susceptible to delays; these include species with long life spans, slow growth, and higher trophic levels (Spencer and Collie 1997). The prevalence of depensation effects is controversial (Gregory et al. 2010); however there is strong theoretical and some empirical evidence that they may occur in fished populations (Liermann and Hilborn 1997, Walters and Kitchell 2001). Species that are likely to show one or a combination of these traits that increase susceptibility to management delays should be a priority for revised management that acts to reduce delays in translating advice into action.

When delays cannot be eliminated, they can be accommodated in a sustainable fishery at the cost of reduced harvests. Previously, focus has often been on biomass reference points, but here these proved less effective controls on probability of collapse under delays, particularly with high observation error. With high observation error, the reference point becomes challenging to estimate. In contrast we found that reducing the upper harvest limit had the strongest and most consistent effects on reducing probability of

collapse and increasing harvest under long delays. Admittedly however, we assumed there was no error in implementation and compliance with maximum harvest, once management applied a new quota. In cases where errors in estimating and regulating harvest are large, the effectiveness of this control will be reduced. The most effective control of harvest under management delays will then be determined by the relative size of the errors in estimating reference points vs. harvest quantities.

In scenarios with long-term stability or declines in intrinsic population growth rate, losses in potential harvest could be offset to an extent by monitoring population growth and accounting for its changes in scientific harvest recommendations. These scenarios reflect the benefits of taking more conservative harvests when there is uncertainty in long-term population growth. However, monitoring is also expensive and the cost of intensive monitoring for management might outweigh the benefits gained (Hansen and Jones 2008). Further work, such as that by Martell and Walters (2002), is needed to consider the relative costs and benefits of monitoring and strategies for implementing alternative management measures in fisheries susceptible to climate-induced impacts.

Future work should consider how unaccounted changes in population growth will affect fishery management and how reference points as well as fishery catches can be updated at appropriate intervals. Changes to the carrying capacity of a population also have the potential to cause fishery collapses if there are delays in acting on environmental change. Though not the focus of this analysis, preliminary simulations showed that allowing carrying capacity to vary in model simulations had similar effects to allowing the intrinsic population growth rate to vary. In reality, changes in carrying capacity and changes in population growth are difficult to distinguish in analysis of fisheries time-series data (Davies and Jonsen 2011). There is, however, the potential for subtle difference between the effects of changes in carrying capacity and changes in population growth. In the harvest-control rules used here, population growth rate and carrying capacity determine the maximum harvest, whereas the reference points are determined as a proportion of carrying capacity alone. This underscores the importance of choosing appropriate baselines for harvest rates and biomass reference points that account for environmental change (Brander 2010).

There is increasing recognition that fisheries systems are dynamic and require management robust to ecological and climatic change. Despite this recognition, inflexible management frameworks promote slow action on population decline and are a neglected factor in fishery collapse. Ideally, delays in management should be minimized to promote long-term persistence and higher catches in fisheries impacted by environmental change. Alternatively, more conservative harvest limits are required to account for long-delays in management

action. Past history shows that such systems are challenging to develop, but critical for long-term sustainability of fishing industries.

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SUPPLEMENTAL MATERIAL

Appendix

Nine figures showing the sensitivity to key parameters of long-term harvest and probability of collapse (*Ecological Archives* A022-018-A1).

ERRATA

Sanz-Lázaro et al. have discovered errors in two of the figures included in their article (“Effect of temperature on biogeochemistry of marine organic-enriched systems: implications in a global warming scenario”), published in the October 2011 issue (*Ecological Applications* 21:2664–2677). The top row of panels in Fig. 3 lacked units for SO_4^{2-} in the published version; the units should have been specified as mmol/L for all three temperatures. Also, the units for the horizontal axis in Fig. 4 were incorrectly given as mmol/cm³; the correct units for AVS and CRS are $\mu\text{mol}/\text{cm}^3$. These errors were apparently introduced by our Graphics Department during preparation of figures for publication. We apologize to the authors and to our readers.

Brown et al. have discovered errors in Table 2 of their paper (“How long can fisheries management delay action in response to ecosystem and climate change?”) in the January 2012 issue (*Ecological Applications* 22:298–310). Two entries in Table 2 may be incorrectly interpreted. The cause under the third row (“North Pacific Minke whales”) should read “scientific uncertainty led to a long process to develop a management scheme, during which catch limits for commercial whaling were zero”.

In addition, the cause in the fourth row (“Whales”) should read “time period required between reviews of management strategy by the International Whaling Commission; this time period was selected using simulations and shown to be adequate”.

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