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Authors
Essington, Timothy
Samhouri, Jameal
Siple, Margaret
et al.

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Author for correspondence:
Adrian C. Stier
e-mail: astier@ucsb.edu

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Avoiding critical thresholds through effective monitoring

Adrian C. Stier[1], Timothy E. Essington[2], Jameal F. Samhouri[3], Margaret C. Siple[1], Benjamin S. Halpern[4,5], Crow White[6], John M. Lynham[7], Anne K. Salomon[8] and Phillip S. Levin[3,9,10]

[1]Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, USA
[2]School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, USA
[3]Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98112, USA
[4]National Center for Ecological Analysis and Synthesis, 1021 Anacapa Street, Santa Barbara, CA 93101, USA
[5]Bren School of Environmental Science and Management, University of California, Santa Barbara, CA, USA
[6]Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407 USA
[7]Department of Economics & UHERO, University of Hawaii at Manoa, Honolulu, HI 96822, USA
[8]School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia Canada, V5A 1S6
[9]School of Marine and Environmental Affairs, University of Washington, Box 355020, Seattle, WA 98195, USA
[10]The Nature Conservancy, 74 Wall Street, Seattle, WA, USA

ACS, 0000-0002-4704-4145; JFS, 0000-0002-8239-3519; MCS, 0000-0002-4260-9856; BSH, 0000-0001-8844-2302; CW, 0000-0002-3141-560X; JML, 0000-0002-5816-9648; PSL, 0000-0003-0611-5688

A major challenge in sustainability science is identifying targets that maximize ecosystem benefits to humanity while minimizing the risk of crossing critical system thresholds. One critical threshold is the biomass at which populations become so depleted that their population growth rates become negative—depensation. Here, we evaluate how the value of monitoring information increases as a natural resource spends more time near the critical threshold. This benefit emerges because higher monitoring precision promotes higher yield and a greater capacity to recover from overharvest. We show that precautionary buffers that trigger increased monitoring precision as resource levels decline may offer a way to minimize monitoring costs and maximize profits. In a world of finite resources, improving our understanding of the trade-off between precision in estimates of population status and the costs of mismanagement will benefit stakeholders that shoulder the burden of these economic and social costs.

1. Introduction

Decision-makers seeking to avoid the collapse of financial, public health or military defence systems often rely on detailed information to manage risk. However, high-precision monitoring of these systems is often costly, requires analysis and storage of large datasets and can delay decision making. In natural resource management, a major question is how much monitoring is needed to maximize the delivery of ecosystem benefits to people while minimizing the risk of species or ecosystem collapse [1–3]?

The status of a species or ecosystem is determined from monitoring or survey data, and assessed relative to one or more minimum thresholds, below which the risk of species or socio-economic collapse surpasses the risk tolerance of management. For example, in the management of a single natural resource like a fishery, management strategies often include lower population limits below which harvest is suspended (i.e. a 'limit reference point'). Thresholds are accounted for in management strategies in the form of decision triggers [4] and in the form of reference points designed to minimize the risk of falling below a productivity threshold [5]. This management threshold is set, in part, because managers recognize that when systems fall below this threshold there is an elevated risk of serious or irreversible harm to populations, ecosystems, economies and societies. Typically, a management threshold is designed to allow sustainable harvest, but also to minimize the chances that a population will cross a biological threshold, below which irreversible harm can occur to a population [6]. When populations are overharvested, they can experience phenomena such as inbreeding depression, predator pits or mate limitation [7], which at critically low densities can lead to population extinction (i.e. an extinction vortex [8]). The consequences of crossing certain thresholds, such as depensatory thresholds, are even greater since depensation can cause irreversible population collapse. The crossing of other thresholds, such as those defined by limit reference points, is often reversible but can also have devastating social and economic consequences [9], particularly when crossing them triggers cessation of harvest or reduced access.

High-precision monitoring can lower the risk of crossing critical thresholds and ensure the delivery of services, but can also be very expensive [2,3]. Even with consistent and intensive monitoring, managers may never have perfect knowledge of how close a population is to crossing a critical threshold, or whether such a threshold exists. For example, Allee effects have long been suspected to occur in fish populations and evidence suggests that they may be the cause of some population collapses, but evidence for these effects can be hard to come by [10,11]. 'Emergent' Allee effects can result from increases in predator abundance even if prey populations remain constant [12]. Even in a case where a threshold is known to exist two factors would prevent managers from knowing how close a stock is to such a threshold. First, shifts in the external drivers that affect natural populations (e.g. the environment) are not always predictable, which means that assessments may not detect the location of a threshold before it is crossed [13]. Second, in any survey, there is measurement error, which even in well-studied populations can be high. Both of these sources of uncertainty mean that an assessment might incorrectly categorize a population as being a 'safe' distance from a threshold, when in reality the population is at or past a threshold beyond which it will take decades to recover. Limited monitoring resources and an incomplete understanding of ecosystems can restrict efforts to devise monitoring strategies that—without crossing a threshold—both maximize ecosystem services and balance risk of harvesting across multiple stakeholders.

Previous studies have emphasized that intensive monitoring is not always beneficial, particularly when such efforts incur high costs that outweigh the management or conservation benefits [3], such as monitoring extremely rare or cryptic threatened species [14], or monitoring a proportion of the population that does not provide a precise index of abundance. Here, we extend these studies by focusing on the value of monitoring information for harvested populations with critical biological thresholds. Our expectation is that the value of monitoring depends not only on how far a population is from the threshold, but also on population state, whereby a population that spends more time close to a critical threshold benefits more from precise monitoring than one that spends time far from it, and that precise monitoring will promote the resilience of degraded populations when they are overexploited. However, these simple expectations may not be fully borne out in a dynamic system. Thus, we seek to explore when and where our expectation holds, and what elements of a natural resource system strengthen the benefit of state-dependent monitoring. We do this by asking four questions:

- (i) How do monitoring precision and harvest rate affect the risk of population collapse and the value of the resource?
- (ii) Does the value of monitoring increase with higher proximity to a critical threshold?
- (iii) Can monitoring allow harvested populations to recover from dangerously low levels?
- (iv) How can managers balance the costs and benefits of monitoring populations prone to collapse?

2. Methods

(a) Closed-loop management strategy evaluation overview

We used a closed-loop management strategy evaluation, a tool that evaluates the likely consequence of applying a harvest strategy, given uncertainty in a system's dynamics [15]. The simulation proceeded in four steps. First, we simulated the biological dynamics of a system. Second, we simulated a monitoring process, where the total biomass of the resource was surveyed with some error. Third, we used an assessment model to simulate the estimation of system biomass based on data from the survey. Fourth, a management model determined the level of resource harvest given the estimated biomass. The harvest was taken out of the true population size each year. The entire process was repeated for a 50-year simulation with 10 000 replicate iterations.

(b) Modelling a natural resource with critical biological threshold

Biological process model*:* to describe how monitoring investment is related to thresholds, we focused on a natural resource system targeting a single species—a management system inspired by a fishery, but is easily transferable to wildlife or forestry resources. We specifically modelled species biomass through time using a reparametrized logistic model with depensation and resource removal [16]. Allee effects are fairly common in animal populations and are thought to occur in fish stocks mainly as a result of predation when prey are at low densities [17]. The model is described as follows:

$$\frac{\Delta B_t}{\Delta t} = rB_t\left(1 - \frac{B_t}{K}\right)\left(\frac{B_t}{K} - \frac{A}{K}\right) - Y_t, \tag{2.1}$$

where r is the intrinsic rate of increase, B_t is the resource biomass in year t, K is the carrying capacity of the resource, A is the theoretical biomass at which the population growth is negative even in the absence of harvest or other removals (i.e. the critical biological threshold, also known as an Allee effect) and Y_t is the yield of harvested biomass at time t (electronic supplementary material, figure S1). The strength of the Allee effect is governed by the value of A. A values ≤ 0 generate scenarios without Allee effects, but low productivity. For example, when $A \cong -500$, the model closely resembles the logistic function. To test the sensitivity of results to stochastic environmental variation, we incorporated environmental variation into our model by examining the role of random temporally uncorrelated lognormal variation in the intrinsic rate of increase, r.

(c) Monitoring and assessment models

Ideally, natural resource managers would have perfect information about resource biomass in a given year (B_{t+1}) based on monitoring of the previous year's biomass (B_t), knowledge about life history and productivity, and some measure of the yield (Y_t). However, managers rely on estimates of biomass (hereafter referred to as $\hat{B}_t$) and often have to make assumptions about the values and uncertainty of certain life-history parameters. The degree to which $\hat{B}_t$ is a precise representation of the true resource biomass (B_t) is determined by monitoring precision. We modelled monitoring (observation) error as a lognormally distributed random variable with mean $-\sigma^2/2$ and variance σ. Hereafter, we refer to monitoring precision by reporting the coefficient of variation (CV) to account for differences in the mean. The degree of monitoring precision in any given system is generally based on the spatial and temporal resolution of monitoring relative to the distribution and dynamics of the resource being harvested. Therefore, at higher monitoring precision (lower σ), $\hat{B}_t$ approaches the true biomass B_t. We assumed that as monitoring becomes less precise, the deviation of the estimated biomass from the true biomass increases exponentially (electronic supplementary materials, figure S1). We also assumed monitoring precision was not autocorrelated and was only dependent upon the current year's monitoring. Note that our simulation of variation in monitoring is focused on precision—variation in estimated biomass ($\hat{B}_t$), not accuracy, which would involve also simulating variation in the mean of estimated biomass ($\hat{B}_t$). Precision is high when monitoring adequately captures the spatial and spatio-temporal distribution of the resource.

(d) Management model

When monitoring data are low resolution, estimates of future biomass can be highly uncertain, which can lead to under- or over-harvesting. To simulate resource harvest in our model, we first calculated the biomass corresponding to maximum sustainable yield of the stock (B_{MSY}), where

$$B_{MSY} = \frac{A}{3} + \frac{K}{3} + \frac{A^2 - AK + K^2}{3}, \tag{2.2}$$

which is a deterministic solution for B_{MSY} under equilibrium conditions. From that we then calculated the maximum sustainable yield (Y_{MSY}) as

$$Y_{MSY} = rB_{MSY}\left(1 - \frac{B_{MSY}}{K}\right)\left(\frac{B_{MSY}}{K} - \frac{A}{K}\right). \tag{2.3}$$

The harvest mortality rate at Y_{MSY} that then produces B_{MSY} is defined as:

$$H_{MSY} = \frac{Y_{MSY}}{B_{MSY}}. \tag{2.4}$$

These estimates of Y_{MSY} and B_{MSY} approximate common reference points in management as the long-term average yield and the biomass that produces it. Our simulated management model implemented an adaptive policy whereby allowable removals are set annually based on estimated population biomass (e.g. [18]). Consistent with many such harvest rules, we introduced a minimum biomass level, here $0.25B_{MSY}$, where no harvest is allowed (i.e. the limit reference point; (e.g. [19])). A generic form of such 'hockey stick' harvest control rules is that the harvest rate in year t, H_t, equals:

$$H_t = H_{\max}\min\left[1, \max\left[0, \frac{\hat{B}_t - B_{\lim}}{B_{\text{tar}} - B_{\lim}}\right]\right]. \tag{2.5}$$

Where $H_{\max}$ is the policy-defined maximum harvest rate (often near the harvest rate that maximizes long-term catch), $B_{\lim}$ is the limit reference point below which no catch is permitted and B_{tar} is the target reference point (often B_{MSY}). Under these control rules, the population is harvested at a specified maximum harvest rate when the estimated population is at or above B_{MSY}, is harvested at decreasing rates as the estimated population falls below B_{MSY} and is set to 0 when the estimated population is below $B_{\lim}$.

The total yield at time t was therefore

$$Y_t = H_t\hat{B}_t. \tag{2.6}$$

This yield was then fed back into the process model described above to determine the true biomass the following year (B_{t+1}) and the model continued for a 50-year simulation. For graphical representation of the management model and examples of 50-year simulations with low and high uncertainty in estimated biomass, see electronic supplementary material, figure S1.

There is no single established value for $B_{\lim}$, but often ranges between near 0 to greater than $0.75B_{MSY}$ for species that have high ecological value like forage fish to values below 0.1 B_{MSY} [19,20]. Here, we chose an intermediate value of $B_{\lim} = 0.25B_{MSY}$, or when $0.25B_{MSY} < A$, we set $B_{\lim} = A$.

We considered variation in harvest pressure that was both less than and greater than harvest rate at maximum sustainable yield by defining maximum harvest rate ($H_{\max}$) as a proportion (p) of the harvest rate at maximum sustainable yield (H_{MSY}):

$$H_{\max} = pH_{MSY}. \tag{2.7}$$

(e) Value of the resource and cost of monitoring

To consider the value and cost of the resource, we used a series of standard expressions in bioeconomic modelling [21]. We estimated the value of the resource extracted at time t (V_t) as

$$V_t = \varphi Y_t - c_e Y_t/B_t, \tag{2.8}$$

where φ is the unit price of the resource and c_e is the cost of extracting that a fraction Y_t/B_t of the total resource at time t (essentially cost per unit fishing effort). If the costs and benefits are borne by the same party then V_t represents profit, but since we consider the costs of monitoring being borne by the same and different parties below, we refer to this loosely as value. We estimated the net present value (NPV) of the resource across the full duration of the simulation as

$$NPV = \sum V_t d_t, \tag{2.9}$$

where the discount coefficient (d) decreases through time following the function:

$$d_t = \frac{1}{1 + \delta^t}, \tag{2.10}$$

and δ is a value between 0 and 1 that represents the rate at which the future value is discounted through time. We assumed that the marginal cost of increasing precision was always positive, such that there was a lower cost to move from low to moderate information than from moderate to high information. NPV is assessed independent of cost of monitoring. The cost of monitoring (C_m) was dictated by two parameters in the monitoring cost function:

$$C_m = \sum_{t=1}^{50} c_i e^{-c_s \sigma_t}, \tag{2.11}$$

where monitoring costs for the duration of the 50-year simulation are determined by the parameters c_i and c_s, which describe the slope and intercept of the cost function andσ_t is the CV the estimate of biomass based on the monitoring at time t. When $c_s = 1$, the cost function is approximately linear, whereas when $c_s > 1$ the cost of increasing monitoring precision is an exponential function. Because our model is heuristic, the absolute values of p, c_e, c_i, and

c_s can be varied without losing generality; therefore, in examining the economic costs and benefits of different harvest rates and monitoring efforts, we focused on the relative financial costs and benefits. For a description of all parameters see electronic supplementary material, table S2.

(f) Scenario analysis

We explored a series of management scenarios using our model to evaluate how variation in monitoring precision affects the harvested population and the return on monitoring investment. Each of the simulations had the same parameterization: $A = 10$, $r = 3.2$, $K = 101$, $B_{MSY} = 70$, $\varphi = 20$ and $c_e = 200$.

(i) How do monitoring precision and harvest rate affect the risk of population collapse and the value of the resource?

We quantified how changes in monitoring precision and the maximum harvest rate ($H_{\max}$) affected the NPV and risk of population collapse by simulating 10 000 iterations of 50-year simulations for a range of monitoring investment (CV of biomass: 0.0–0.5) and a proportion of maximum harvest rates (pH_{MSY}). Here, the proportion of maximum harvest rate (p) was explored from 0.0–2.0 with a starting population size at carrying capacity (K). To visualize the model and dynamics at the extreme ends of monitoring precision, we extracted example time series from low-precision (CV = 0.5) and high-precision monitoring (CV = 0.1) harvest at $p = 1$. We then estimated the median NPV and the probability of population collapse for a range of combinations of monitoring precision and maximum harvest rates.

(ii) Does the value of monitoring increase with higher proximity to a critical threshold?

We hypothesized that populations spending higher amounts of time close to a critical threshold would benefit most from high-precision monitoring. To test this hypothesis, we compared how the amount of time a simulated population spent in the danger zone ($< 0.8B_{MSY}$) affected the NPV of populations for simulations with high and low monitoring precision. To simulate populations where the resource spent increasingly more time close to the critical threshold, we conducted simulations across a range of harvest rates. Higher harvest rates tend to drive the resource down in biomass and cause the resource to spend an increasingly frequent amount of time near the critical threshold. Therefore, we examined how the difference in NPV between high-precision (CV = 0.1) and low-precision (CV = 0.5) monitoring changed as harvest rates increased and populations spent increasingly higher amounts of time near the critical threshold. We conducted these simulations similarly as above, with 10 000 iterations of 50-year simulations, with a starting biomass at carrying capacity (K), and a biological threshold of $A = 10$. Then, for each simulation, we calculated the fraction of the time series where the population was categorized in the danger zone ($<0.8B_{MSY}$) and correlated the precision of monitoring to the median fraction of time a population spent categorized as overharvested.

(iii) Can monitoring allow harvested populations to recover from dangerously low levels?

We hypothesized that high-precision monitoring can increase the probability a depleted resource will recover from an overharvested state. High monitoring precision can allow managers to quickly identify when populations are overharvested and reduce or stop harvest until the population has recovered. To test this hypothesis, we determined what combination of monitoring precision and harvest pressure maximized population recovery from the danger zone ($< 0.8B_{MSY}$) to sustainable harvest levels ($> 0.8B_{MSY}$)across replicate time series. Similar to the previous scenarios, we then ran 10 000 50-year simulations of our management strategy evaluation model for a range of different harvest and monitoring efforts (CV of biomass: 0.0–0.5; pH_{MSY} 0.0–2.0). For each simulation of a combination of monitoring and harvest efforts, we estimated the number of times a population recovered from below to above the $0.8B_{MSY}$ threshold and then estimated the median number of recoveries across the 10 000 iterations.

(iv) How can managers balance the costs and benefits of monitoring populations prone to collapse?

Managers are presented with a challenge of determining what combination of harvest rates and monitoring investment are appropriate for a given system given the costs of improving monitoring precision and the negative economic consequences of harvesting modestly. The appropriate solution will depend on their tolerance to risk of population collapse and their access to monitoring resources. One option presents stakeholders with different 'safe' combinations of monitoring precision and resource extraction rates, given a willingness to accept some probability of population collapse. Thus, a 'safe operating space' [22] that includes a suite of different monitoring and harvest levels can be defined for a given risk tolerance. Here we provide an example of this type of safe operating space for a range of risk tolerance levels defined by a willingness to accept a 20%, 10%, 5% or 1% probability of population collapse. To determine the safe operating space, we conducted a suite of 50-year simulations with 10 000 iterations with the same parameter combinations detailed above, and calculated the minimum precision (max CV in estimated biomass) needed to avoid crossing a critical threshold given a resource extraction rate and risk tolerance. We then plotted the combinations of monitoring and harvest rates that afford a certain level of risk for crossing the biological or management critical threshold.

One approach that might mitigate the cost of monitoring is a precautionary biomass level below which monitoring is conducted with high precision and above which low-precision monitoring is implemented. To demonstrate the utility of such a precautionary buffer, we quantified the NPV, the probability of crossing a critical threshold, and the cost of the resource given three monitoring approaches: (i) high precision (CV = 0.1), (ii) low precision (CV = 0.5) and (iii) an adaptive approach where monitoring precision changes every year based on estimated biomass (precision is low (CV = 0.5) when $\hat{B}_t > B_{MSY}$ and is high (CV = 0.1) when $\hat{B}_t < B_{MSY}$). For many populations, B_{MSY} may serve as an appropriate trigger for increased monitoring, both because B_{MSY} is likely far away from a depensation threshold in most populations. Depending on the ecosystem type and management organization, the cost of monitoring may be borne by the industry or by the government. Because we use a heuristic model, the exact monetary cost from increased monitoring or profit from increased harvest effort is arbitrary. Therefore, we explore the relative cost of monitoring and profit from harvest by plotting the ratio of NPV to monitoring costs for a range of maximum harvest efforts.

3. Results

(a) How do monitoring precision and harvest rate affect the risk of population collapse and the value of the resource?

Populations with lower monitoring precision are more volatile through time and more likely to spend time at low biomass and categorized as in the 'danger zone' (figure 1). These conditions arise because low monitoring effort leads to imprecise estimates of true biomass, which causes the population to experience frequent under- and over-harvesting. Consequently,

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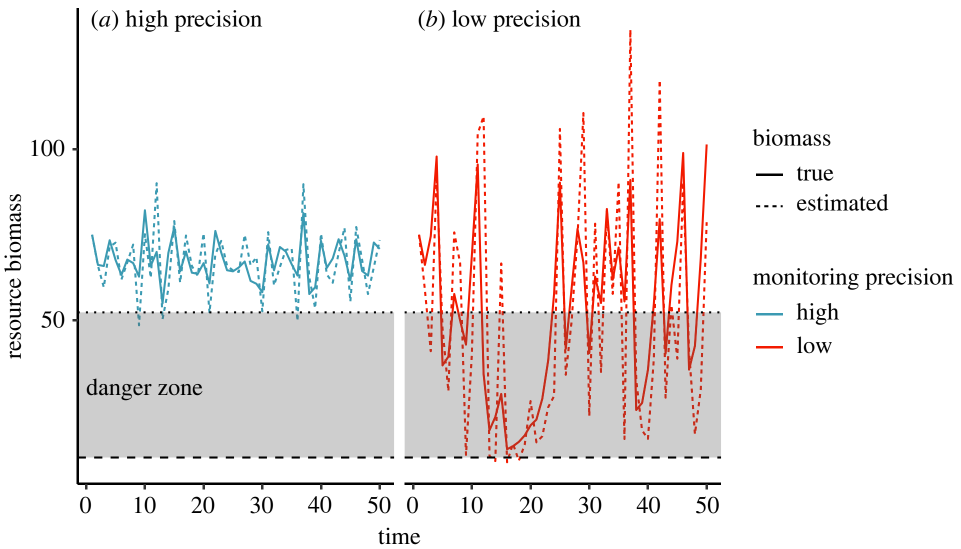

Figure 1. Different population dynamics of a harvested resource with (*a*) high monitoring precision (blue) and (*b*) low monitoring precision (red) at rate H_{msy} for a single replicate run of the simulation model. Model output represents true biomass (solid line) and estimated biomass (dashed line). Grey area represents overharvest 'danger zone' region calculated as $\hat{B}_t < 0.8B_{MSY}$ (dotted line). Bottom of danger zone is *A* value, below which the population crashes ($A = 10$). Increased monitoring precision produces different population dynamics, with lower volatility and less time spent categorized as 'overharvested' at high monitoring precision. (Online version in colour.)

the population is most likely to cross a critical threshold at high harvest rates and under low monitoring precision (figure 2*a*). Furthermore, over- and underestimates of population abundance due to low monitoring precision (CV = 0.5) leads to economic inefficiencies. NPV of a resource is highest when monitoring precision is high (CV = 0.1), and harvest pressure is at H_{MSY} (figure 2*b*). High-precision monitoring allows the population to be harvested close to B_{MSY}, which maximized population growth and yield. The benefits of high monitoring precision (i.e. CV = 0.1 relative to CV = 0.5) is minimal when the maximum harvest rate is low, but increases as harvest rate exceeds $0.5H_{MSY}$. The benefits of high monitoring precision increase from $0.5H_{MSY}$ to H_{MSY} and stabilize but remain highly beneficial for values greater than H_{MSY}. These effects of monitoring and maximum harvest rates generally hold for systems where the critical threshold happens at higher biomass (e.g. $A = 20$ or $A = 30$), but the consequences of low-precision monitoring and higher harvest rates tend to increase as depensation intensifies (electronic supplementary material, figure S3).

Importantly, our model is also highly relevant to populations without critical thresholds ($A = 0$), where high-precision monitoring and moderate maximum harvest rates lead to the highest NPV. The effects of monitoring precision and harvest rate were also contingent on the environmental stochasticity and the harvest model. When environmental stochasticity is integrated into the model in the form of variation in intrinsic growth rate, the probability of population collapse increases and NPV declines for a given level of monitoring precision (electronic supplementary material, 4, figure S4). A more conservative harvest model where harvest ceases when the population is estimated below maximum sustainable yield produced marginal decreases in the probability of population collapse and a decrease in NPV (electronic supplementary material 5, figure S5).

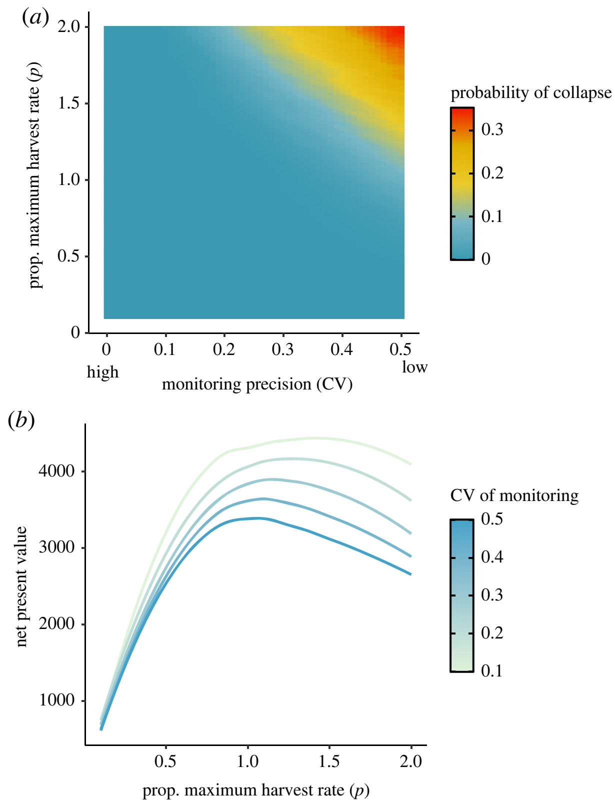

Figure 2. Summary of the probability of population collapse (*a*) and the median NPV (*b*) for 10 000 iterations of 50-year simulations across a range of monitoring investment. The probability of population collapse increases as the maximum exploitation rate increases and as monitoring precision decreases. Combinations of exploitation rate and monitoring precision with higher probability of collapse are in warmer red colours and combinations with lower probability of collapse are in colder blue colours. NPV of the resource increases as the harvest rate peaks at harvest at maximum sustainable yield and is highest for high-precision estimates. In (*b*), precision (CV of the population) is plotted as high precision in light green and low precision in blue.

(b) Does the value of monitoring increase with higher proximity to a critical threshold? If not, why?

Our results suggest higher monitoring precision always leads to higher economic value than low-precision monitoring (figure 3). However, the return on monitoring investment for the most precise monitoring (CV = 0.1) is low when harvest rates are very low, because low harvest rates are typically

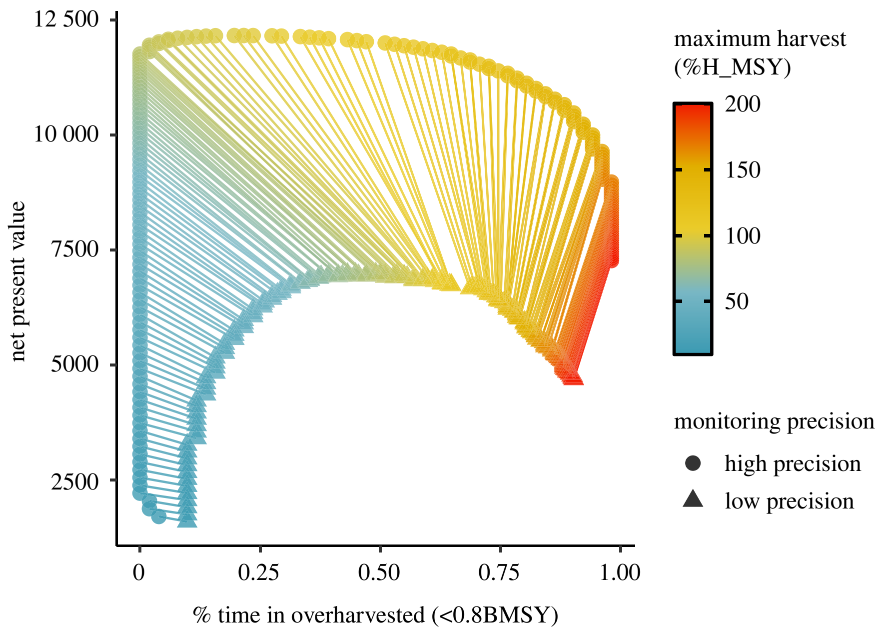

Figure 3. Summary of NPV for 10 000 50-year simulations for low (CV = 0.5, triangles) and high (CV = 0.1, circles) monitoring investment and across a range of maximum harvest mortality rate (proportion of H_{MSY} : pH_{MSY}). Populations with higher maximum harvest rates spend a larger fraction of their time classified as overharvested. Generally, NPV increases as harvest rates approach (H_{MSY}, $p = 1$), then declines as over-harvesting occurs ($> H_{MSY}$, $p > 1$). Return on investment is proportional to the length of the line connecting any two points harvested at the same rate (i.e. same colour), which depicts how much NPV changes when you go from low to high monitoring precision.

associated with very high biomass and consequently have low risk of collapse. Even when monitoring is imprecise, very conservative harvest rates still lead to very high relative resource biomass through time. The value of precise monitoring increases substantially as the population spends an increasing amount of time at low biomass and at higher risk of collapse (proportional to line segment lengths in figure 3). However, the relative benefits of heavy monitoring decline somewhat as populations spend increasingly high amounts of time overharvested at very high harvest rates $> 1.0H_{MSY}$. Thus, heavy harvest rates increase the risk of collapse, but can be profitable if the population is carefully monitored.

(c) Can monitoring promote resilience of harvested populations?

Populations that are poorly monitored and heavily harvested tend to regularly dip into the danger zone (figure 1). This effect of poor monitoring precision is exacerbated by heavy harvest pressure, which can lead to rapid dips in population biomass in short periods of time when populations are incorrectly estimated as abundant and subsequently overharvested. However, high-precision monitoring and modest harvest pressure increase the frequency at which populations recover from the danger zone (figure 4). Carefully monitored populations with high harvest pressure still occasionally become overharvested and approach a critical threshold, but have a much higher frequency of recovery back to a biomass that will maximize yield compared to populations with less monitoring. This increased recovery afforded by high-precision monitoring is a critical complement to the economic benefits that maximize return on investment.

(d) How can managers balance the costs and benefits of monitoring populations prone to collapse?

The higher recovery potential of heavily monitored populations can be actualized for a manager interested in balancing risk and economic gain in a population. Higher exploitation rates and lower monitoring investment increase the risk that a population's biomass will fall below a critical threshold. We defined a safe operating space as a combination of exploitation effort and the minimum precision required to avoid crossing a critical biological threshold. The safe operating space becomes narrower as the manager or stakeholder's aversion to risk increases (figure 5). In other words, risk-averse managers or stakeholders will benefit from a more conservative approach with lower harvest rates and higher monitoring precision.

Precautionary buffers offer a clear opportunity for managers to maintain high profits, reduce monitoring costs and significantly reduce the risk of population collapse. The least expensive monitoring option where monitoring precision is always low (CV = 0.5) offers the highest relative return on investment, but is risky, with the highest probability of crossing the biological threshold (figure 6, triangles). By contrast, the most expensive monitoring option of always monitoring with high precision (CV = 0.1) offers the highest NPV, the lowest probability of crossing a critical threshold, but also a relatively low return on investment (figure 6, circles). However, always maintaining high-precision monitoring may be unattainable given the high cost. A precautionary buffer offers an intermediate solution where the cost of monitoring is substantially reduced, in exchange for minor reductions in NPV, a higher return on investment and a moderate increase in the risk of collapse (figure 6, squares). Therefore, a precautionary buffer may be an effective approach for balancing these trade-offs by maintaining relatively high profits while minimizing monitoring. Naturally, the costs and benefits of any given strategy will potentially change for any given system depending on the specific costs and benefits of monitoring and the perceived consequences of crossing a threshold.

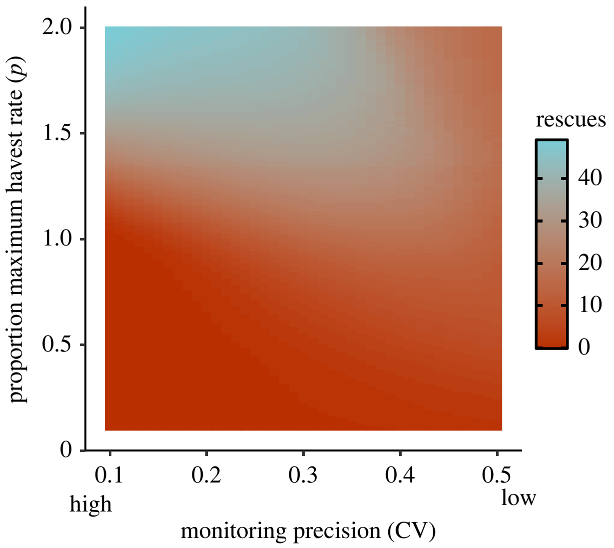

Figure 4. The number of successful rescues of a population when it dips into the danger zone state ($\hat{B}_t < 0.8B_{MSY}$). Number of recoveries is calculated as the average from 10 000 iterations of 50-year simulations for each of a range of monitoring precision and proportion of maximum harvest rates. Recovery is most frequent when monitoring precision is highest and harvest rate is low, but declines as harvest rate increases and monitoring precision decreases. Recovery is high in blue and low in red.

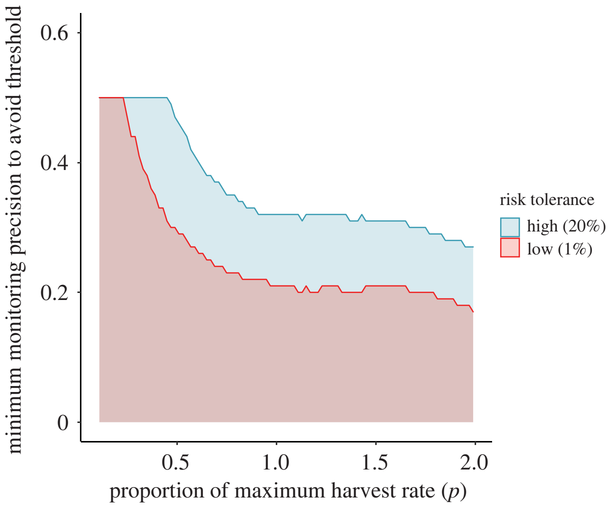

Figure 5. Suite of safe combinations of monitoring and harvest rates that avoids crossing a critical biological threshold ($A = 10$) given high (blue) and low (red) risk tolerance. The minimum amount of monitoring precision needed (maximum allowable CV where high CV corresponds to less monitoring) for a given maximum harvest rate (pH_{MSY}) to avoid a threshold under two different risk scenarios (1% and 20% of crossing a threshold). A higher precision of monitoring and lower rate of harvest is required to avoid a crossing a threshold, thus as maximum harvest rate increases, a decline occurs in the minimum allowable monitoring precision is needed to avoid crossing a threshold. The total safe area of potential combinations of monitoring precision and maximum harvest increases as tolerance to risk increases from 1% (dashed red) to 20% (solid blue). Lines represent median of 10 000 50-year simulations across a range of monitoring investment (CV of true biomass) and percentage of the maximum harvest rate (pH_{MSY}). (Online version in colour.)

4. Discussion

The monitoring of biological systems is typically constrained by financial and logistical resources. Our results demonstrate that high-precision monitoring can promote the recovery of an overharvested population, mitigate the risk of population collapse and maximize the economic value of a resource. While our case study was inspired by fisheries management strategies and focused on a single species, our findings are generally applicable to other management systems and taxa. Our results also provide insights for monitoring and management at the ecosystem-level, where human impacts such as over-harvesting, nutrient limitation and habitat fragmentation can cause ecosystems to cross critical thresholds and undergo regime shifts [23], which can have major socio-economic consequences [24]. Generally, managers seeking to avoid crossing critical thresholds, recover from overuse and maximize value, will increasingly benefit from high-precision monitoring as systems spend more time near their critical biological or management threshold.

Conservation biologists are increasingly aware that not all monitoring is equally valuable [2,3]. Rather, as resource exploitation rates increase and the system approaches a critical threshold, the risk of collapse increases. Consequently, the value of monitoring information also increases the more a population spends time at low biomass in proximity to a critical biological threshold beyond which recovery is impossible. While the notion that the value of information changes is intuitive and has been used in resource management (e.g. the design of protected areas [25]), it is rarely used to justify a change in monitoring effort. Instead, monitoring investment often is a product of funding, availability of technology, personnel logistics, and perceptions of risk among managers and resource users. Improving our understanding of how ecosystem characteristics dictate the trade-off between precision in estimates of population status and the costs of mismanagement will benefit both stakeholders, scientists and managers who are working with finite resources.

Variation in the value of monitoring, therefore, requires an approach that balances cost of monitoring with the risk of catastrophe. Our results support previous studies highlighting the utility of precautionary management approaches as a way to prevent populations from falling below critical thresholds, especially when there is uncertainty in stock status and risk is thought to be high [26]. We demonstrated how an adaptive monitoring programme that takes advantage of precautionary buffers, but does not track changes intensively when population biomass is high, can minimize monitoring costs, increase profits, prevent a system from collapsing and promote the recovery of overharvested systems.

(a) What if the existence or location of the critical threshold is ambiguous?

In systems with critical biological thresholds, decision makers are rarely fortunate enough to have perfect knowledge of biological thresholds until after the threshold has been crossed [27]. Indeed, surprises such as crossing a threshold are inevitable in many systems [28]. Uncertainty about the location of a threshold presents challenges, particularly in the face of global change, where the strength and location of thresholds may well change as ecosystems transform. Gaining greater certainty about the location of a critical threshold can be achieved through adaptive management [29], which has a long history in ecological literature and has been widely used to inform fisheries management based on optimal control [30]. The closed-loop simulation we employed here takes

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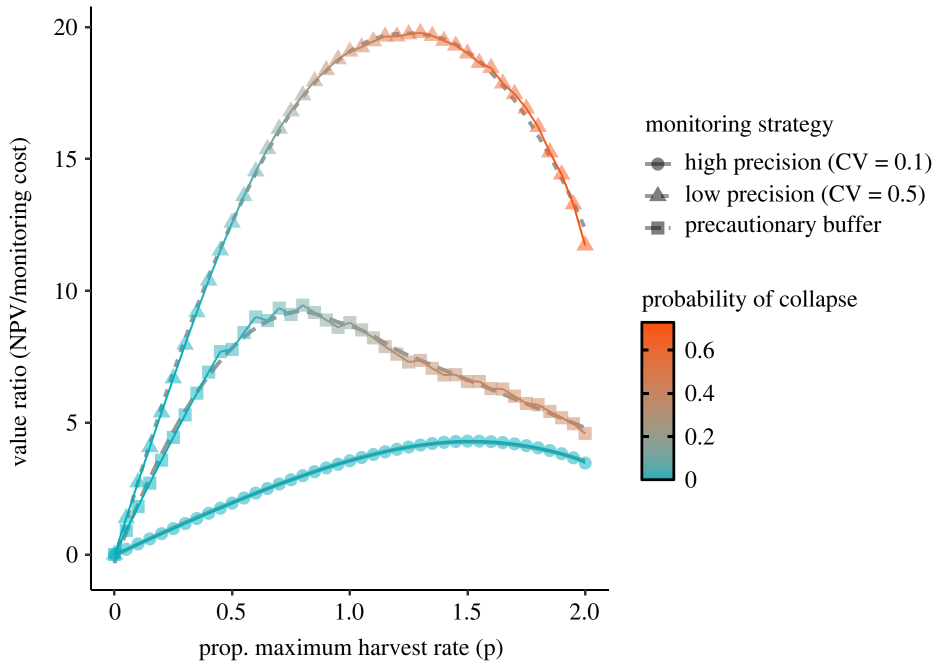

Figure 6. Financial benefits of a precautionary buffer approach when the industry bears the cost of monitoring. Comparison of constant but fixed monitoring investment (i.e. high monitoring precision [CV = 0.1, solid line and circles] or low-precision monitoring [CV = 0.5, short-dash line and triangles]) to a precautionary buffer where when estimated biomass is above this buffer (i.e. $\hat{B}_t > B_{MSY}$) monitoring is low precision [CV = 0.5] and below which (i.e. $\hat{B}_t > B_{MSY}$) monitoring is high precision (long dash line and squares). Cost function slope ($c_s = 5$). Median results from 10 000 simulations shown for a range of maximum harvest efforts (*x*-axis), and blue and red points represent the low and high probability of population collapse, respectively.

a different approach, providing insight into how a fixed set of management strategies performs with various levels of monitoring investment and in the face of multiple forms of uncertainty. Future work could marry our ideas with those emerging in the decision optimization literature [31]. For example, Gaussian process stochastic dynamic programming, which makes few structural assumptions about population production functions, can allow managers to identify optimal control rules in light of uncertainty in threshold locations [32]. Alternatively, early warning indicators such as rising variance or changes in autocorrelation may offer a signal for when a system is approaching a threshold [33,34], though detection of a threshold using these indicators likely requires high-precision and frequent precise monitoring. However, even with better monitoring and analysis, some uncertainty is irreducible [35]. Such irreducible uncertainty (e.g. due to stochasticity in recruitment) can amplify the risks associated with limited monitoring effort and are critical for managers to consider.

(b) The value of monitoring depends on the stakeholder

Determining the value of monitoring information also likely extends beyond the organization bearing the monitoring costs to include the value to other stakeholders. The high volatility that emerges from low monitoring investment may be particularly challenging to some stakeholders while others might be less affected. For example, surveys of Kenyan fishers suggest that socio-economic background drives willingness to leave a fishery; wealthy individuals were more likely to leave the fishery after large declines in catches, whereas low-income households would become stuck in poverty traps due to a lack of resources to switch occupations [36]. By contrast, large industrial fishing operations may have higher travel capacity to harvest in another location where the resource remains plentiful, or are capable of investing in the gear and infrastructure needed to switch to harvesting a different resource [37]. To achieve equity among stakeholders, management will need to account for asymmetry in risk aversion among stakeholders, which in turn will be a critical step in integrating the value of information as a driver of monitoring investment.

(c) Consideration of moral hazards

Our examination of the relative costs and benefits of different monitoring strategies suggests that high-precision monitoring is always the most effective way to maximize yield and avoid crossing a limit reference point or critical biological threshold. However, high monitoring precision can be extremely expensive, and the feasibility of payment depends on the state of the system and the resources that industry, stakeholders, non-governmental organizations or government agencies have to cover the costs of monitoring. In some circumstances 'moral hazards' can emerge, where one organization is involved in a risky activity (harvest) but is protected against risk by another party that incurs the cost [38]. When contracts are initially based on payoff alone and intensive monitoring is cost prohibitive, lower monitoring precision combined with shared risk among multiple parties is a common solution applied to moral hazards.

In the case of resource monitoring, shared risk strategies can include the industry sharing monitoring costs with government agencies. However, shared monitoring costs do not always align with economic incentives. For example, our model suggests that an economic incentive exists for an organization to support increased monitoring as long as the expected financial benefit from resource extraction exceeds the financial cost of monitoring. By contrast, agencies are incentivized to keep the population at a valuable biomass, but to minimize taxpayer's costs. This asymmetry in incentives for different stakeholders poses a challenge, because agencies often have limited resources to provide high-precision monitoring, while the industry is often incentivized to harvest as much of the resource as possible at the lowest cost. Thus, context-appropriate solutions that are economically viable and cost-effective, and that incentivize environmental protection, are critical.

Commercial fisheries offer an interesting case study in placing the burden of monitoring costs on the industry versus the government. For example, a subset of fisheries in New Zealand, Canada and Australia, the fishing industry is primarily responsible for monitoring costs, with the philosophy that the burden of proof for sustainability is on the stakeholder interested in exploiting the system [15]. An example of this is the commercial Pacific herring fishery in the Canadian North Pacific, where monitoring of spring herring spawns was historically funded by one of several stakeholders, the fishing industry. However, the fishery crossed a limit reference point over a decade ago and has not fully recovered [37]. As a consequence, monitoring effort has declined, which impacts the precision of biomass estimates, and may prolong closures. This case highlights a key consideration in monitoring programmes: if information is most valuable as a fishery approaches and recovers from collapse, it is best to ensure that funding for monitoring is independent from stock size.

(d) Looking forward

Our model is a simplified harvested system that illustrates how monitoring precision can be more or less valuable depending on how close an ecosystem is to a biological or management threshold. Our goal in this study was to provide strategy; however, to develop tactics based on the principles described above, managers will need to integrate additional ecological and economic complexity. Ecologically, shifts in productivity, species interactions and environmental variability can change a species' carrying capacity and rebound potential [39], and consequently alter what harvest rates maximize yield and avoid collapse. Moreover, including age or size structure in the model has the potential to change the autocorrelation structure in the model and likely modify the importance of monitoring. Economically, it will be important to consider additional complexity in the shape of the cost function for monitoring, and dynamic prices for a harvested species such as increases in price as species become rare [40]. Moreover, as motoring technology advances (e.g. through remote sensing), the relative cost of high-precision monitoring may decrease, allowing high frequency monitoring at all times. Consideration of all of these additional sources of complexity will benefit managers considering how to optimize their monitoring strategies now and in the future as ecosystems change.

5. Conclusion

Managers, policy makers and stakeholders are tasked with connecting monitoring effort, thresholds and the state of the system to short-term management decisions. This will be difficult given the inherent limitations in assessing the state of the system and because the location of critical thresholds is not always known. Additional difficulties emerge because of misaligned economic incentives and structures that deter or constrain heavy monitoring when yields are near a critical threshold, and because stakeholders differ in their risk of collapse given their divergent ability and flexibility to adapt once a population or ecosystem has crossed a critical threshold. Seeking creative strategies that promote investment in monitoring when it is most valuable has the potential to increase sustainable natural resource use and conservation.

Data accessibility. The data are provided in electronic supplementary material [41].

Authors' contributions. A.C.S.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing—original draft and writing—review and editing; T.E.E.: conceptualization, formal analysis, writing—original draft and writing—review and editing; J.F.S.: conceptualization, formal analysis, funding acquisition, supervision, visualization, writing—original draft and writing—review and editing; M.C.S.: formal analysis, methodology, visualization and writing—review and editing; B.S.H.: conceptualization and writing—review and editing; C.W.: formal analysis and writing—review and editing; J.M.L.: writing—review and editing; A.K.S.: conceptualization and writing—review and editing; P.S.L.: conceptualization and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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