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Course corrections responding to climate impacts produce divergent effects on population biomass and harvest in fisheries

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Abstract

Climate change will alter ecological dynamics, affecting the relative abundance of species. A primary challenge is whether and how to modify natural resource management practices to address these changes. We explored a model of a harvested fish population experiencing climate-driven changes in demography, finding that climate impacts impose a choice between management strategies that favor fishery yield or population biomass but not both. When climate caused a population's carrying capacity to increase, or its productivity to decrease, a climate adaptive strategy relying upon this updated information maintained higher population biomass but produced similar or lower yield than fixed management pegged to historical conditions. In contrast, when climate caused a population's carrying capacity to decrease, or its productivity to increase, a climate adaptive strategy produced greater yield but maintained lower population biomass. Both strategies prevented a population from becoming overfished (too small to achieve maximum yield), but the fixed management strategy could impose more excessive annual harvest rates (overfishing). These insights suggest climate adaptive management may not always outperform a fixed strategy. Yet in U.S. fisheries we found routine assessment of population status modifies demographic parameters, implicitly shifting management reference points that affect fishery yield and population biomass. Participatory processes can illuminate these impacts, creating opportunities to co-develop weightings for conservation and harvest objectives.

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Introduction

Maintaining effective food security amidst global climate change and a growing human population is one of the most significant environmental challenges of the 21st century. The impacts of climate change on natural resources that provide food, such as fisheries, are already visible, and climate models predict additional future changes in productivity and disturbances that will disproportionately affect those most dependent on them [1,2]. Policies that steer changes to maintain food security under the new environmental conditions, while avoiding risks of major population declines, can achieve regional, national, and international sustainability goals. However, in most cases it remains unclear what type and rate of response is appropriate, especially given the potential that corrections for anticipated climate impacts can have negative consequences in the near-term [3]. Identifying the right approaches will help mitigate the predicted loss of food security anticipated under business-as-usual management, while maintaining progress toward conservation goals.

The success of the technology, medical, and economic sectors in implementing adaptive strategies highlights the potential merits of moderate, incremental interventions over business-as-usual. For example, phased rollouts in the technology sector that stay ahead of consumer needs offer advantages over static platforms, ensuring system continuity and easier troubleshooting [4]. Similarly, in medicine, gradual treatment adjustments consistently yield better patient outcomes by mitigating severe side effects associated with failing to change treatment plans [5]. In economics, measured financial market reforms, which address both contemporary and anticipated trends, can prevent losses associated with rigid regulations [6]. The success of these gradual interventions relies on regular updates to current understanding based on two key pieces of information: (i) monitoring and analysis of recent data, and (ii) forecasts of potential future trends.

A gradual adjustment approach is particularly relevant to adaptive fisheries management in the face of climate change. Climate change will reshuffle geographic distributions, alter body sizes, and modify catch of fisheries species [7–11]. However, these predictions are rarely integrated into strategic or tactical fisheries management. In contrast, in other natural hazard management contexts such as wildfire and drought risk, forecasts that integrate environmental information are widely used to inform policy [12,13]. Threshold harvest control rules that adjust fishery catch based on estimated biomass are protective against some aspects of climate change [14], but may be insufficient when the effects of climate change go beyond increasing or decreasing population size. An outstanding question remains: how should managers react and adjust the amount of fish harvested in anticipation of a different future? For instance, if the long-term abundance of a fisheries species is projected to decline due to warming ocean temperatures over the next half-century, how should that information influence today's harvest management? Fundamentally, these questions speak to whether climate-ready fisheries could learn from technology, medicine, and economics where gradual, adaptive responses are highly effective.

Recent studies have explored the relative effectiveness of integrating climate impacts into fisheries management. For instance, Szuwalski et al. [15] simulated a sudden, climate-induced decline in a population's carrying capacity with no correspondingly sudden change in population biomass (a potentially unrealistic juxtaposition). Counterintuitively, they found that immediately matching fisheries management targets to the reduced carrying capacity — a climate adaptive strategy — depressed population biomass and did not create marked gains in harvest compared to business-as-usual management. In contrast to the sudden decline in carrying capacity and sudden change in management envisioned by [15], many real-world changes are expected to be gradual and detectable in population trends or predictable with forecasts. Furthermore, carrying capacity and other demographic rates may respond favorably, not just unfavorably, to climate influences (e.g., range expansions underpinned by a climate driver; [16]). In cases where such changes can be observed or anticipated, there is room for harvest rates to adjust as climate drivers express their influence on a population and assessments of population status are updated [17–22]. Collectively this work points to a gap in understanding of the consequences of adaptation in fisheries as climate impacts happen or are projected to take effect [23]. Specifically, there is a need to compare business-as-usual and adaptive fishery management with: (i) both positive and negative gradually-occurring climate impacts, and (ii) adjustments to harvest rates that occur at different lagtimes relative to actual shifts in one or more demographic rates.

In this paper, we focus on potential future scenarios where climate change causes a gradual change in the productivity (intrinsic growth rate) and/or carrying capacity of a population subject to fishing. In contexts where monitoring and evaluation of harvested populations are possible, these changes to demographic parameters may be observed and estimated based on recent trends [17,21] or forecast based on climate projections or other factors [8]. Using a well-grounded model, we develop scenarios where evidence or forecasts signal these demographic shifts, and management reference points are, or are not, routinely updated. We examine whether climate adaptive course corrections to harvest rates that keep up with demographic shifts are more effective at producing a higher population size and greater fishery yield than maintaining a fixed harvest strategy. We hypothesize that a climate adaptive management strategy that dynamically responds to changes in productivity and carrying capacity will optimize fishery yield, and also protect population biomass, compared to a fixed, or business-as-usual, management strategy. Our focus is on the transient dynamics occurring during the period in which carrying capacity or productivity is changing. We conclude by relating our insights about the application of adaptive management strategies to real-world estimates of population change in several harvested stocks from the U.S. West Coast. This focus invites the opportunity to bring greater specificity to notions of adaptive management and climate-ready fisheries.

Methods

Model framework

We developed a time-varying, surplus production model to explore the impacts of climate adaptive and fixed management on a harvested resource. In this model, the biomass B_t of the population depends on productivity (or intrinsic growth rate) r_t and carrying capacity K_t, and is subject to an annual harvest rate (or exploitation fraction) U_t:

$$B_{t+1} = B_t + r_t B_t \left(1 - \frac{B_t}{K_t}\right) - U_t B_t \tag{1}$$

In the base case where r_t and K_t are constant (i.e., $r_t = r^*$ and $K_t = K^*$), the maximum sustainable yield (MSY) is achieved by setting $B_{MSY} = \frac{K^*}{2}$ [24]. We imposed a sloped harvest control rule specified such that the harvest rate declines linearly from a target maximum sustainable harvest rate (in the base case, $U_{MSY} = \frac{r^*}{2}$) as the biomass of the resource declines below $B_{MSY,t}$ and falls to zero when B_t is below $\alpha B_{MSY,t}$, as

$$0 \text{ if } \frac{B_t}{B_{MSY,t}} < \alpha \tag{2a}$$

$$U_t = \frac{U_{MSY,t}\left(\frac{B_t}{B_{MSY,t}} - \alpha\right)}{1 - \alpha} \text{ if } \alpha \leq \frac{B_t}{B_{MSY,t}} < 1 \tag{2b}$$

$$U_{MSY,t} \qquad \text{if } \frac{B_t}{B_{MSY,t}} \geq 1 \tag{2c}$$

In equation 2, $\alpha \in [0, 1)$ determines the slope of the harvest control rule as

$$\frac{U_{MSY,t}}{(1-\alpha)B_{MSY,t}}, \tag{3}$$

such that changes in productivity, carrying capacity, and α together influence the rate at which the maximum sustainable harvest rate is reached. The qualitative form of this harvest control rule is inspired by widespread federal fisheries management practice in the U.S. and beyond [14]. It is used because under assumptions of stationarity (where *r* and *K* are constant) the decline in harvest rate accelerates the rebuilding of the population to levels consistent with maximizing long-term yield and protects the population from declining to very low levels [25]. Note that this model excludes uncertainties common in real fisheries systems, such as observation error (inherent to estimating population biomass and demographic parameters) and implementation error (common due to time lags involved with governance of coupled social-ecological systems, among other reasons). We explore the model assumptions and limitations more fully in the *Discussion*.

The defining feature of the model presented in equation 1 is that it allows both the carrying capacity and productivity to vary through time, reflecting the potential effects of a climate driver on a population. Before we develop simulations to understand the consequences of such temporal variation, it is useful to describe the general response of a population and harvest to changes in productivity (r_t) and carrying capacity (K_t). In this model, if the population is unharvested and a climate driver causes productivity or carrying capacity to increase, the population biomass will increase. Conversely, if productivity or carrying capacity declines, population biomass will also decline. In populations with these different characteristics, if a fishery were to develop and operate under a sloped harvest control rule it would rely upon distinct management reference points (Fig 1). The changes in harvest rate triggered by shifts in productivity are intuitive, but the differences in harvest rate with changes in carrying capacity may be initially surprising.

Populations with higher productivity after a climate impact will have a greater maximum sustainable harvest rate $U_{MSY,t}$, while those with larger carrying capacity after a climate impact will have greater biomass associated with maximum sustainable yield $B_{MSY,t}$. A higher value of $U_{MSY,t}$ will increase the slope of the harvest control rule (equation 3, Fig 1), causing the harvest rate to increase faster at lower population biomass. In contrast, a higher value of $B_{MSY,t}$ will have two consequential effects on the harvest control rule. First, it will cause the harvest rate to remain at zero for a larger absolute range of values of population biomass (because $\alpha B_{MSY,t}$ is larger). Second, and counterintuitively, it will reduce the slope of the harvest control rule (equation 3), causing the harvest rate to *increase more slowly* at lower population biomass (because the unchanged $U_{MSY,t}$ is reached at a larger population biomass). In populations experiencing a climate impact causing lower productivity or smaller carrying capacity, $U_{MSY,t}$ or $B_{MSY,t}$ will be smaller. A smaller value of $U_{MSY,t}$ will reduce the slope of the harvest control rule (equation 3), causing the harvest rate to increase more slowly at lower population biomass compared to fixed management. In contrast, and again counterintuitively, a lower value of $B_{MSY,t}$ will both cause the harvest rate to remain at zero for a smaller range of values of population biomass (because $\alpha B_{MSY,t}$ is smaller) and increase the slope of the harvest control rule (equation 3), causing the harvest rate to *increase more quickly* at lower population biomass (because the unchanged $U_{MSY,t}$ is reached at a smaller population biomass).

Simulations and analyses

Climate change will challenge some species (losers) and benefit others (winners). Below we consider situations where a climate driver alters the productivity, carrying capacity, or both features of a population. For example, warming waters and reduced predation could increase productivity, while habitat expansion and nutrient enrichment may boost carrying capacity. Conversely, thermal stress and elevated metabolic costs can decrease productivity, while habitat loss and

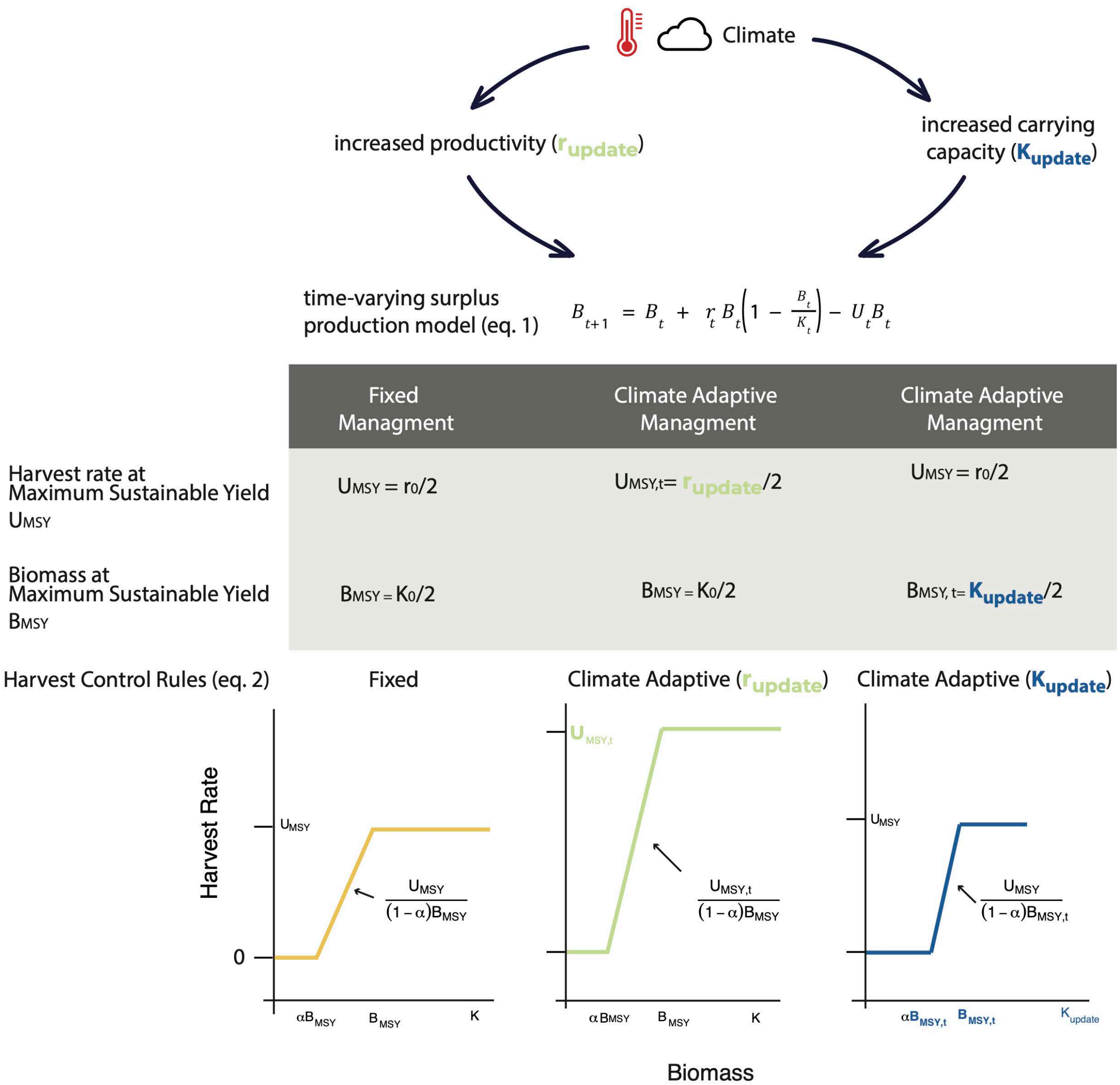

Fig 1. Conceptual schematic of climate impacts on demographic rates and alternative harvest control rules. Conceptual schematic describing how climate impacts to productivity and carrying capacity were incorporated into the dynamics of a time-varying surplus production population model (equation 1) and associated harvest control rule (equation 2). In this model, populations with higher productivity or larger carrying capacity after a climate impact will have a greater maximum sustainable harvest rate $U_{MSY,t}$ or biomass associated with maximum sustainable yield $B_{MSY,t}$, compared to a fixed management strategy that uses a harvest control rule that retains initial values of these quantities. Under a climate adaptive management strategy, a higher value of $U_{MSY,t}$ will increase the slope of the harvest control rule (equation 3), causing the harvest rate to increase faster at lower population biomass compared to fixed management. In contrast, a higher value of $B_{MSY,t}$ will have two consequential effects on a climate adaptive harvest control rule. First, it will cause the harvest rate to remain at zero for a larger range of values of population biomass (because $\alpha B_{MSY,t}$ is larger) compared to fixed management. Second, it will reduce the slope of the harvest control rule (equation 3), causing the harvest rate to increase more slowly at lower population biomass (because the unchanged $U_{MSY,t}$ is reached at a larger population biomass) compared to fixed management. In populations experiencing a climate impact causing lower productivity or smaller carrying capacity, the opposite effects on $B_{MSY,t}$ will occur (not shown).

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ocean deoxygenation can reduce carrying capacity [26]. These situations present a choice about whether to maintain a *fixed management strategy* with a harvest control rule (equation 2) tied to a historical estimate of carrying capacity and/or productivity (i.e., business-as-usual management), or to adopt a *climate adaptive strategy* with a harvest control rule that adjusts to a new estimate of carrying capacity or productivity (Fig 1). In fisheries, population status is commonly determined via a stock assessment, which in turn informs harvest decisions. We define a climate adaptive strategy as one in which a stock assessment incorporates (i) updated information about the impacts of climate on the population, and/or (ii) a forecast of expected climate-induced change in the population. We assume a direct consequence of this climate-adaptive assessment is a harvest control rule that integrates observed or forecasted demographic changes, allowing the resource manager(s) to make course corrections to harvest rates over time. In our model, a climate adaptive strategy is reflected through the incorporation of an updated carrying capacity K_{update} to calculate the biomass reference point $B_{MSY,t}$ and/or an updated productivity r_{update} to calculate the harvest rate reference point $U_{MSY,t}$. In contrast, the fixed strategy retains initial values K_1 and r_1 in calculating biomass and harvest rate reference points.

We simulated the dynamics of the population described in equations 1–3, assuming that (i) the productivity declined linearly or increased linearly without any change to K_t, (ii) the carrying capacity declined linearly or increased linearly without any change to r_t, and (iii) both productivity and carrying capacity declined linearly or increased linearly (S1-S2 Tables). Specifically, we assumed a climate driver γ exerted influence on carrying capacity and/or productivity between $t=1$ and $t=t_{change}$, as

$$K_{update,t} = K_1 + \gamma_K t, \tag{4a}$$

and

$$r_{update,t} = r_1 + \gamma_r t, \tag{4b}$$

where $t_{change}=50$ and reflects the time point when K_t and/or r_t reaches its new stable value following the climate-induced changes. In the fixed management strategy scenario, the harvest control rule (equation 2) relied on constant values of $K_t=K_1$ and $r_t=r_1$, without integrating the effects represented by γ. In the climate adaptive management strategy scenario, the harvest control rule used the updated carrying capacity $K_{update,t}$ to calculate the annual biomass reference point $B_{MSY,t}$ and/or an updated productivity $r_{update,t}$ to calculate the annual harvest rate reference point $U_{MSY,t}$. To understand how lag times in updating the harvest control rule relative to actual shifts in demographic rates affected outcomes for population biomass and fishery yield, we explored application of equation 4 at annual, 4-year, and decadal intervals. While these four scenarios (fixed, decadally updated, 4-year updated, and annually-updated) are not intended to reflect operational practice for any specific region or stock, they do bracket common stock assessment recurrence frequencies and resulting options for gathering inference about the influence of fixed and climate adaptive management and assessment strategies on population and harvest dynamics (also see *Discussion*).

The default parameters (S1-S2 Tables) in our simulations imposed a 75% decrease or 300% increase in productivity and/or carrying capacity, and focused on an annual update interval. In all simulations, we initialized the system at equilibrium, i.e., with biomass at B_{MSY} and harvest rate at U_{MSY} for $K_t=K_1$ and $r_t=r_1$. This approach minimized the effects of initial transient dynamics unrelated to shifts in K_t and/or r_t. The interpretations below are based primarily on summaries of mean annual population biomass and cumulative harvest between $t=1$ and $t=50$, and visual inspection of three equal time bins (16 years each) to better interpret the transient dynamics during the gradual change in demographic rates. In the Supporting Information, we report the effects of these demographic changes on the time series of population biomass, harvest rate, harvest, cumulative harvest, the sloped harvest control rule, and cumulative discounted revenue.

In addition to describing the population and harvest dynamics in these simulations, we report differences between fixed and climate adaptive management strategies for each climate impact scenario in relation to specific conservation and fishery objectives. We specified the conservation objective as maintaining population biomass at a level 20% greater than $B_{MSY,t}$ [27]. While this objective is a proxy for maximum economic yield [28], it also implicitly maintains sufficient population biomass for other ecosystem processes of conservation concern [29]. The fishery objective was specified in two ways: (i) avoid overfishing (annual rate of catch is too high) by maintaining the harvest rate $U_t < U_{MSY,t}$, and (ii) avoid an overfished population (a population considered too small to achieve maximum sustainable yield) by maintaining the population biomass $B_t > 0.2 * B_{MSY,t}$ [30].

To span a wide range of potential climate impacts on demographic rates, we explored the sensitivity of our results by running simulations with 15, 30, 45, 60, 75 (default), and 90% gradual decreases in K_t and/or r_t, and 50, 100, 150, 200, 250, 300 (default), 350, and 400% gradual increases in K_t and/or r_t. Because our results are potentially sensitive to the degree of prior exploitation and the value of t_{change}, we repeated simulated declines in productivity and carrying capacity with the population initiated at $B_1 = K_1/2,\ 0.8K_1/2,\ 0.6K_1/2,\ 0.4K_1/2,\ \textit{and}\ 0.2K_1/2$, and separately, for values of t_{change} = 10, 30, 50, 70, and 90 (with lower values of t_{change} corresponding to a faster rate of change in r_t and/or K_t). Finally, as a supplemental analysis, we investigated how integrating stochastic population growth affects the performance of fixed versus climate adaptive management strategies, which allowed us to quantify changes in the interannual variability in population biomass and harvest (see S1 Text).

Application to groundfish along the U.S. West Coast

To link our theory to real-world fisheries management practices, we evaluated whether published stock assessments of several harvested stocks from the U.S. West Coast show evidence of changes in equilibrium unfished spawning biomass. A common reference point used in determining harvest advice, unfished spawning biomass is analogous to the use of carrying capacity K in our model simulations. While other studies have demonstrated that climate change can influence productivity and that shifts in productivity can have implications for reference points (reviewed by [23]), the groundfish application presented here provides an opportunity to explore these dynamics directly and in relation to the theory above.

For many federally-managed species in the U.S. and elsewhere, stock assessment models are developed and updated with fishery-dependent and fishery-independent data to understand how populations change over time. Resulting information is leveraged to adjust fishing regulations to changing conditions captured by the stock assessment. In this way, updates to stock assessment models may implicitly change reference points used to inform harvest setting processes, similar to how we have implemented K_{update} and r_{update} in our simulations. We explored this possibility by quantifying variation in estimated equilibrium unfished spawning biomass (hereafter, unfished biomass) in Pacific Fishery Management Council (PFMC) groundfish stock assessments from the U.S. West Coast. We extracted unfished biomass (or spawning output) from the stock assessments available on the PFMC website (https://www.pcouncil.org/stock-assessments-star-reports-stat-reports-rebuilding-analyses-terms-of-reference/groundfish-stock-assessment-documents/) for 2005–2022. We acknowledge that changes in estimates of unfished biomass in stock assessments over time represent retrospective patterns which could arise for a variety of reasons including inaccurate or additional data, incorrect or changed model assumptions, or actual temporal variation in unfished biomass [31,32].

We chose stocks to compare and explore based on assessment frequency and continuity in the units of biomass reported. Thirteen groundfish stocks have been assessed four or more times over 2005–2022. For illustrative purposes we focus here on Pacific hake (*Merluccius productus*), petrale sole (*Eopsetta jordani*), and sablefish (*Anoplopoma fimbria*). All three of these stocks report reference points in terms of units of spawning biomass, are highly valuable, and benefit from regular, Congressionally-mandated monitoring surveys and frequent stock assessments.

Results

Model simulations

We analyzed a time-varying surplus production model for a population in which a climate driver altered productivity, carrying capacity, or both, to evaluate the effects of fixed and climate adaptive management strategies on population biomass and fishery yield. The choice of a climate adaptive or fixed management strategy favored greater population biomass or greater cumulative harvest but not both at the same time (Figs 2-3, S1-S5 Figs, Table 1). Both management strategies met fishery objectives to avoid overfishing and an overfished population in most scenarios, though climate adaptive management was more likely to avoid overfishing (Fig 4). However, fixed management also met the conservation objective to maintain population biomass at a level 20% greater than $B_{MSY,\,t}$ under more climate impact scenarios than climate adaptive management (Fig 4). These results were qualitatively robust to variation in initial population biomass (S6 Fig), the rate

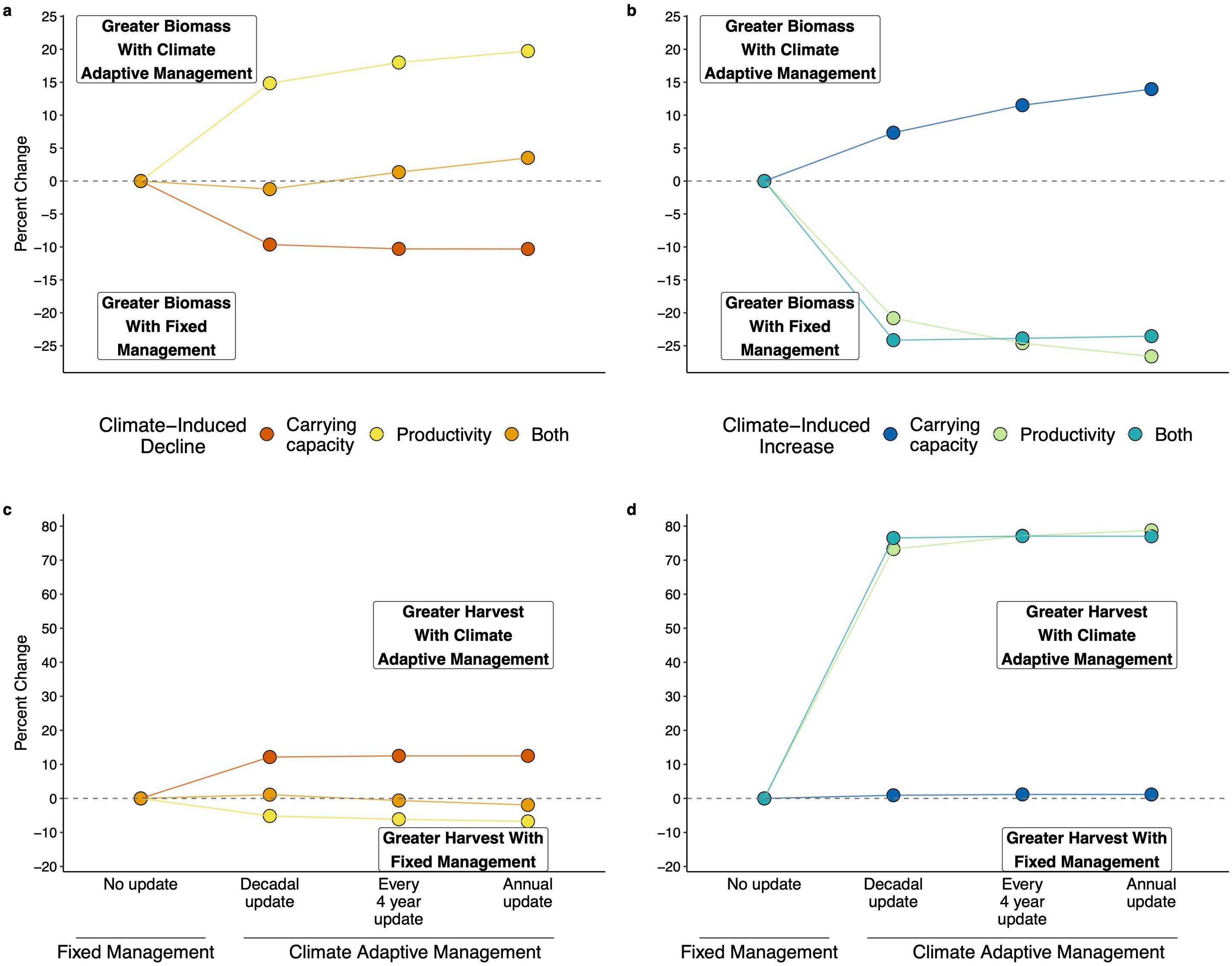

Fig 2. Percent change under climate adaptive management versus fixed management in population biomass and cumulative harvest. The percent change under climate adaptive management compared to fixed management in (a-b) mean population biomass and (c-d) cumulative harvest with changes in productivity, carrying capacity, or both. The figures show responses when updates to the harvest control rule never occur (fixed management) or are climate adaptive and occur decadally, at 4-year intervals, or annually. All parameters are at their default values (S1-S2 Tables). The horizontal dashed line at zero is for reference only.

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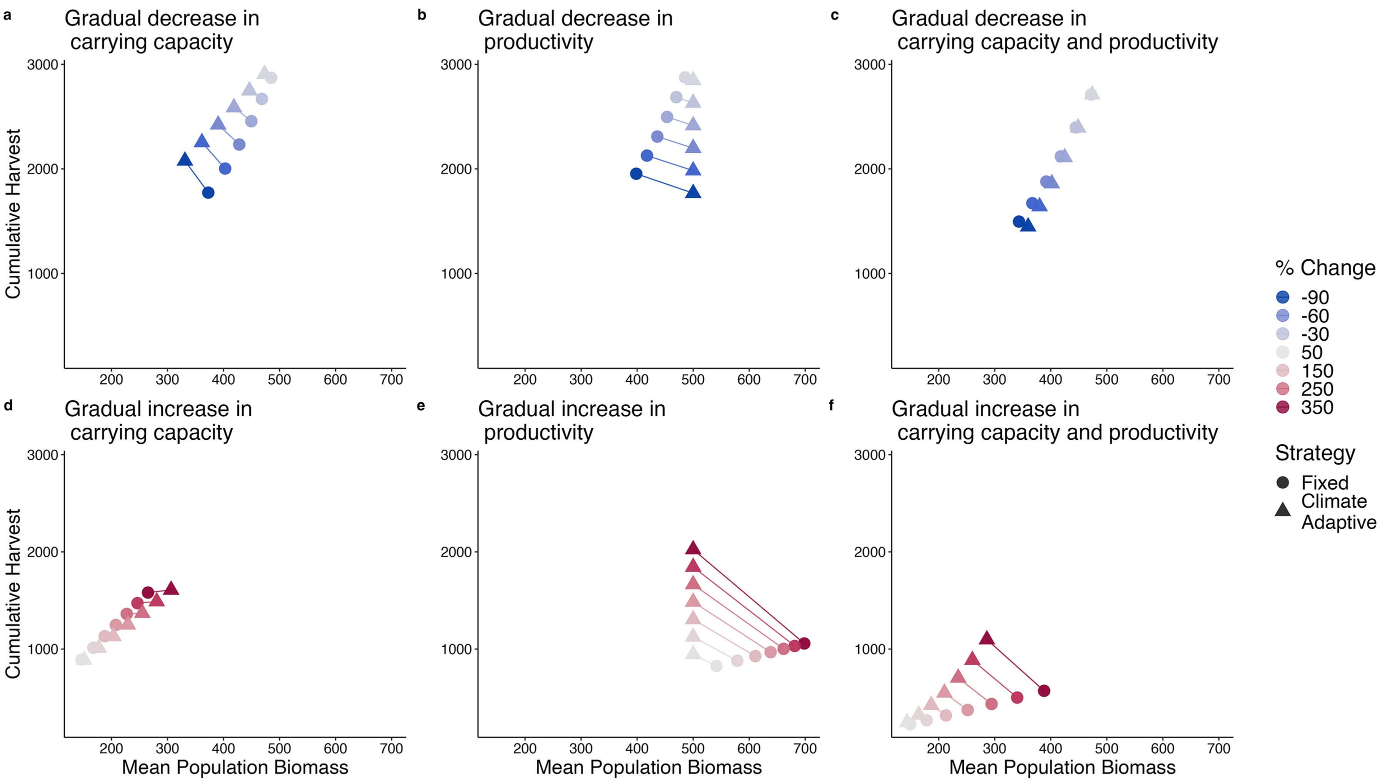

Fig 3. Sensitivity of biomass and cumulative harvest to magnitude of climate impacts under alternative management strategies. Outcomes of implementing fixed versus annual climate adaptive harvest management strategies on mean population biomass and cumulative harvest over 50-year simulations in a population subject to a gradual decrease or increase in carrying capacity **(a, d)**, productivity **(b, e)**, and both carrying capacity and productivity **(c, f)**. All parameters except for the percent change in demographic parameters are at their default values; note that initial and final values of productivity and carrying capacity differ in the decreasing versus increasing scenarios (S1-S2 Tables).

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Table 1. Summary of outcomes for population biomass and cumulative harvest under a climate adaptive versus fixed fishery management strategy.

Climate scenario	Effect on *Umsy,t*	Effect on *Bmsy,t*	Population biomass	Cumulative harvest
$r\downarrow$ $K\uparrow$	– 0	0 +	climate adaptive > fixed	fixed > climate adaptive
$r\uparrow$ $K\downarrow$	+ 0	0 –	fixed > climate adaptive	climate adaptive > fixed
$r\downarrow K\downarrow$together	–	–	climate adaptive ~ fixed	fixed ~ climate adaptive
$r\uparrow K\uparrow$together	+	+	fixed > climate adaptive	climate adaptive > fixed

Summary comparison of outcomes for population biomass and cumulative harvest under a climate adaptive versus fixed fishery management strategy, including how harvest and biomass reference points are modified under climate adaptive management. Down/up arrow indicates a decline/increase in the associated demographic parameter due to a climate impact, while a negative/positive/0 sign indicates a decline/increase/no change in the reference point.

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at which carrying capacity and/or productivity changed (S7 Fig), and whether climate adaptive management strategies responded to demographic change at annual, 4-year, and decadal intervals (Fig 2).

When productivity declined, the lower harvest rate for small population biomass implied by $r_{update,t}$ under climate adaptive management resulted in higher population biomass and lower cumulative harvest than under fixed management (Figs 2ac, S1, S3 Figs). During the 50-year simulation of declining productivity, mean population biomass was as much as

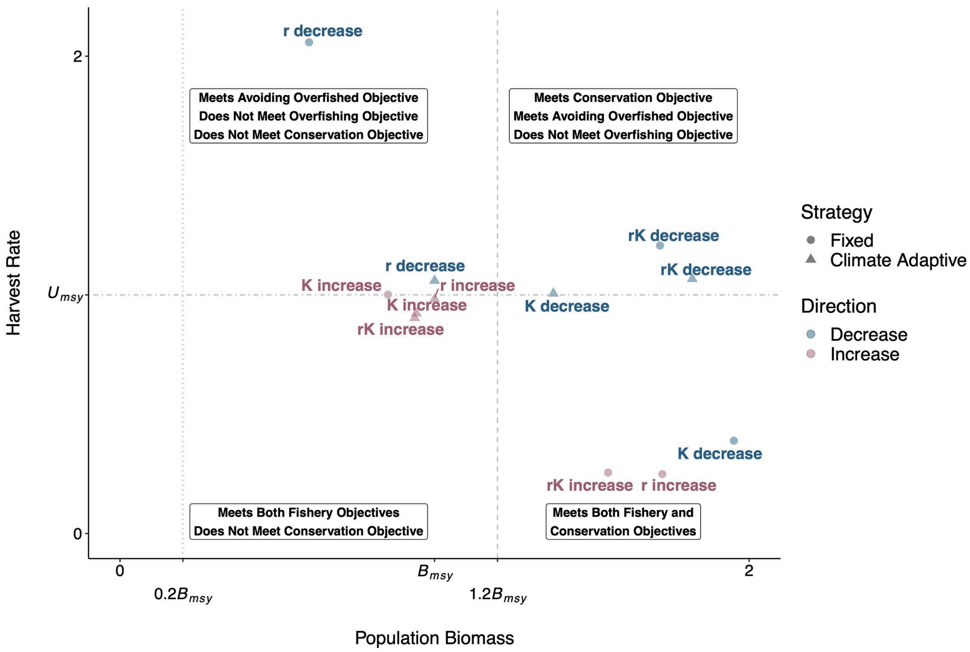

Fig 4. Performance of climate adaptive and fixed management strategies in relation to fishery and conservation objectives. The ability of climate adaptive and fixed management strategies to meet two fishery objectives and a conservation objective given different climate impacts on population demographic parameters. Climate impacts cause decreases or increases in productivity (*r*), carrying capacity (*K*), or both (*rK*). The fixed management strategy does not incorporate these demographic changes into fishery reference points, while the climate adaptive management strategy does so on an annual basis. Fishery objectives were specified in two ways: (i) avoid overfishing by maintaining the harvest rate $U_t < U_{MSY,t}$ (points below the horizontal dot-dash line), and (ii) avoid an overfished population by maintaining the population biomass $B_t > 0.2 * B_{MSY,t}$ (points to the right of the dotted vertical line). The conservation objective is to maintain population biomass above $B_t > 1.2 * B_{MSY,t}$ (to the right of the dashed vertical line). Values indicative of $t = 50$ in each scenario.

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42% greater under climate adaptive management compared to fixed management (years 33–48) but differences in cumulative harvest were smaller and more consistent over time (S5c Fig). Similarly, when carrying capacity increased climate adaptive management resulted in higher population biomass than fixed management, with comparable cumulative harvest (Figs 2bd, S1-S2 Figs). In this scenario, increasing values of $K_{update,t}$ caused reductions in harvest rate at low population biomass. However, compared to the declining productivity scenario, differences between the management strategies in population biomass and cumulative harvest were small (<15%; Fig 2) and more consistent over the 50-year simulation (S5b Fig).

In contrast, when productivity increased, climate adaptive management resulted in a higher harvest rate, lower population biomass, and higher cumulative harvest than fixed management (Figs 2bd, S1, S3 Fig). During the gradual transition to increased productivity, cumulative harvest was at times more than 100% greater under climate adaptive management compared to fixed management (years 33–48) but differences in population biomass were smaller (<40%) and more consistent over time (S5d Fig). Similarly, when carrying capacity declined climate adaptive management resulted in lower population biomass and higher cumulative harvest than fixed management (Figs 2ac). In this scenario, decreasing values of $K_{update,t}$ caused higher harvest rates at small values of population biomass (S1-S2 Figs). During the 50-year simulation of decreasing carrying capacity, cumulative harvest was as much as 36% greater and mean population biomass 22% lower under climate adaptive management compared to fixed management (S5a Fig, years 33–48).

For the scenario in which productivity and carrying capacity declined together, the climate adaptive strategy confronted a tension between higher harvest rates at low population biomass triggered by decreasing $K_{update,t}$ values and lower overall harvest rates triggered by decreasing $r_{update,t}$ values. These forces largely counteracted one another, leading to small differences between fixed and climate adaptive management in population biomass and fishery yield (Figs 2ac, S1, S4 Figs). However, simultaneous increases in productivity and carrying capacity caused the climate adaptive management strategy to produce similar outcomes to increases in productivity alone: the result was lower population biomass and higher cumulative harvest than the fixed strategy (Figs 2bd, S1, S4 Figs). In this scenario, the climate adaptive strategy triggered higher overall harvest rates due to increasing $r_{update,t}$, which dominated the lower harvest rates at small population biomass implied by increasing $K_{update,t}$. Differences in population biomass and cumulative harvest were fairly consistent over time in scenarios with simultaneous increases or decreases in both productivity and carrying capacity (S5ef Fig). The magnitude of contrast between the climate adaptive and fixed management strategies was much greater when both productivity and carrying capacity increased (<25% differences in population biomass and >50% differences in cumulative harvest; Figs 2bd) than when they both decreased (<10%; Fig 2ac).

On average across all climate impact scenarios and the range of demographic parameters we explored, quantitative differences between the climate adaptive and fixed strategies were larger for population biomass than for cumulative harvest (Figs 2-3). However, the positive effects of climate adaptive management on cumulative harvest were especially large in the scenarios with increasing productivity and increasing productivity and carrying capacity (Figs 2, 3ef). Overall, scenarios involving changes in productivity magnified differences between the climate adaptive and fixed strategies compared to scenarios involving changes in carrying capacity.

These outcomes can be contextualized in relation to specific conservation and fishery objectives (Fig 4). Across four of the six types of climate impacts on demographic rates explored here, we found that after 50 years the fixed management strategy met a conservation objective to maintain population biomass $> 1.2 * B_{MSY,t}$ (the exceptions were the declining productivity and increasing carrying capacity scenarios). In contrast, the climate adaptive strategy met the conservation objective for only two of the six types of climate impacts (declining carrying capacity, declining productivity and carrying capacity). However, the fixed management strategy failed to meet the fishery objective to avoid overfishing (i.e., $U < U_{MSY,t}$) by a greater margin than the climate adaptive strategy at the end of the 50-year simulations in which productivity alone, or both productivity and carrying capacity, declined. Both climate adaptive and fixed management strategies met the avoid an overfished population objective (i.e., maintain $B > 0.2 * B_{MSY,t}$) in all of the climate impact scenarios.

Changes in management targets for groundfish on the U.S. West Coast

To better ground the theory developed above in real-world fisheries management, we quantified variation in estimated unfished biomass (analogous to carrying capacity in the model simulations) for three federally-managed species along the U.S. West Coast. Scrutiny of stock assessments for Pacific hake, petrale sole, and sablefish shows that as new information has become available from fishery-independent and fishery-dependent surveys over the last two decades, estimates of unfished biomass have changed substantially (Fig 5). Specifically, between 2005 and 2022 the minimum estimate of (median or mean) unfished biomass was 25–65% lower than that of the maximum for these species. If these estimates, which were generated at one-, two- and four-year intervals, are interpreted as revealing declines in unfished biomass (a proxy for carrying capacity), rather than retrospective patterns emerging for a different reason [31,32], then there is a direct implication based on the results of our simulations. During periods when unfished biomass estimates were low, a fixed management approach relying on a static reference point in the harvest control rule (e.g., a long-term average; [33]) would be more likely to maintain higher population biomass and avoid overfishing, while sacrificing the potential for greater harvest. In contrast, the dynamic management approach currently used for these species tracks demographic changes in a manner equivalent to the climate adaptive strategy we simulated (e.g., updating the estimated unfished biomass each time an assessment is conducted), thereby maintaining higher harvest but lower population biomass than expected from a fixed strategy.

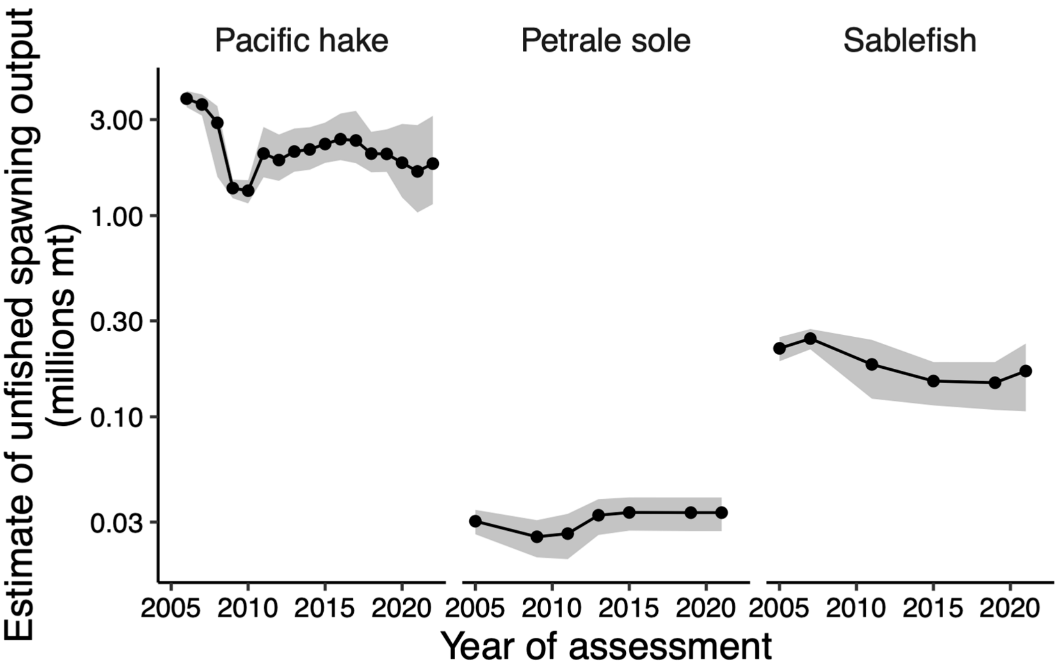

Fig 5. Changes in estimated unfished biomass from stock assessments of three groundfish species. Changes over time (2005-2022) in estimated unfished biomass (log10-scale) from stock assessments of three groundfish species on the **U**.S. West Coast: **(a)** Pacific hake, (b) petrale sole, and (c) sablefish. For Pacific hake **(a)**, the central tendency is a median of the posterior distribution and shading indicates the 95% credible intervals. For petrale sole (b) and sablefish **(c)**, the central tendency is the mean point estimate and shading indicates the 95% asymptotic confidence intervals.

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Discussion

A primary challenge arising from climate change lies in determining how environmental decision makers can best plan to achieve social and ecological outcomes of shared interest across society. Here we compared fixed and climate adaptive strategies for a harvested fish population undergoing climate-driven demographic change, revealing a primary tradeoff such that a climate adaptive strategy may enhance population biomass or fishery yield, but not both simultaneously. This finding contrasted with our hypothesis that a climate adaptive management strategy that dynamically responds to changes in productivity and carrying capacity would optimize fishery yield, and also protect population biomass, compared to a fixed, or business-as-usual, management strategy. Specifically, we found that in scenarios where a climate adaptive strategy favored higher biomass, the fixed strategy favored greater fishery yield, and vice versa (Table 1). Hence, the responsiveness of management to climate change did not necessarily improve outcomes for all management objectives. In such cases, climate considerations may be an important component of management frameworks that evaluate competing objectives and quantify risk profiles [34,35]. Overall, the results fill a gap in understanding the effects of gradual course corrections to fisheries management on transient population and harvest dynamics under both favorable and unfavorable non-stationary environmental conditions. These findings have implications for assessing and adapting to climate risk in other sectors of natural resource management and beyond.

The outcomes of climate adaptive and fixed strategies differed because of the influence of demographic change on harvest rates, as expressed through the sloped harvest control rule. For example, in scenarios with increasing productivity, managers can choose to maintain a constant harvest rate U_{MSY}, or alter course to track the productivity change by increasing the harvest rate. In this scenario, the climate adaptive strategy produced greater yield over time by allowing the fishery to more effectively capture surplus production when compared to fixed management. From a food security perspective, in the increasing productivity case (all else being equal) climate adaptive management outperformed fixed management. In contrast, if climate acted to increase carrying capacity K_t without altering productivity r_t, the climate adaptive course resulted in higher equilibrium biomass, but a lower optimum fishery yield, because the shallower slope of the harvest control rule (Fig 1, equations 3–4) constrained the capture of surplus production during the period of demographic transition. From a food security perspective, in the increasing carrying capacity case (all else being equal) fixed management outperformed climate adaptive management. These and other results were generally robust to whether climate adaptive management updated reference points annually or at less frequent intervals. Less frequent updating of reference points only slightly diminished the contrast with a fixed management approach.

Previous research has also explored climate impacts on demographic rates and the consequences for population dynamics and harvest of fishery species. Burgeoning empirical evidence links environmental change to stock productivity [36–38]. Concurrently, modelling studies demonstrate that climate adaptive management strategies that account for declining productivity can preserve population biomass (as we found here), despite challenges and uncertainty associated with these changes on decision-relevant timescales [15,17,22,23,36]. However, these studies disagree about the effect of climate adaptive management strategies on fishery harvest. Our research suggests that harvest may be reduced when productivity declines under climate adaptive management, consistent with recent findings for Bering Sea snow crab under simulated declines in productivity [15]. However, Kaplan et al. [22] found that harvest may increase (Pacific hake in the California Current ecosystem) or may not change (mackerel in the Nordic and Barent Seas) under climate adaptive management like that simulated here (their harvest control rule 4) in the face of declining productivity. Although simpler in its analytical approach than other work (e.g., the management strategy evaluations considered by [19]), the present study helps to contextualize these previous results by outlining the general conditions under which we would expect climate adaptive management to lead to increases or decreases in harvest. The contrasting results from our alternative climate scenarios and other published studies also emphasize that a climate adaptive strategy can be, but is not necessarily, more likely to conserve population biomass. Future research to explore the specific environmental, demographic, and governance contexts in which greater or lesser population biomass and fishery yield should be expected may provide further insight for regional management issues.

The surplus production model we relied on in this study is a simplification of reality that assumes the assessment and implementation of management procedures observe the true state of the population without error. Similar model formulations have been employed usefully to understand stock status and changes in productivity globally [38–40] and for non-marine species [41]. Surplus production models can represent the end result from a combination of many complex demographic processes through just two parameters, the carrying capacity K and productivity r, that immediately connect to a range of biological processes. For example, higher recruitment due to environmentally-driven improvements in early life history survival (e.g., [42]) can be interpreted as affecting carrying capacity and B_{MSY} [43]. In contrast, directional changes in natural mortality due to temperature-mediated effects on metabolism [44] or predation rates [21] modify productivity and U_{MSY}, as well as carrying capacity and B_{MSY} [45]. Productivity and carrying capacity parameters can also covary [41] and have been used successfully to estimate the influence of environmental change on fish population dynamics [46]. Our purpose here is not to link changes to a specific biological process but rather to reveal general themes and tradeoffs between scenarios under directional climate change. While future work may add additional features of populations (e.g., age- or size-structure, stochasticity) and management systems (e.g., uncertainty associated with estimation of population parameters or implementing management actions), the conclusions drawn here about biomass-harvest tradeoffs resulting from employing climate adaptive versus fixed management strategies are unlikely to be altered by them [15].

The consequences of interactions between climate-driven changes and harvest management strategies are only beginning to reveal themselves, and our work suggests promising future directions of inquiry. For example, extending the model to include multiple interacting species with distinct climate responses may offer important additional context [22,47,48]. Linking changes in productivity and/or carrying capacity explicitly to specific biological or ecosystem processes (e.g., changes in size at maturity or mortality regimes with predator-prey dynamics) and management rules (e.g., size-selective harvest) would help parse the effects of specific climate-driven changes. Importantly, the models presented here provide testable management predictions. For instance, we show that a fixed management strategy maintains population biomass at larger values, making it more likely to achieve the conservation objective across a range of climate scenarios when using a commonly structured (sloped or "hockey-stick") harvest control rule. Therefore, a testable prediction is that fixed management strategies are better aligned with precautionary principles that conserve stock biomass. The importance of this type of precautionary management may be especially acute in systems where there is large uncertainty in the ability to estimate stock status or about the existence of tipping points [49–51]. These types of considerations related to increased complexity, stochasticity, and uncertainty could be well-addressed using a management strategy evaluation framework [52].

Our study adds to the field of climate-ready fisheries by illuminating biomass-harvest and fishery-conservation tradeoffs that emerge as climate impacts occur. These tradeoffs arise whether or not the fishery management system responds to the climate impacts or if the climate impacts improve or diminish productivity and carrying capacity. Amid widespread calls for modernizing fishery management systems to address non-stationary population dynamics emerging from changing ocean and climate trends [53–55], it is important to be transparent and specific when describing counterintuitive outcomes for focal stocks, fishing-dependent communities, and broader ecosystem structure. Indeed, a binary framing of whether a climate adaptive management strategy is an improvement over a fixed one is misleading. Decision makers would do better to consider directly how they wish to negotiate these tradeoffs. In doing so, the larger body of research on the topic of climate-ready fisheries highlights the opportunity to bring in new information flows, develop participatory fishery management processes, and embrace co-management (e.g., by integrating on the water observations of fishers; [55]).

Observations of climate-driven changes, and forecasted changes, in demographic rates are increasingly common [15,35,56]. In the examples we provide for U.S. West Coast groundfish, estimates of baseline productivity (e.g., equilibrium spawning biomass; also referred to as unfished biomass) and associated biomass reference points are updated each time an assessment is made (every 1, 2, or 4 years). This adaptive management approach, which is consistent with the climate adaptive management strategy we simulated, is implicit but its effects on fishery and conservation objectives follow explicitly: declines in estimated unfished biomass will favor increasing harvest, while increases will favor maintaining larger population biomass. These consequences can emerge despite the fact that in operational settings practitioners cannot know whether estimated changes in unfished biomass are due to data or model issues, real demographic changes due to a host of climate (or other) factors, or some mix of the two. Finally, we emphasize that the implicit changes to estimates of unfished biomass described here are distinguished from an assessment model and management process that incorporates a time-varying unfished equilibrium biomass ("dynamic B_0"), representing the biomass at any time that would result if fishing did not occur [36]. Time-varying parameters could potentially yield larger interannual variability in reference points and associated harvest control rules, complicating harvest advice in ways not explored here.

In contrast to U.S. West Coast groundfish, many management reference points for another group of species, Pacific salmon, remain fixed, despite well-documented age truncation that implies reduced productivity [57,58]. Though our model is not intended to represent the particulars of salmon life histories, the inference from our simulations associated with this fixed management strategy is that population biomass will be lower and cumulative harvest higher than if a climate adaptive management approach were implemented. While these two examples come from the Northeast Pacific, similar issues are arising in many regions around the world [22,37,48,59]. These empirical examples illustrate that the findings from the theory we developed here have real-world relevance, calling attention to the difficult choices inherent to continuing with business-as-usual management approaches or keeping pace with changing environmental conditions.

Just as rapid changes in economic policy can unsettle markets, sudden restrictions or alterations in fishing policies can disturb marine ecosystems and the human communities that rely on them. In contrast, more incremental adjustments to regulations can provide continuity in income and business practices while potentially affording opportunities to make changes that substitute for relinquished opportunity [60]. Conceptually, the ideas we explored here have potential for application in fields beyond fisheries, such as disaster management associated with hurricanes and wildfires where adjustments to decision-making are necessary based on changing environmental conditions. There too it will be important to recognize whether the consequences of climate adaptive management are heterogeneous across different societal values. Our key argument is not that there is one clear way forward to best navigate the challenges of climate change. Rather, it is that there is value in directly addressing the environmental management tradeoffs imposed by directional shifts in population dynamics forced by climate change. This study has helped to specify at least one definition of climate-ready fishery management: the intentional implementation of climate-adaptive course corrections to management practices, or the lack thereof. In fisheries, course corrections to management are no panacea, but the decision to evaluate their effects will avoid unintended and potentially undesirable predicaments.

Supporting information

S1 Text. Analysis of discounted cumulative revenue and stochastic population growth.
(DOCX)

S1 Table. Parameters, definitions, and default values for single-species surplus production model subject to a sloped harvest control rule.
(DOCX)

S2 Table. Default values for productivity (r_t), carrying capacity (K_t), and the rate of climate impact (γ) under each of the scenarios.
(DOCX)

S1 Fig. Time series of simulated population biomass. Time series of simulated population biomass when a climate impact causes carrying capacity, *K*, to decrease (a) or increase (b), productivity, *r*, to decrease (c) or increase (d), or both carrying capacity and productivity to decrease (e) or increase (f), and harvest is managed using either a fixed or climate adaptive strategy. All parameters are at their default values (S1 Table); note that initial and final values of *r* and *K* differ in the decreasing versus increasing scenarios (S2 Table).
(TIFF)

S2 Fig. Time series of simulated harvest rate, harvest, cumulative harvest, and example harvest control rules related to climate impacts on carrying capacity. Time series of simulated harvest rate (a, b), harvest (the product of population biomass and harvest rate; c, d), and cumulative harvest (the sum of harvest from *t*-1 to *t* at each time step; e, f) when a climate impact causes carrying capacity, *K*, to decrease (a, c, e) or increase (b, d, f), and harvest is managed using either a fixed or climate adaptive strategy. The bottom panels show the harvest control rule when a climate impact causes carrying capacity to decrease (g) or increase (h), and harvest is managed using either a fixed or climate adaptive strategy (at two example time points, years 25 and 50). All parameters are at their default values (S1 Table); note that initial and final values of *r* and *K* differ in the decreasing versus increasing scenarios (S2 Table).
(TIFF)

S3 Fig. Time series of simulated harvest rate, harvest, cumulative harvest, and example harvest control rules related to climate impacts on productivity. Time series of simulated harvest rate (a, b), harvest (the product of population biomass and harvest rate; c, d), and cumulative harvest (the sum of harvest from *t*-1 to *t* at each time step; e, f) when a climate impact causes productivity, *r*, to decrease (a, c, e) or increase (b, d, f), and harvest is managed using either a fixed or climate adaptive strategy. The bottom panels show the harvest control rule when a climate impact causes

productivity to decrease (g) or increase (h), and harvest is managed using either a fixed or climate adaptive strategy (at two example time points, years 25 and 50). All parameters are at their default values (S1 Table); note that initial and final values of r and K differ in the decreasing versus increasing scenarios (S2 Table).
(TIFF)

S4 Fig. Time series of simulated harvest rate, harvest, cumulative harvest, and example harvest control rules related to climate impacts on carrying capacity and productivity. Time series of simulated harvest rate (a, b), harvest (the product of population biomass and harvest rate; c, d), and cumulative harvest (the sum of harvest from t-1 to t at each time step; e, f) when a climate impact causes carrying capacity, K, and productivity, r, to decrease (a, c, e) or increase (b, d, f), and harvest is managed using either a fixed or climate adaptive strategy. The bottom panels show the harvest control rule when a climate impact causes carrying capacity and productivity to decrease (g) or increase (h), and harvest is managed using either a fixed or climate adaptive strategy (at two example time points, years 25 and 50). All parameters are at their default values (S1 Table); note that initial and final values of r and K differ in the decreasing versus increasing scenarios (S2 Table).
(TIFF)

S5 Fig. Percent differences between the fixed and climate adaptive harvest management strategies in mean biomass and cumulative harvest at different time intervals in the simulations. Percent differences in mean biomass and cumulative harvest between the fixed and climate adaptive harvest management strategies for 16-year time intervals throughout the 50-year simulations in populations subject to a gradual decrease in (a) carrying capacity, (c) productivity, (e) both carrying capacity and productivity, or a gradual increase in (b) carrying capacity, (d) productivity, (f) both carrying capacity and productivity. All parameters are at their default values (S1-S2 Tables).
(TIFF)

S6 Fig. Sensitivity of mean population biomass and cumulative harvest to initial biomass. Mean population biomass (a,b) and cumulative harvest (c,d) under fixed and (annual) climate adaptive management, showing sensitivity to initial biomass ($B_1 = K_1/2,\ 0.8K_1/2,\ 0.6K_1/2,\ 0.4K_1/2,\ and\ 0.2K_1/2$). All parameters are at their default values (S1 Table); note that initial and final values of r and K differ in the decreasing versus increasing scenarios (S2 Table).
(TIFF)

S7 Fig. Sensitivity of mean population biomass and cumulative harvest to initial biomass to the rate of demographic change due to climate impacts. Mean population biomass (a,b) and cumulative harvest (c,d) under fixed and (annual) climate adaptive management, showing sensitivity to t_{change}, the time point at which the changing parameters (carrying capacity and/or productivity) reach their new value. For each simulation, mean biomass and cumulative harvest were calculated for the transient period from the year 1 to t_{change}. All parameters are at their default values (S1 Table); note that initial and final values of r and K differ in the decreasing versus increasing scenarios (S2 Table). Values of t_{change} = 10, 30, 50, 70, and 90 (with lower values of t_{change} corresponding to a faster rate of change in r_t and/or K_t).
(TIFF)

S8 Fig. Percent change under climate adaptive management compared to fixed management in cumulative discounted revenue and cumulative harvest. The percent change under climate adaptive management compared to fixed management in (a-b) cumulative discounted revenue and (c-d) cumulative harvest with changes in productivity, carrying capacity, or both. The figures show responses when updates to the harvest control rule never occur (fixed management) or are climate adaptive and occur decadally, at 4-year intervals, or annually. All parameters are at their default values (S1-S2 Tables). The horizontal dashed line at zero is for reference only.
(TIFF)

S9 Fig. Percent change under climate adaptive management compared to fixed management in mean population biomass and cumulative harvest in stochastic simulations. The percent change under climate adaptive management compared to fixed management in (a-b) mean population biomass and (c-d) cumulative harvest with changes in productivity, carrying capacity, or both, in a time-varying, surplus production model with stochasticity in population growth. The figures show responses when updates to the harvest control rule never occur (fixed management) or are climate adaptive and occur decadally, at 4-year intervals, or annually. The central tendency is the median point estimate from 100 stochastic realizations and shading indicates the minimum and maximum values. All parameters are at their default values (S1-S2 Tables). The horizontal dashed line at zero is for reference only.
(TIFF)

S10 Fig. Percent change under climate adaptive management compared to fixed management in the coefficient of variation (CV) in population biomass and harvest in stochastic simulations. The percent change under climate adaptive management compared to fixed management in the CV of annual (a-b) population biomass and (c-d) harvest with changes in productivity, carrying capacity, or both, in a time-varying, surplus production model with stochasticity in population growth. The figures show responses when updates to the harvest control rule never occur (fixed management) or are climate adaptive and occur decadally, at 4-year intervals, or annually. The central tendency is the median point estimate from 100 stochastic realizations and shading indicates the minimum and maximum values. All parameters are at their default values (S1-S2 Tables). The horizontal dashed line at zero is for reference only.
(TIFF)

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