

Climate-mediated stock redistribution causes increased risk and challenges for fisheries management

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The environmental conditions that marine populations experience are being altered because of climate change. In particular, changes in temperature and increased variability can cause shifts in spatial distribution, leading to changes in local physiological rates and recruitment success. Yet, management of fish stocks rarely accounts for variable spatial dynamics or changes in movement rates when estimating management quantities such as stock abundance or maximum sustainable yield. To address this concern, a management strategy evaluation (MSE) was developed to evaluate the robustness of the international management system for Pacific hake, an economically important migratory stock, by incorporating spatio-temporal population dynamics. Alternative hypotheses about climate-induced changes in age-specific movement rates, in combination with three different harvest control rules (HCR), were evaluated using a set of simulations that coupled single-area estimation models with alternative operating models representing spatial stock complexity. Movement rates intensified by climate change caused a median decline in catches, increased annual catch variability, and lower average spawning biomass. Impacts varied by area and HCR, underscoring the importance of spatial management. Incorporating spatial dynamics and climate change effects into management procedures for fish stocks with spatial complexity is warranted to mitigate risk and uncertainty for exploited marine populations.

Keywords: climate change, management strategy evaluation, movement, Pacific hake.

Introduction

The marine environment is experiencing significant transformation due to climate change, fishing pressure, and environmental change (Cheung et al., 2009; Worm et al., 2009; Hastings et al., 2020). The cumulative impacts of these changes present challenges for management of renewable resources that transcend management boundaries, as well as impose new constraints on the biological dynamics of species. Complex spatial dynamics and movement are common in fish populations. However, stock assessments frequently assume that abundance, life history parameters, and fishing mortality can be aggregated to a single spatial area (Berger et al., 2017; Cadrin et al., 2019; Punt, 2019). Here, we ask in what way ignoring spatial dynamics in fish populations affect an exploited stock subject to changes in movement rates initiated by climate change across a range of alternative harvest scenarios.

Using a two-area operating model (OM) and a standard age-based estimation model (EM) with no spatial resolution, a management strategy evaluation (MSE) was conducted to jointly evaluate the potential consequences of climate change and choice of harvest control rule (HCR) for a stock that exhibits interannual migration between two distinct management areas separated by an international boundary. Movement rates and distribution shifts amplified by climate change have the potential to negatively influence management (e.g. setting sustainable annual total allowable catches, TACs), but appropriate management procedures can act to mitigate risks associated with stock redistribution and related changes in cumulative fishing pressure.

We investigate these issues by applying our model to Pacific hake (*Merluccius productus*). Pacific hake is currently managed without explicit regard to spatial stock structure or movement, regardless of evidence of migratory movements (Agostini *et al.*, 2006; Malick *et al.*, 2020). The current stock assessment estimates total spawning biomass and is used to apply a fishing mortality-based HCR (Berger *et al.*, 2019). The coastwide TAC is set annually by an international management committee set forth by the joint US and Canada Pacific Hake Treaty (2004) using a HCR that specifies the maximum TAC that the management committee can apply. The coastwide TAC is apportioned by country (73.88% to the USA and 26.12% to Canada) based on historical catch as specified in the Treaty.

A common issue with area-specific allocation of fishing quotas from a single area model is that the allocation is often based on regional historical catch or abundance rather than current estimates of population distribution such as from a survey (Bosley *et al.*, 2019; Baudron *et al.*, 2020). This problem is exacerbated with seasonally migratory stocks. A static division of quotas might become incompatible with altered stock distribution and dynamics due to increasing ocean temperatures, hydrophysical changes, and other climate-driven impacts on population dynamics (Pinsky and Fogarty, 2012; Punt *et al.*, 2014; Baudron *et al.*, 2020). Climate change may also increase or decrease stock productivity (Free *et al.*, 2019),

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or contribute to differential production among areas. Additionally, conflicts over a resource shared across political borders may arise when the resource is present in a country at one time of the year, but subsequently migrates into another country ("downstream effects"). For example, the "mackerel wars" led to significant political conflict over the share of the TAC between EU, Faroe Islands, Iceland, and Norway due to the migratory behaviour of Atlantic mackerel (Jensen et al., 2015). Simulations exploring Atlantic Mackerel management procedures showed that spatially explicit models can have a significant demographic effect on stock estimates (Boyd et al., 2018). Many fisheries are managed as single biological stocks, e.g. implying that when stocks are transboundary, quotas need to be distributed among regional stakeholders in the fishery. Thus, changes in future population distribution due to fishing, climate change, or stochastic spatial dynamics may cause conflicts and present challenges for the management of marine resources.

The presence of unique or interacting population segments of a stock is of potential concern for fisheries management, because statistical models assessing the status and abundance of exploited stocks very rarely include spatial components (Goethel *et al.*, 2011; Berger *et al.*, 2017), which can lead to biased management advice especially when movement among areas is not acknowledged. In particular, not including spatial dynamics can result in misleading reference points and biological quantities, and consequently cause lower yields or higher risks of overfishing (Kerr *et al.*, 2014; Goethel and Berger, 2016). Harvesting can also lead to changes in spatial distributions of fish stocks by causing local depletion, changes in size or age composition of the stock, or alterations to the traits or genetic composition of the stock (Ciannelli *et al.*, 2013).

Climate change has the potential to alter a stock's distribution relative to geographic coordinates. For example, some fish stocks have already shown localized and global shifts in their spatial distribution in response to climate change (Perry *et al.*, 2008; Pinsky and Fogarty, 2012; Cheung *et al.*, 2013). In general, fish stocks are expected to either move poleward (Parmesan and Yohe, 2003) or to deeper waters to mitigate the impacts of changing temperatures. Understanding how climate change can impact connectivity of stocks and sub-stocks can help guide management decisions (MD) and set appropriate HCRs.

Robust procedures that acknowledge uncertainty in both biological characteristics and management choices are paramount for the rational management of marine resources, particularly when unique management areas have stock connectivity (Fogarty and Botsford, 2007; Kerr et al., 2014) or distribution patterns alter due to environmental pressures (e.g. climate change; Goethel et al., 2021). A tool to explore the consequences of uncertainty, alternative biological hypotheses, and alternative management strategies is MSE (Punt et al., 2016). MSE is a structured decision-making process that evaluates the performance of management alternatives over many possible futures with regard to managing the fishery or changing biology (Smith et al., 1999). MSEs offer a flexible framework that can be used in support of diverse management needs, such as choosing a HCR, evaluating the long-term consequences of decisions about the structure of a stock assessment model (e.g. Wiedenmann et al., 2017), or the frequency of observation and assessment of a population (e.g. Hutniczak et al. 2019). In the context of climate change, MSEs have been used to evaluate HCRs when recruitment was impacted by rising temperatures for Walleye pollock (A'Mar *et al.*, 2009) and nearshore changes in sea level for Sablefish (Haltuch *et al.*, 2019). Climate-induced changes to movement can also lead to incorrect estimation of abundance, in particular for stocks that exhibit poleward movement intensified by temperature changes (Goethel *et al.*, 2021).

We use the California current population of Pacific hake (M. productus) to construct a two-area OM, where each area represents linked management areas (US and Canadian territorial waters) in the North Pacific. This population is commercially important and is known to migrate within years to spawn and feed (Agostini et al., 2006). The transboundary nature of the stock as well as its expected response to a changing climate makes it an excellent study system to explore the potential impacts of shifts in the spatial distribution of the stock on the future performance of the management system. The hake fishery is the largest groundfish fishery on the US contiguous west coast with a total yield over 400 000 tons in recent years. While little is known about the specific movement rates of individuals in the stock, there are biennial surveys of abundance and age compositions in US and Canadian waters, as well as country-specific age-based catches, which collectively indicate general ontogenetic-based northward movement patterns (Bailey et al., 1982; Agostini et al., 2006). The dominant movement hypothesis is that fish spawn in the Southern California Current in winter, and migrate northward into Canadian waters to feed in summer. The extent of northward migration is assumed to be positively related to fish size. Recent research supports this hypothesis and further suggests that the annual variability in the extent of adult northward movement each year is related to sea temperature at a depth of 100 m with movement farther north in warmer years potentially leading to a larger proportion of the stock in the Canadian management area as sea temperatures increase (Malick et al., 2020).

The objectives of this study are to evaluate the impact of climate-induced changes in movement patterns when (1) alternative HCRs (e.g. harvest decisions) are implemented, and (2) spatial processes are ignored in the stock assessment process for an economically valuable transboundary stock. We do this by comparing the spawning biomass, potential future catches, and catch variability among a range of scenarios pertaining to climate change-induced movement and MDs. To address these objectives, an MSE simulation framework was developed for Pacific hake that incorporates hypotheses about seasonal ontogenetic movement rates among management areas, conducts an estimation procedure similar to the existing stock assessment model used for management, employs alternative HCRs, and measures the performance of these alternatives using metrics informed by stakeholders and incorporating stakeholder input. The results presented here underscore the performance of the Pacific hake fishery as it relates to existing management objectives, including the quantification of uncertainty and risks associated with harvest decisions under an uncertain future with respect to climate-mediated stock redistribution.

Methods

We used a simulation model to evaluate how climate-induced changes in ontogenetic migration patterns could influence the performance of alternative HCRs for the Pacific hake fishery. We investigate these changes by implementing an MSE consisting of a closed-loop simulation with a spatial OM that includes movement of Pacific hake and an EM similar to the current stock assessment model used to calculate the TACs each year. Closed-loop refers to the EM fitting parameters to output from the OM, such that the models can be simulated any number of years into the future. In particular, the closedloop simulation consisted of four components: (1) an OM, (2) data generation from the OM, (3) an EM, and (4) a management model. Each component is described in detail below. The model framework is available as an R-package from https: //github.com/nissandjac/PacifichakeMSE with accompanying code to reproduce figures and supplementary material.

The OM in the MSE contained two spatial areas, which are defined by different quota allocations between the United States and Canada, as well as varying biological characteristics. We refer to the "initialization period" as the historical years 1965–2018, and the "projection period" from 2019 to 2048 (30 years) where we evaluated the management strategies in light of the climate-induced changes in movement.

We compared three HCRs (the default, baseline rule, and two alternatives based on historical management recommendations and actual catch levels) under each of three movement scenarios, resulting in nine sets of projections, each replicated 500 times with unique recruitment deviations and observation error on the biennial survey.

OM

The OM is an age-based model with movement occurring between spatial areas *i*, Canada (i = 1) and the United States (i = 2), and across seasons *t* (four seasons per year evenly divided) and years y. Parameters and variables used in the model are listed in Supplementary Table S1 and the mathematical representation of the population dynamics governing the OM are listed in Supplementary Table S2 [Equations (1)–(23)]. The OM was initialized using observed catch and externally estimated recruitment from the Pacific hake stock assessment (Berger *et al.*, 2019) over the period 1965–2018. The OM then simulated hake population dynamics forward in time using stochastic recruitment, and future removals from the fisheries were specified according to a management model that uses an HCR to set annual TACs based on biomass estimates from the EM.

The equilibrium numbers at age were based on unfished recruitment and natural mortality [Equation (1)], from which the unfished spawning biomass (S_0) was calculated, assuming equal sex ratio [Equation (2)]. The initial stock size was adjusted with a set of historical recruitment deviations [Equation (3)] leading into the first year of the fishery (i.e. 1966). Recruitment was calculated as an area-specific Beverton-Holt stock recruitment function with annual deviations that were assumed to be the same in both spatial domains, and occur in the beginning of the year [Equation (4)], based on the spawning stock biomass, $S_{\gamma, i}$, in the population in that specific year (γ) , and area (i). The recruitment function furthermore included a bias adjustment to ensure that the median unfished spawning biomass across simulations was similar to the equilibrium unfished biomass estimated by the Pacific hake stock assessment (Supplementary Figure S1; Equation (5)). The bias adjustment used in the operational benchmark hake assessment was used in the initialization period to obtain a temporally similar total spawning biomass abundance in the OM as in the operational stock assessment.

We assumed that recruitment occurred in the first season of the year. Cohort survival to the following season depended on annual and seasonal rates of mortality [Equation (6)] occurring simultaneously (i.e. constant natural mortality and time-dependent fishing mortality). Seasonal fisheries mortality in the projection period was calculated based on the season where catches occurred in the last 10 years (Supplementary Figure S2). At the end of a year (i.e. at the end of the fourth quarter), the OM projected each cohort a year forward in time as a standard age-based model [Equation (7)].

Selectivity was modelled for both the fishery and the scientific survey as an approximation of a trawl selectivity curve with four and five parameters for the survey and fishery, respectively [Equations (8)–(10)]. The fisheries selectivity was constant from 1965 to 1991 and then time-varying from 1991 to 2018 to match the stock assessment (Berger *et al.*, 2019; Equation (10)). For the projection period (i.e. after 2018) time invariant selectivity was used across years and seasons, but selectivity was area-specific and adjusted as a part of the conditioning process. The selectivity primarily targets ages 2+, and therefore, the mature part of the Pacific hake population. Selectivity in the operational stock assessment model is implemented to implicitly account for unaccounted variables, such as spatial effects on selectivity estimation (Hicks *et al.*, 2016).

Catch, C, was calculated using the Baranov catch equation by season and area [Equations (11)–(13)]. The OM calculated the fishing mortality rate, F_t , using the specified total catch each season and year using the "Hybrid method" (Pope, 1972; Methot and Wetzel, 2013). Total catch was used as an input in the initialization period, and is specified according to each HCR examined during the projection period (see Alternative HCRs).

The spatial dynamics occur between two areas (Canada and the US) connected through ontogenetic seasonal movement. First, the equilibrium distribution was spread between the two areas using a fixed ratio in the first year of the initialization period [Equation (14)]. Subsequently, each cohort moved between areas with transition probabilities dependent on age, season, and area after seasonal total mortality was applied, as a function of the movement matrix $f(\omega)$ (Equation (15); Figure 1). Transition probabilities were used to model movement as the fraction of fish that leave an area (thus, in a two-box model, the fish that remain in the area is simply the complement of that probability). Mortality was assumed to occur at the beginning of each season followed by movement. The movement rates were modelled as a saturating function of age [Equation (16)] as a two-parameter function that is defined by an area-specific maximum movement rate κ_i and a slope γ_i that determines the rate at which age the fish reach the maximum movement rate. This parameterization causes older fish to have higher northward movement probabilities than younger fish, as newly born recruits and small individuals are less likely to swim large distances into the other area. We additionally add movement predominantly southwards in the last season to let the mature fish return to the United States to spawn. Detailed movement parameters are described in the conditioning section.

Model conditioning and assumptions

The parameters and variables in the OM were based on the single-area 2018 Pacific hake stock assessment (Berger *et al.*, 2019; Supplementary Table S1) with regards to life history,



Figure 1. Movement rates as a function of age and season in the OM. Full lines indicate the fraction of the population moving into Canadian waters (red), and the dashed lines represent the fraction of fish into US waters (blue). The number above each plot represents the season.

fisheries selectivity, and weight at age. To condition the spatial OM, the unfished recruitment parameter R_0 and parameters related to movement were adjusted in order to produce spatial patterns that are similar to the observed data. The observed survey data is available every second year from 1995 to 2018. Additionally, we adjusted the area-specific fisheries selectivity specifically for the Canadian area to get improved agreement between observed and modelled catch at age. The available spatial data are survey biomass (assumed to represent biomass in the third season of the year), survey age compositions, and age compositions from country-specific catch. The movement parameters were adjusted by testing a range of parameters in the initialization period to determine a viable combination of two crucial parameters, (1) the maximum movement rate, κ , which determines the maximum fraction of the population that moves from the United States into Canada, and (2) the return rate, κ_{return} , which determines the fraction of the population that returns to spawn in the United States in the last season (Figure 1). A set of parameters is viable if the OM was able to run the initialization period with the historical catch per country (e.g. a set of parameters is unviable if all stock biomass is constantly present in one area, as the historical catch in the other area then cannot be realized). We then proceeded to adjust the parameters (from within the viable range) to match the spatial survey data and catch age compositions.

The unfished recruitment used in the stock-recruitment relationship R_0 was distributed between Canada and the US marine areas as $R_{0, i=1} = 0.25R_0$ and $R_{0, i=2} = 0.75R_0$, respectively. This procedure was required to obtain comparable biomass and age distribution in the OM and the observed data. The distribution corresponds to the median relative biomass observed for the youngest fish in the historical surveys, and represents the spawning capacity of each of the areas. Steepness, h, was assumed to be the same in both areas. This distribution of spawners causes the effective production to have higher potential in the southern area, in correspondence with the current theory of Pacific hake spawning (Bailey et al., 1982). Total catch during the projection was divided between the two areas with 73.88% allocated to the United States and 26.12% allocated to Canada, following specification in the hake Treaty. However, if the allocated catch exceeded 75% of the vulnerable biomass in an area, the model assumed that the catch was capped at 75% of the vulnerable biomass in that area and season in order to account for decreased catchability during low biomass simulations, which is a general concern by fishers and managers in the fishery. This meant that the simulated catch could be lower than the applied TAC because of a mismatch between the distribution of Pacific hake and the area-specific fisheries. In the OM, we assumed that 85% of all spawning biomass present in the Canadian area moved to the southern area to spawn at the end of the last season of the year, so they were effectively present to spawn during the first season the following year, following current understanding of Pacific hake spawning patterns (Agostini et al., 2006; Figure 1). After fish have moved to the Canadian area during the year, they only rarely $(5\%, \kappa_{out})$ move back to the southern area before the last season. Similarly, we do not assume a large influx to Canada in season one when spawning is occurring $(5\%, \kappa_{out})$.

Data model

The OM produces data categorized by season, area, and year, but it is aggregated to represent the data available to the current stock assessment. The data output is summarized for the EM as total annual catch [Equations (18) and (19)], fisheries age compositions ($\tau_{C, y}$; Equation (20)), and an annual index of abundance from a survey (I_y) reported with lognormal error with a standard deviation of 0.26 (as estimated in the stock assessment; Supplementary Table S2; Equation (22)). The survey also produces age compositions ($\tau_{s, y}$, Equation (23)). The survey for the stock assessment is standardized by kriging acoustic data, and as such has its own uncertainty associated with this standardization. The age compositions were reported without error, as this implementation would have no impact on the interplay between the EM and OM. The survey data (age compositions and biomass index) were provided to the EM in the same years as the survey occurred (Berger et al., 2019), and every second year in the future projections. The OM assumed that the survey takes place in the third season. The OM calculates survey index in each area, but the data model generates a single survey index summed over areas for the EM. The total annual catch each year in the projection period is determined by the management model, described in detail below.

ΕM

The EM is an age-based model with similar dynamics as the OM (i.e. Equations (1)–(12)), but excluding the spatial aspects (i.e. movement, area-specific spawning, and selectivity) and using an annual time step. The equations governing the model are described in detail in Methot and Wetzel (2013), and the specific Pacific hake operational stock assessment model is described in Berger et al. (2019). For the purposes of this MSE, we rebuilt the necessary elements of the operational stock assessment model built using Stock Synthesis using the software "TMB" (Kristensen et al., 2016) to increase computational efficiency, as well as code transparency for the specific needs of this study. The only differences between the EM and the operational stock assessment model are that the EM does not include ageing error in age compositions, and we estimated annual fishing mortality rates. In total, the model estimates 276 parameters (from year 1965 to 2018; the "initialization" period) with the number of parameters increasing with two per extra year modelled into the future (the "projection" period), with one annual recruitment deviation and one annual fishing mortality estimate. The parameters are estimated by minimizing the negative joint log-likelihood function that consists of eight different components, of which four are fits to data and four are penalty functions for parameter deviations (see Supplementary Table S3, Equations (25)–(33)); (1) fit to bi-annual survey, (2) fit to total catch (3) Dirichlet-Multinomial fit to age in survey, (4) Dirichlet-Multinomial fit to age in catch, (5) penalty on recruitment deviations, (6) penalty on selectivity deviations (initialization period), (7) prior on steepness (beta distribution), and (8) prior on natural mortality. For details and more thorough descriptions of likelihood functions in Stock Synthesis see Berger et al (2019) and Methot and Wetzel (2013).

Management model—alternative HCRs

The MSE requires a management model that calculates the TAC in each yearly time step. The management model we employed here takes the ratio of the current terminal year spawning biomass estimate (S_0) to the equilibrium unfished spawning biomass estimate (S_0) from the EM and translates that ratio into an annual TAC, which is then applied to the OM in the following year (y + 1). The TAC is determined using one of three possible HCRs (see Supplementary Table S4) based on the spawning potential ratio (SPR; Equation (35)) with a 40:10 adjustment (Figure 2). We examined the performance of



Figure 2. (a) The three different management scenarios (HCR₀, *MD*, and *AC*) as a function of the TAC (thousand tons) specified by the default HCR specified in the Hake Treaty, denoted by full, dashed, and dotted lines, respectively. Crosses denote the historical MDs on the TAC (*MD*) and triangles denote AC attained (*AC*) as a function of the maximum TAC allowed by the default HCR during the years (2002–2014). (b) The exploitation rate from figure (a) relative to the total unfished biomass for the three catch scenarios. The dashed and dotted lines for *MD* and *AC* indicate the linear fit used to model *MD* and *AC* in future projections.

three alternative HCRs; a baseline HCR specified in the Pacific hake Treaty (HCR_0 ; Equation (36)) and two more precautionary alternatives based on historical management recommendations and actual catch (AC) levels, denoted as MD and AC HCRs, respectively. HCR_0 is the threshold rule articulated in the Pacific Hake Treaty (2004) with a maximum fishing mortality rate defined by applying a fishing mortality leading to *SPR* being 40% of the unfished state (%).

SPR is calculated by first defining the equilibrium number of fish under a given fishing mortality and then converting it to a ratio with regards to the unfished spawning biomass (Equation (35)). We then calculate the F that leads to SPR = 0.4, % and convert it to a harvest rate as $H = 1 - e^{\%}$. The management model furthermore implements a 40:10 adjustment, which means that below $0.4S_0$ the quota is linearly decreased to $0.1S_0$, and below $0.1S_0$ all fisheries are suspended (Equation (36); Figure 2).

While the default HCR defines the maximum catch that may be removed the following year, TACs have historically been set more conservatively in practice by management authorities. Furthermore, the TACs that have been set by management were not fully attained by the fisheries. Therefore, we evaluated two alternative functions for setting TACs that may better represent how stock status in a given year relates to catches removed the following year. For simplicity, we refer to these functions as alternative HCRs, even though in some



Figure 3. (a) Changes in maximum northward movement rate, κ and (b) southward return rates, κ_{return} for the three different climate scenarios (base scenario, moderate increase in movement, high increase in movement denoted by full, dashed, and dotted lines, respectively).

instances practitioners refer to these formulations as the result of partial controllability, or implementation error, in management systems (Williams, 2011).

The first alternative [Equation (37)] is derived from the relationship between the actual historical TACs set by managers in the fishery and the maximum TACs specified by HCR_0 (termed the management decision, MD, HCR; Figure 2a). The second alternative [Equation (38)] is based on the relationship between the actual historical catches and the maximum TACs allowed by the default HCR (termed the actual catch, AC, HCR; Figure 2a). We constructed the alternative HCRs by fitting linear models to describe the relationship between MDs or ACs and the baseline HCR for the years 2004-2017 (Figure 2, fitted parameters in Equations (37) and (38)). All three HCRs were configured to be identical at stock sizes that enacted the 40:10 adjustment (i.e. below $0.4S_0$), following HCR_0 ; Figure 2b).

Climate-induced movement scenarios

We constructed three scenarios describing hypothesized change in movement of Pacific hake ("baseline," "moderate," and "high") in response to increases in temperature due to climate change. The climate scenarios assume that future increases in temperature will increase northward movement rates and decrease southward movement rates as suitable habitat for feeding and spawning shifts northward (Figure 3). The baseline scenario represented constant movement rates with no impact of climate change, i.e. same movement in the future as in the conditioned initialization period. The "moderate" scenario represented climate-mediated movement with a slow increase in the maximum movement rate northward over time of $\Delta \kappa = 0.02 yr^{-1}$ and a slow decrease in the southward return rate $\Delta_{return} = 0.005 \ yr^{-1}$, where Δ represents the

change in movement rate towards an upper limit $\max(\kappa) =$ 0.8, and a lower limit for the return rate at $\min(\kappa_{return}) = 0.5$). The "high" scenario represented climate-mediated movement with a more rapid increase in movement over time such that $\Delta \kappa = 0.04 \ yr^{-1}$ and $\Delta \kappa_{return} = -0.02 \ yr^{-1}$. We implemented the same upper and lower limits on κ and κ_{return} in the "moderate" and 'high scenarios. These movement rates were chosen based on plausible expectations of stock redistribution given potential warming of the waters (Agostini et al., 2006; Malick et al., 2020). Additionally, the movement rates were applied such that they provide a realistic distribution of fish in a historical context, i.e. (see Supplementary Figure S3), as well as of an increase in movement rates that culminates with maximum movement before and after the model is stable (around 2030; Supplementary Figure S1).

Performance metrics

We compare the alternative states of nature (movement scenarios) and HCRs using a range of common performance metrics. The performance of the resulting nine combinations, three alternative HCRs, and three movement scenarios, were evaluated by compiling summary metrics across 500 simulations of 30-year projection period. For generality, performance metrics commonly evaluated in MSEs were reported and include spawning biomass time series, total catch, and a metric describing the average annual variation (Cox and Kro-

nlund, 2008) in yield (*AAV*), defined as $AAV = \sum_{y=1}^{y} \frac{|C_y - C_{y-1}|}{\sum_{y=1}^{y} C_r}$.

Additionally, 'risk' was defined as the probability spawning biomass declined to under 10% of the unfished biomass, as that level triggers a fishery closure, i.e. zero TAC (for a discussion of reference levels see Smith et al., 2009; Worm et al., 2009; Thorpe and De Oliveira, 2019).

Sensitivity to TAC allocation

Additionally, we ran a set of scenarios where the static quota allocation (i.e, 74% assigned to the United States and 26% assigned to Canada) changed with the distribution of observed biomass in the previous year's survey. We add this simulation experiment to allow fishing to follow the fish, by assuming the survey provides an annual estimate of the spatial fish distribution. We describe this as a time-varying quota allocation strategy, defined by annually revisiting the quota allocation based on the fraction of biomass observed in each area in the survey

We compare the time varying quota allocation approach with the HCR_0 static allocation approach across each of the three movement scenarios. Comparisons were conducted across 100 simulations of each movement scenario with each of the two quota allocation approaches.

Results

Conditioning the OM resulted in general agreement between the age compositions in the data and in the model for both the survey in the United States (Figure 4a) and the catch (Figure 4b). In Canada, the average age in the survey data was higher than model estimates from 2009 to 2015, potentially due to variable movement rates or changes in catchability over time. The mean age in the catch was well-represented on average in the OM in most years in both areas (Figure 5b). Furthermore, the agreement between modelled and observed area-specific



Figure 4. Conditioning of the OM. Thick lines indicating model output and thin lines with dots indicating fishery or survey data. Dashed lines (blue) represent the fish present in the southern (United States) area and full lines indicate fish present in the northern (Canada) area (red). Panels show model conditioning performance related to the (a) mean age in the survey, (b) mean age in the catch, and (c) total survey biomass.



Figure 5. Median relative error (lines) associated with estimated spawning stock biomass in the HCR_0 scenario. Each line represents a climate scenario. Shading represents the 5th and 95th quantiles.

biomass in the survey was considered adequate (Figure 5c), with the dominant trends being well-represented.

The baseline EM performed relatively well on average (median relative error of less than 1%), however ,the distribution of spawning biomass estimates was negatively skewed and rather uncertain (-50% and 17% for the 5th and 95th quantiles, respectively, Figure 5). In the climate change scenarios, the redistribution of biomass led to deteriorating EM performance, with a 13% and 19% on average underestimation of spawning biomass for the moderate and high climate change scenarios, respectively. The uncertainty in the two climate scenarios was similar to the baseline scenario. The underestimation of spawning biomass in the climate scenarios is driven by changes in movement causing a larger fraction of the spawning stock biomass to reside in Canada during spawning, while the "baseline" scenario has a majority of the spawning biomass in the United States, causing the coastwide EM to more accurately estimate spawner recruit dynamics. The three climate scenarios had similar variation between runs, where the EM tended to underestimate the spawning biomass (see shading Figure 5). In the other catch scenarios, there were larger differences between the OM and the EM (i.e. MC and AC; Supplementary Figure S4), except for the "high" climate scenario, which has similar estimation precision across all scenarios.

The risk profile for fishery closures was similar between the three different HCRs, with the median risk being less than 2% of years with a fishery closure in the short term, but incrementally increasing over time. The short-term risk is low because the stock in the first year of the MSE simulation is high and constant. There was little difference in risk between the three different HCRs because the TAC in each case is the same at low spawning biomass, i.e. under approximately $SS B_0= 0.3$ (Figure 2). Conversely, the climate change scenarios had a large impact on the risk, with the average risk of closing the fishery increasing from 3% for the baseline scenario to approximately 12% around year 2050 for the "high" effect of climate on movement rates (Figure 6).

Under the HCR₀ rule, climate-induced movement negatively affected total catch and SSB and increased catch variability (Table 1, Supplementary Figure S5). Long term (i.e. after 2040) median catch was 18% lower in the high movement scenario compared to baseline movement (Table 1). Climate change scenarios had negative impact on catch in all scenarios (Supplementary Figure S5, Table 1). Median spawning biomass in the high climate-induced movement scenario was 158 000 tons lower (a 19% decline) than the baseline movement scenario by the end of the simulation (Figure 7b), whereas the moderate climate-induced movement scenario caused a 14% decline. The climate-induced movement scenarios additionally caused increased inter-annual variability in catch, despite the overall median catch being lower (29% and 33% increase in average AAV for the moderate and high scenario, respectively). The lowered catches and declining spawning biomasses are driven by the spawning biomass being pushed into the Canadian waters, which have lower recruitment potential than the US area (Figure 7). Additionally, the TAC is a larger fraction of the available biomass in the United States, which eventually leads to lower catches (if there is not enough biomass present to fulfill the TAC) or overall lower biomass if recruitment is im-



year

Figure 6. Time series of total risk (fraction of years where $S < 0.1 S_0$) under the three different climate and three different catch scenarios. Movement scenarios are denoted by solid, dashed, and dotted lines for the baseline, moderate, and high scenarios, respectively. Panel sets describe alternative catch scenarios defined as HCR_0 baseline HCR, MD: management decision rule, and AC: actual catch. The horizontal dashed line represents 0.05, which is the desired risk threshold for the fishery managers.

Table 1. Differences (%) of long-term (after 2030) medians for catch, spawning biomass, and AAV in all climate and HCR scenarios. The values are percentage change relative to the baseline scenario (no movement and HCR_0). Note that colour scales are reversed in the AAV column to represent blue as the more desirable attribute.

HCR	climate	catch	SSB	AAV
HCR_0	Baseline	0	0	0
MD	Baseline	14.7	14.2	-41.9
AC	Baseline	9.7	28.1	-69.1
HCR_0	Moderate	-14.6	-13.5	29.3
MD	Moderate	11.1	8.1	-37.2
AC	Moderate	2.3	4.3	-42.3
HCR ₀	High	-17.8	-18.9	32.5
MD	High	-7.9	-5.8	4.4
AC	High	-9.2	9	-27.7

paired. The lower catches are amplified by the EM underestimating the total biomass in the climate scenarios (Figure 5), which leads to the management model setting lower TACs.

The two alternative HCRs (MD and AC) both provided higher median catches than the default model, despite setting lower TACs (Table 1). Furthermore, the catch variability was up to 30% lower in the AC scenario providing more stable catches to the fishery, but also reducing the probability of years with very high catch (Supplementary Figure S5). The consequences for the fish population from either the HCR or the climate scenarios are cumulative (Table 1), where the combination of HCR_0 and the "high" climate-induced movement scenario results in lower catch, lower spawning biomass and higher catch variability than all other scenarios. The spawning biomass was highest with the AC rule (at approximately 803 000 tons), while MD rule provided approximately 21% higher median spawner biomass in comparison with HCR₀, when considering the moderate climate-induced movement scenario. For the case with the "high" climate-induced movement scenario paired with the AC rule, the spawning biomass increased in Canada and decreased in the United States compared to the other climate-induced movement scenarios (Figure 7).

The climate scenarios additionally led to tradeoffs between the two countries in terms of the performance metrics: catch, relative spawning biomass, and catch variability. Increased northward movement in the first season and decreased southward movement in season three caused the median spawning biomass in the US waters to decline 113% in the high climate-induced movement scenario compared to the baseline scenario after 2040 (Figure 7). Spawning biomass in Canadian waters increased 37% (Figure 7). Interestingly, both Canadian and US median catches declined by 28% and 34%, respectively, in the high climate-induced movement scenario compared to the baseline scenario using the HCR_0 . This occurred because the total spawning biomass is approximately 26% lower despite a relatively higher amount being present in Canada. Additionally, Canada is still restricted by their allocation fraction of the total TAC. Climate-induced movement increased catch variability in both areas; 32% and 34% for Canada and the United States, respectively for the high compared with the *baseline* scenario (Figure 7c).



Figure 7. Violin plots showing three long term (i.e, data summarized after year 2030) area-specific (Canada left panels; United States right panels) performance metrics for each alternative HCR. Colour of the violin plots denote the climate scenario. The TACs are defined as *HCR*₀: baseline HCR , *MD*: management decision rule, and *AC*: actual catch.

Finally, we tested the sensitivity of the country-specific TAC allocation by changing it dynamically in the projection period dependent on the observed survey biomass (see supplementary information). By adjusting the catch allocation each year, the EM has lower relative error compared with simulations where allocation was constant (Supplementary Figure S6). Time varying TAC allocation causes lower risk in the fishery for all climate-induced movement scenarios (Supplementary Figure S7). Additionally, it increases total yield, but at the expense of lowered spawning biomass in the baseline climate-induced movement scenario (Supplementary Figure S8), while there were consistently net positive effects for both the moderate and high climate-induced movement scenarios.

Discussion

Here, we used MSE to evaluate climate change-induced movement in conjunction with three alternative HCRs, and the results highlight some potential risks and challenges associated with changing stock distribution patterns. We show that climate change has the potential to cause a decline in catches and lowered spawning biomass through redistribution of spawning biomass to areas with lower TACs and lower reproductive potential, despite assuming that recruitment was not directly influenced by temperature. The magnitude of these effects is proportional to the impact climate change may have on the system as the negative effects increased with climateinduced changes. In our study, the Canadian area experienced an increase in spawning biomass present in the area due to climate-mediated movement changes, but could not benefit from this effect due to the pre-allocated TAC for that area, and consequently also experienced a decrease in catch. We also showed that an adaptive, time varying TAC allocation could mitigate some of these effects, similar to simply fishing in the areas where fish are present irrespective of political borders, but that is not often feasible for international transboundary stocks.

Using the baseline HCR, Pacific hake had a high risk of dropping below a level of biomass (i.e. $0.4SSB_0$) where TACs become a lower fraction of the available biomass. This leads to lower catches, and catch reductions may be amplified when the baseline HCR is utilized in combination with unknown distribution changes caused by climate change. Additionally, the increased AAV may be problematic from an economic perspective, as revenue stability decreases from year to year, and thus may limit investments in the fishery. The baseline HCR used for the fishery is based on a general SPR 40:10 rule, which is not implemented specifically with Pacific hake life history taken into account. The high recruitment variability observed in Pacific hake, leads to high uncertainty in short term productivity and forecasting. These issues can lead to management challenges, and potentially to management failure if not taken into account.

We assumed in the projection period that selectivity, natural mortality, and somatic growth remained constant in the OM. Misspecification of any of these can cause estimated reference points to be inaccurate (Butterworth *et al.*, 2014; Horbowy and Luzeńczyk, 2017; Punt *et al.*, 2021). One way to mitigate changes in selectivity and vital rates is time varying reference points (O'Leary *et al.*, 2020), which could be an alternative solution towards sustainability in highly variable fisheries. Alternative approaches include stochastic reference points that help include the uncertainty associate with assessment and natural variability (Mildenberger *et al.*, 2021).

Fisheries selectivity estimated in a stock assessment model is a combination of gear selectivity and spatiotemporal availability (arising from movement and vertical distributions or spatial demography). Therefore, changes in movement could be implicitly reflected in selectivity estimation. Including spatial information in a stock assessment model could improve reference point estimation, and potentially provide more accurate catch advice (Kapur et al., 2021). Similarly, spatial differences in growth and natural mortality can be a challenge for stock assessments that assume homogenous life history parameters across entire populations. MSE frameworks, such as the one presented here, provide an excellent opportunity to investigate such issues and their impact on exploited population managements (Punt et al., 2016), and an MSE was previously used to incorporate time varying selectivity in the Pacific hake stock assessment (Hicks et al., 2016).

Climate-induced movement scenarios represented hypotheses about potential states of nature, not forecasts, of future movement rates that may cause the range distribution of the stock to be more northerly over time. While consistent with a recent analysis of hake distribution as it relates to annual variability in temperature (Malick et al., 2020) and previous hypotheses of hake movement (Bailev et al., 1982; Agostini et al., 2006) no long-term changes in movement rates or species distribution have yet been observed for this population. However, the empirical approach we used here is supported by other climate change MSE studies (Punt et al., 2014). Climate change-induced shifts in distributions have been observed in other ecosystems (Perry et al., 2008; Cheung et al., 2009; Engelhard et al., 2014). The link between these and our study is that we assume that subsurface water temperature will increase along with the predicted changes in global surface temperatures (Pachauri et al., 2014). Because our results show sensitivity in the performance of the current management strategy for hake, further work to develop projections of future subsurface temperature may allow for more realistic projections of movement. The CMIP6 framework (Eyring et al., 2016) may provide an outlet for a global resource that could be used as input to models that model distribution changed on the basis of temperature. Additionally, localized circulation models could provide input for stocks that exhibit a smaller distribution range.

One of the major assumptions in our OM is that the two areas modelled represent management areas rather than specifically modelling areas based on population biology, which may induce localized depletion and subsequent problems, such as decreased recruitment (Smedbol and Stephenson, 2001; Bosley *et al.*, 2019). A model that specifically modelled recruitment hotspots or areas with high prey availability would be useful to simulate fisheries impact on demographics. In a stock like Pacific hake, modelling management areas is reasonable, as (1) it is considered one biological stock (i.e. no genetically distinct subpopulations within the modelled area (Iwamoto et al., 2004), and (2) fisheries (which operates in management areas) are one of the main drivers of population abundance. We make the assumption concerning the interannual migration pattern, where most fish spawn in the south, and then go north to forage, and while the specific movement rates change, there is no qualitative change to this behaviour. Additionally, we assume that there has been no interannual changes to movement in the initialization period. While this pattern follows the current knowledge of the stock, it is not well-grounded in data. Movement rates and interannual spatial distribution could be better estimated if tagging data was available, or if sub-stocks could be identified by genetic analysis (Goethel et al., 2011; Berger et al., 2017), which would also help identify changes and scale to distribution patterns.

Climate change may affect other vital rates for Pacific hake that we did not explore here. Other groundfish in the California Current (e.g. Sablefish) have shown responses to ocean conditions through recruitment patterns (Tolimieri et al., 2018; Haltuch et al., 2019). We did not include explicit relationships between climate change and recruitment success, but the alteration of spawning biomass distribution caused by climate change led to lower overall spawning biomass caused by the spawners being present in an area that we assumed had less recruitment potential, due to recruits rarely being observed there. The link between climate change and recruitment deviations in Pacific hake could improve the realism and ecological context in the model, and is currently being investigated. Establishing robust links between climate change and spatial dynamics is vital to understand implications of not including spatial considerations in management.

Pacific hake is characterized by having substantial recruitment variation, which causes high uncertainty in future stock status and management performance. Quantifying uncertainty, through process error and measurement error, is a key part of an MSE (Punt et al., 2016). Due to the high process error in recruitment, the uncertainty intervals for the performance metrics are quite large, and can be a cause for concern for decision-makers. We used the same recruitment variability as used by the current stock assessment, although this number may be inflated due to the assessment assuming constant natural mortality (Jacobsen et al., 2019), variable growth, or the selectivity estimation not being able to sufficiently account for spatial patterns or gear variability (Hurtado-Ferro et al., 2014). Additional research on recruitment dynamics (also with respect to climate change and spatial scale) would lead to better understanding of reference points and the uncertainty in future stock abundance (Dippner, 1997; Szuwalski and Hollowed, 2016; Punt, 2019).

The results shown here underestimate total uncertainty because the OM was initialized using the median value of parameters estimated in the official stock assessment (e.g. natural mortality, stock-recruitment steepness, or fisheries selectivity). Including uncertainty in these values would better represent the structural uncertainty of both the assessment model and the implementation of HCRs. Additional uncertainty would also occur from the structural uncertainty in the OM, where we assumed a single population with two areas and four seasons. Additional complexity in terms of density dependence, predator abundance, and life history parameter variation could lead to further insights in hake population biology.

Our study shows some potential impacts of climate-driven shifts and ignoring spatial stock structure on the ability of fisheries management to achieve its objectives; maintaining high catch, low variability, and sustainable spawning biomass. While we focus on Pacific hake under a limited range of climate and fishing scenarios, the main results can be extrapolated to other fish stocks, as quotas are generally distributed based on historical catches, and distribution shifts due to climate change impacts are now becoming well-documented (Pinsky et al., 2013; Fossheim et al., 2015; Lenoir and Svenning, 2015; Post et al., 2020). In a world where fish stocks change their distribution, spatial quota allocations specified based on assumed historical distribution may cause overexploitation in recruitment hot spots, or disruption to the stock structure. Adaptive and proactive management that takes into account the ecological impacts of climate change and fisheries can be used to improve management systems where species are vulnerable to overexploitation and climate change effects.

Data availability

The software and data used to produce the simulations and figures are available on Github at https://github.com/nissand jac/PacifichakeMSE.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contributions

NSJ performed all the calculations and wrote the initial draft with help from KNM. All authors contributed to reviewing and editing the final version, and gave the final approval. All authors were involved in the methodology and conceptualization of the study.

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Conflict of interest

The authors declare no conflict of interest.

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