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RESEARCH

Modeling the interactive effects of sea surface temperature, fishing effort, and spatial closures on reef fish populations

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Abstract

Climate change can affect reef fish both directly (e.g., mortality, growth, fecundity) and indirectly (e.g., habitat degradation). The extent to which the effects of rising water temperature could drive changes in fish populations and if and how these effects may interact with potential management interventions remain unclear. The objective of this study was to test various hypothesized mechanisms by which sea surface temperature (SST) could affect reef fish population dynamics and explore these effects in combination with fishing effort restrictions and spatial closures. To do this, we modeled hypothesized relationships between SST and two governing parameters of the fish populations: intrinsic growth rate (r) and carrying capacity (K). We coupled these temperature-dependent fish population models with a fisheries harvest model and explored interactions between thermal effects, fishing effort level, and spatial closures. Under small closure scenarios, we found that the thermal effects models predicted substantially lower fish population biomass and harvest compared to the baseline (constant r and K) model. Under large closure scenarios, the thermal effects models more closely resembled the baseline. Generally, incorporating spatial closures mitigated some of the detrimental thermal effects on fish biomass and allowed for increased harvest under certain fishing effort levels. Whether intrinsic growth or carrying capacity most affected fish population levels also depended on the fishing effort and the spatial closure area. Overall, we described how fishing effort and spatial closures can influence the relative importance of key processes and the extent to which rising water temperatures affect fish populations and harvest.

Keywords Climate change · Coral reef fisheries · Fisheries model · Marine reserves · Population dynamics · Temperature

Introduction

Nearshore fisheries provide food security and support livelihoods for hundreds of millions of people (Cisneros-Montemayor et al. 2016) but are experiencing the consequences of widespread habitat degradation and overexploitation (Mullon et al. 2005). Fisheries management aims to maintain, protect, and enhance fish populations to ensure long-term sustainability of stocks and their associated ecosystems, as well as provide fishing and job opportunities. To meet these goals, fisheries managers use a variety of methods to regulate the frequency and/or intensity of fishing effort, including strategies like spatial closures, bag limits, seasonal closures, and gear restrictions (Woodward and Griffin 2003; Carvalho et al. 2019; Carvalho and Humphries 2021). Implementing these strategies is far from simple, as successful management also requires enforcement, compliance, and community support (Pendleton et al. 2018).

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Fisheries management is further complicated by climate change, as changing ocean conditions can affect fish populations in both direct and indirect ways (Pratchett et al. 2015). Direct effects of warming waters on fish populations include changes in their distribution and life histories (Wang et al. 2020). In general, the geographic ranges of warm-water species are experiencing poleward expansion, while cold-water species are becoming increasingly vulnerable as they approach their thermal limits (Williams et al. 2015). In terms of effects on life history, general trends include faster metabolism, faster growth and maturity, smaller size at maturity, higher mortality, and decreased fecundity in warmer waters, although these vary across species and functional groups (Ospina and Mora 2004; McClanahan 2010; Cheung et al. 2013; Donelson et al. 2014; Pratchett et al. 2015; Wang et al. 2020). Overall, these physiological changes can lead to declines in population growth for many functional groups (Wang et al. 2020).

Fish populations are also indirectly affected by climate change through habitat loss and changes in competition and predation due to range shifts of other species (Pratchett et al. 2011a, b). An example of the former occurs when rising water temperatures cause mass coral bleaching and death, leading to a subsequent loss of an important habitat for many reef fishes (Pratchett et al. 2015). This degradation often leads to a decline in topographic complexity (Bozec et al. 2015). Reef fish and invertebrates depend on coral reefs for food and/or shelter and are highly sensitive to the loss of this habitat (Munday 2004; Pratchett et al. 2006). When reefs degrade, there become fewer places for reef-associated species to shelter from potential predators and competitors, with the result that degraded reefs support fewer individuals and fewer species (Sano et al. 1987; Jones et al. 2004; Wilson et al. 2006; Graham et al. 2006). Fish carrying capacity, diversity, and abundance have been found to decrease as topographic complexity decreases (Friedlander et al. 2007; Noonan et al. 2012; Pratchett et al. 2015; Folpp et al. 2020; Fukunaga et al. 2020). Although climate change affects many aspects of fish life histories, the potential of water temperature to act as a driver of reef fish population patterns remains uncertain. This uncertainty is especially problematic given that certain management strategies may unintentionally interact with climate-driven changes in fish life history traits (Serpetti et al. 2017). For example, climate drivers can cause demographic parameters, which are used to determine biological reference points and harvest rules, to vary on decadal time scales (Free et al. 2019; Tableau et al. 2019).

The objective of this study was to explore the hypothesized mechanisms by which temperature could affect reef fish populations and to subsequently test the extent to which they interact with fishing effort and spatial closure scenarios. To do this, we reviewed the literature and identified potential relationships between sea surface temperature (SST) and two key population parameters in reef fish populations: intrinsic growth rate (r) and carrying capacity (K). Then, we incorporated multiple formulations of the temperature-growth rate and temperature-carrying capacity relationships into a theoretical model of a reef fish population and compared projected population biomass. We then coupled this population model to a fisheries harvest model and different fishing effort and spatial closure scenarios to evaluate any potential interactions between temperature effects and management interventions on outputs of fish biomass and harvest.

Material and methods

Thermal effects functions

For all scenarios, we used Insular Pacific-Hawaiian Sea Surface Temperature Anomaly (relative to the 1976–2005 climatological mean) Projections for the CMIP6 SSP2-4.5 scenario (Figure S1). To relate SST to reef fish intrinsic population growth rate, we used a quadratic formulation where the maximum intrinsic growth rate (r) corresponded to an optimal temperature, and deviations from this optimum led to declines in the growth rate. There is an abundance of literature that supports this formulation (summarized in Table S1), in particular that reef fish population growth rate will decrease as water temperature increases from an optimum. However, fish population responses to rising temperature are not universal, because different species have different optimal conditions for growth (Jobling 1997). To address this uncertainty, we tested three formulations relating intrinsic growth rate to SST, each representing populations with differing optimal temperatures. For the first formulation, $r1$, we set the maximum growth rate to correspond to a 0° yearly anomaly (i.e., optimal temperature is the 1976–2005 climatological mean; Fig. 1A; Eq. 1), representing a population where growth was highest under historical conditions. For the second formulation, $r2$, we set the maximum growth rate to correspond to a $+1$ °C anomaly (i.e., optimal temperature is 1 °C higher than the climatological mean; Fig. 1A; Eq. 2), representing a population where growth is highest under warmer waters. For the third formulation, we set the maximum growth rate to correspond to a -1 °C anomaly (i.e., optimal temperature is 1 °C lower than the climatological mean; Fig. 1A; Eq. 3), representing a population where growth is highest in cooler waters. We chose a maximum growth rate of $r=0.3$, because it generally represents species targeted in coral reef fisheries such as parrotfishes and wrasses (Labridae) (Carvalho et al. 2019; Froese and Pauly 2023), and established the function so that $r=0$ with an anomaly of 9 °C (Ospina and Mora 2004; Table S1).

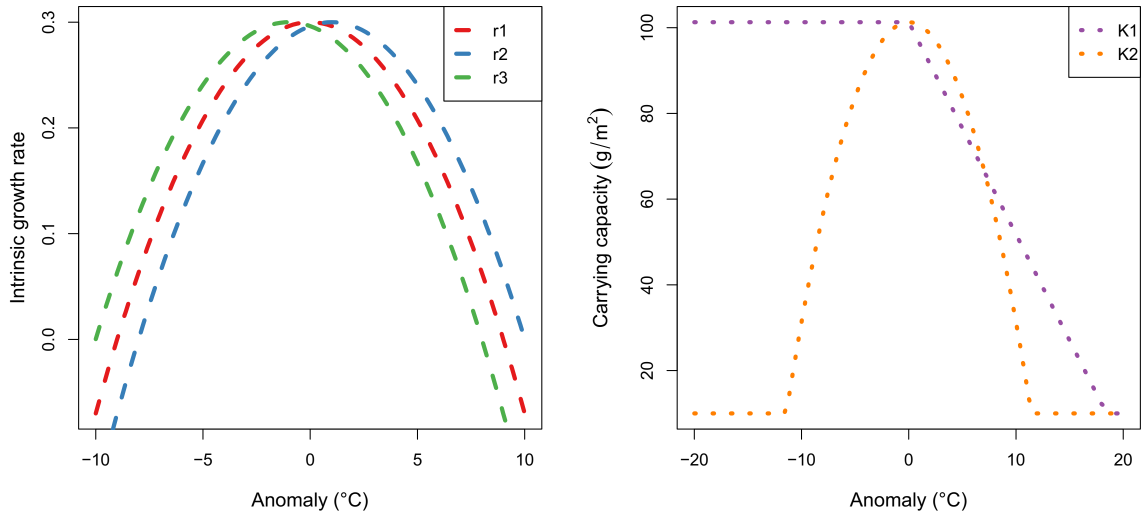

Fig. 1 **A** Temperature-dependent intrinsic growth rate and **B** temperature-dependent carrying capacity as a function of the sea surface temperature anomaly

$$r_{1,t} = 0.3 - 0.0037 * \text{anomaly}_t^2 \tag{1}$$

$$r_{2,t} = 0.3 - 0.0037 * (\text{anomaly}_t + 1)^2 \tag{2}$$

$$r_{3,t} = 0.3 - 0.0037 * (\text{anomaly}_t - 1)^2 \tag{3}$$

To relate SST to reef fish carrying capacity (K), we tested two different formulations. For the first formulation ($K1$), we assumed a linear relationship where increases in SST anomaly led to declines in K (Eq. 4; Fig. 1B). This relationship was based on findings that reef fish carrying capacity is expected to decline ~ 6% by 2040, assuming a 2% annual loss of coral cover (MacNeil et al. 2015). The points used to establish our linear relationship were as follows: 0° anomaly, 101.3 g/m^2 (the maximum K from MacNeil et al. 2015), and 1.23° (2040 anomaly), 95.22 g/m^2 (0.94 K, representing a 6% decline). We established upper and lower limits on the linear function so that it did not extend indefinitely. Maximum K was bounded at 101.3 g/m^2 (the global average expected unfished biomass for resident diurnally active reef fish from MacNeil et al. 2015) and minimum K was bounded at 10 g/m^2 (derived from Darling et al. 2017, where ~ 10 g/m^2 fish biomass was maintained with no habitat complexity). For the second formulation ($K2$), we used a quadratic function where maximum K (101.3 g/m^2) corresponded to an optimal temperature anomaly (0°) and deviations from the optimum led to declines in K, and minimum K was again bounded at 10 g/m^2 (Fig. 1B). We chose to test a quadratic formulation due to its prevalence as a pattern found in the temperature performance curves of ectothermic organisms (Pratchett et al. 2011a, b), and it has previously been found to be a realistic formulation for the response of tuna carrying capacity to SST deviations (Mediodia et al. 2023). We did not test a formulation where K is projected to increase under warming waters (i.e., a higher optimal temperature scenario), because coral habitat complexity has been shown to decline with rising water temperatures (Alvarez-Filip et al. 2011; Bozec et al. 2015).

$$K_{1,t} = \begin{cases} -4.95243768 * \text{anomaly}_t + 101.3 if 10 < K_{1,t} < 101.3 \\ 10 if K_{1,t} < 10 \\ 101.3 if K_{1,t} < 101.3 \end{cases} \tag{4}$$

$$K_{2,t} = \begin{cases} 101.3 + -0.7 * \text{anomaly}_t^2 if 10 < K_{2,t} < 101.3 \\ 10 if K_{2,t} < 10 \\ 101.3 if K_{2,t} < 101.3 \end{cases} \tag{5}$$

Fish population and harvest model

All values for the following parameters and state variables are given in Table 1.

We calculated fisheries harvest:

$$h_t = X_{t-1} f\left(E_t\right) A \tag{6}$$

where fisheries harvest (h_t) was simulated as a function of stock biomass at the beginning of time t (X_{t-1}), fraction of the stock harvested ($f\left(E_t\right)$), and fishing area (A, White and Costello 2014). We used an exponential survival function to calculate the fraction of the stock harvested:

$$f\left(E_t\right) = 1 - \exp\left(-E_t q_t\right) \tag{7}$$

Table 1 Defined parameters and their data source for the fish population and harvest model. *t* indicates the timestep and *i* and *j* refer to the respective patch

Parameter	Units	Description	Value and data source
h_t	g/m^2	Fisheries harvest at time *t*	Calculated from Eq. 6
$f(E_t)$	Proportion	Fraction of the stock harvested time *t*	Calculated from Eq. 7
E_t	Proportion	Fishing effort at time *t*	Varies
q_t	Proportion	Catchability at time *t*	1
N_t	g/m^2	The fish population after harvest	Calculated in Eq. 8
G_t	g/m^2	The fish population after growth	Calculated in Eq. 9
r	Rate	Baseline intrinsic rate of population growth	0.3 (Froese and Pauly 2023), previously used for reef species in fisheries models (Boncoeur et al. 2002; Carvalho et al. 2019; Cabral et al. 2019). Varied in *r* models
K	g/m^2	Baseline carrying capacity	101.3 (MacNeil et al. 2015). Varied in *K* models
X_t	g/m^2	The fish population after dispersal	Calculated in Eq. 10 for spatial scenarios; for nonspatial scenarios, $X_t = G_t$; $X_0 = 10$
A_i	Proportion	Area of patch *i*	1 for nonspatial scenarios; varied in spatial closure scenarios. $A_i + A_j = 1$
D_{ji}	Proportion	Dispersal kernel between patches	Calculated in Eq. 11
Q_{ji}	Proportion	Proportion of individuals in patch *j* that disperse to patch *i*	Equal to A_i
S	Unitless	Site fidelity parameter used to s6cale $Q_{s,d}$	0.5 in management strategy runs; varied in sensitivity analysis

where the fraction of the stock harvested ($f(E_t)$) was based on fishing effort (E_t) and catchability (q_t, White and Costello 2014). We calculated the post-harvest population for time *t* (N_t):

$$N_t = X_{t-1} - h_t \tag{8}$$

We then simulated logistic fish population growth:

$$G_t = N_t + r * N_t * \left(1 - \frac{N_t}{K}\right) \tag{9}$$

where the fish population biomass after growth (G_t) was a function of the population biomass after harvest (N_t), intrinsic population growth rate (r), carrying capacity (K, Schaefer 1957). For the temperature-dependent model versions, *r* and *K* were replaced by the respective temperature-dependent version of the variable at each time step (e.g., baseline *r* replaced by r_1).

Fishing effort and spatial closure scenarios

We tested different scenarios of fishing effort and spatial closures in conjunction with the *r* and *K* thermal effects models. First, we varied fishing effort (E_t) from 0 to 0.5, to represent measures taken to regulate the amount of fishing. The fishing effort value range was set to range from no fishing (0) to the value that led to extinction of the stock in the baseline (nonspatial, constant *r* and *K*) model (0.5, Figure S2). Then, we tested a range of spatial closures (0 to 100% of area designated as no-take spatial closures). To incorporate spatial closures, we used a two-patch model framework where each patch has a fish population and, at each time step, the two populations can disperse and move from one patch to another (Fig. 2). We used dispersal methods from White and Costello (2014) where, after harvest, the fish biomass disperses from one patch to another:

$$X_{i,t} = \frac{\sum_{j=1}^{N} D_{ji} A_j G_{j,t}}{A_i} \tag{10}$$

where the final stock biomass in patch *i* at time *t* ($X_{i,t}$) was a function of the dispersal kernel (D_{ji}), patch areas (A_i, A_j), and fish biomass after growth ($G_{j,t}$, White and Costello 2014). The dispersal matrix was calculated by modifying a common pool matrix by a site fidelity term (S) using methods from White and Costello (2014):

$$D = \begin{bmatrix} Q_{i,i} + \left(1 - Q_{i,i}\right)S & Q_{i,j} - Q_{i,j}S \\ Q_{j,i} - Q_{j,i}S & Q_{j,j} + \left(1 - Q_{j,j}\right)S \end{bmatrix} \tag{11}$$

where $Q_{s,d}$ represented the proportion of individuals moving from a source (s) to destination (d) patch. For the common pool matrix (i.e., $S = 0$), the fraction of individuals that disperse to each patch was proportional to the relative size of the patches (e.g., if patch *i* covers 70% of the domain, then 70% of all individuals go to patch *i*). Higher values of site fidelity increased the fraction of the population that remained in their original patch. $S = 1$ represents completely isolated patches (i.e., no movement between patches). A more detailed explanation of how S modifies the common-pool matrix can be found in White and Costello (2014). Note that our model was strategically designed using simplifying

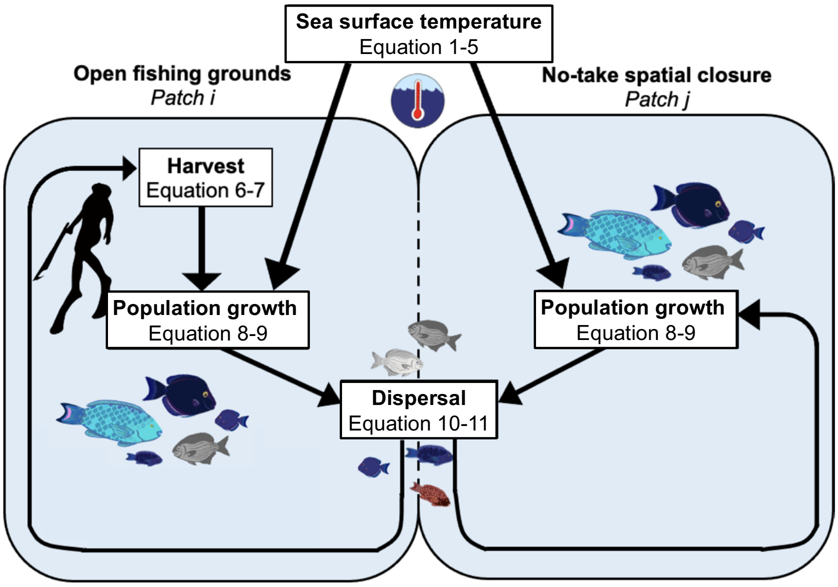

Fig. 2 The structure and flow of the full model framework, evaluating thermal effects, fishing effort, and spatial closures (graphics by A. Innes-Gold). We begin by calculating a temperature-dependent growth rate or carrying capacity (with the exception of the baseline model with no temperature dependencies), followed by fisheries harvest, fish population growth, and fish dispersal

assumptions to compare relative population dynamics in response to fishing and temperature scenarios (Levins 1966) and therefore should not be viewed as generating absolute, quantitative predictions of reef fish populations.

For our analyses, we tracked outputs of fish population biomass (calculated as $X_i * A_i + X_j * A_j$) relative to (1) the baseline model fish population biomass and (2) the optimal nonspatial management scenario. For the biomass relative to the baseline model, we divided each model's projected biomass by the baseline model's projected biomass. We determined the optimal nonspatial management scenario by running the baseline fish population and harvest model with no spatial closure and a variety of fishing efforts (Figure S2). From this, we determined the fishing effort scenario that maximized harvest and termed this the "optimal nonspatial management scenario" ($E = 0.16$). We then divided each model's projected biomass by the optimal nonspatial management scenario's biomass (51.35 g/m^2), giving us biomass relative to the optimal nonspatial management scenario. We also divided the projected harvest from each model by the respective harvest of the optimal nonspatial management scenario (7.59 g/m^2). All analyses were conducted in R 4.2.1 (R Core Team 2024).

Simulations

We first ran the baseline fish population model (no thermal effects) and then again with each of the five different thermal effects model versions ($r1$–$r3$, $K1$–$K2$). For these trials, there was no fishing ($E = 0$) or spatial closure ($A_j = 0$). We then ran the same thermal effects model versions while varying fishing effort. Finally, we ran the same model versions and fishing effort values under varying spatial closure scenarios (5%, 10%, 30%, and 50% of area closed to fishing). We compared outputs of fish biomass (relative to the baseline model and relative to the optimal nonspatial management scenario) and harvest (relative to the optimal nonspatial management scenario). We analyzed the average outputs from the last 20 years of the simulation (corresponding to SST anomalies 2070–2089), chosen because the baseline model had reached equilibrium by this point.

Results

Thermal effects

We ran simulations with six model versions of thermal effects (baseline model with no thermal effects; $r1$–$r3$; $K1$–$K2$; Figure S3). Aside from the baseline model, the $r2$ model (+ 1° anomaly as the optimal temperature) reached the carrying capacity most quickly, followed by the $r1$ model (0° anomaly as optimal temperature), and eventually the $r3$ model (– 1° anomaly as the optimal temperature). The $K2$ model (quadratic formulation) projected a final biomass ~ 3% lower than the baseline and r model versions, while the $K1$ model (linear formulation) projected a fish biomass ~ 10% lower than the baseline and r model versions. The $K1$ and $K2$ models showed a decreasing biomass trend from years 25–60 (Figure S3). The time-varying, temperature-dependent intrinsic growth rates ($r1$–$r3$) and carrying capacities ($K1$–$K2$) all showed declining trends over time as temperature anomaly increased (Figure S4). The largest parameter changes due to temperature reduced intrinsic growth rate to 0.26 (from baseline 0.3) and carrying capacity to 91 g/m^2 (from baseline 101.3; Figure S4).

Interactions between thermal effects and fishing effort

We then simulated these six model versions with a range of fishing effort values, finding notable interactions between model version and fishing effort level (Fig. 3). For example, at low fishing effort, the r models predicted fish biomass similar to the baseline model, whereas at higher fishing effort levels, the r models diverged from the baseline and predicted lower biomass (Fig. 3A, B). The magnitude of difference between the r models and the baseline varied by model version, with the r2 model predicting ~ 0.95 biomass relative to the baseline model, while the r3 model predicted ~ 0.35 biomass relative to the baseline model at high fishing effort (Fig. 3A). At low fishing effort levels, there was a more notable difference between the K models and the baseline, whereas at high fishing effort levels they converged (Fig. 3A). The fishing effort that produced the maximum relative harvest also varied slightly between model versions (Fig. 3C). In the baseline model, maximum harvest occurred at a fishing effort of 0.16. When using the r3 model, maximum harvest occurred at a slightly lower fishing effort level (0.15). The baseline model produced the highest maximum harvest, followed by the r2 model, the k2 model, the r1 model, the k1 model, and the r3 model (Table S2).

Interactions between thermal effects, fishing effort, and spatial closures

Finally, we ran the same model versions and fishing effort values with a range of spatial closure scenarios (Figs. 4 and 5, Fig. S5). In small and intermediate spatial closure scenarios (5, 10, 30%), the K1 model predicted the lowest relative biomass under low fishing effort while the r3 model predicted the lowest biomass under high fishing effort (Fig. 4). Under the large spatial closure scenario (50%), the K1 model predicted the lowest relative biomass across all fishing effort levels. As the amount of spatial closure increased, the spread of relative biomass across model versions was reduced (Fig. 4). For example, under small spatial closures, the projected biomass relative to the baseline model ranged from 0.35 to 1, depending on the model version and fishing effort level. Under a large spatial closure scenario, all projected biomass relative to the baseline model fell within 0.9–1.

Similarly, there were interactive effects of model version, fishing effort, and spatial closure area on harvest relative to the optimal nonspatial management scenario (Fig. 5). Under small spatial closure scenarios (5, 10%), there was more difference in projected harvest across model versions, particularly at high fishing efforts (> 0.2), compared to large spatial closures (30, 50%), where they were similar regardless of fishing effort. Notably, under small spatial closures, the r3 model predicted the lowest harvest relative to the optimal nonspatial management scenario for high fishing effort levels, but under the large spatial closure scenario, the K1 model predicted the lowest harvest relative to the optimal nonspatial management scenario. Finally, the harvest relative to the optimal nonspatial closure reached higher levels under the large spatial closure scenarios for all models, but required higher fishing effort to do so (Fig. 5).

For all scenarios, site fidelity (S) was held constant at 0.5. We conducted a sensitivity analysis varying S for the full range of possible values (from 0 to 1) but found there were minimal interactions between S and the thermal effects models across spatial closure scenarios under low fishing effort (0.16; Figure S6). Under high fishing effort (0.5), the crossover point between the r and K models shifted based on site fidelity (Figure S7).

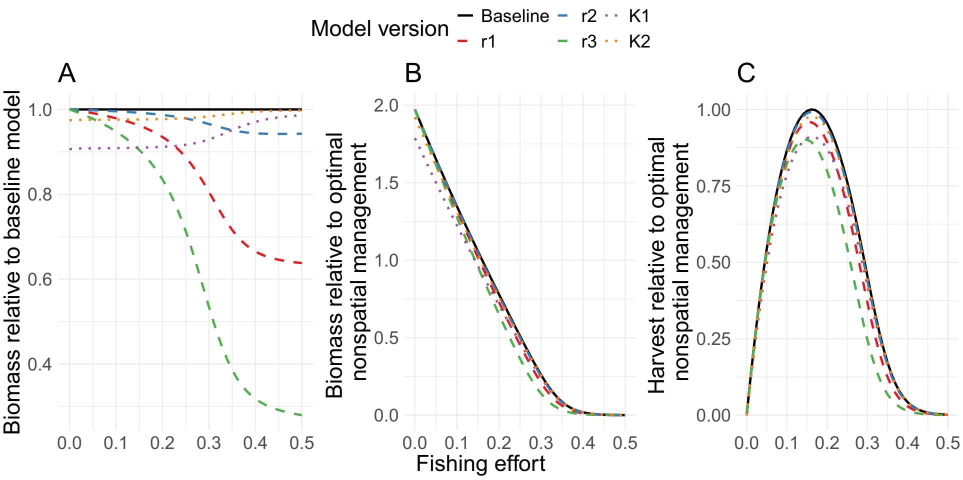

Fig. 3 **A** Fish biomass relative to the baseline model, **B** fish biomass relative to the optimal nonspatial management scenario, and **C** harvest relative to the optimal nonspatial management scenario across model versions and fishing efforts. Because we assumed linear harvest, harvest relative to the baseline model appears identical to biomass relative to the baseline model and thus is not shown. There were no spatial closures

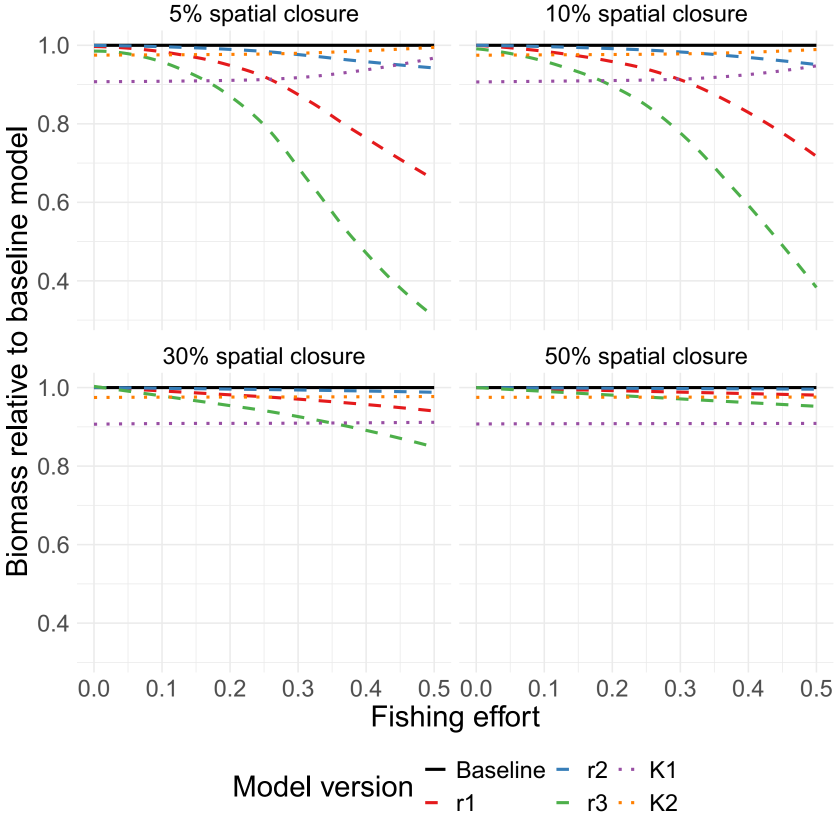

Fig. 4 The effects of fishing effort (*x*-axis), thermal effects model version (color), and spatial closure area (panel) on fish biomass. Fish biomass is relative to the baseline model

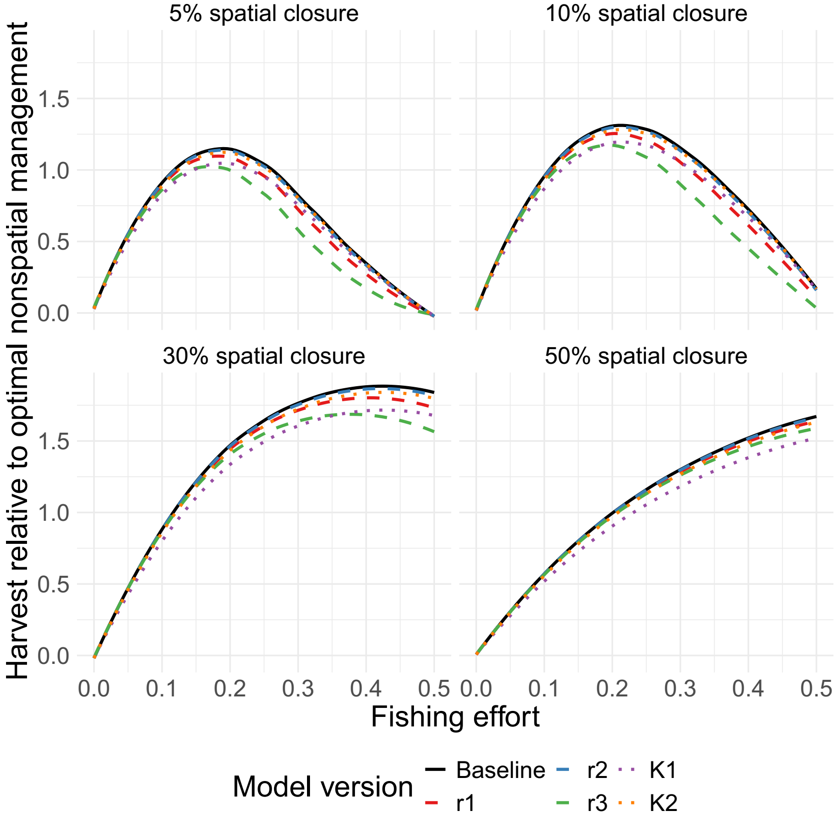

Fig. 5 The effects of fishing effort (*x*-axis), thermal effects model version (color), and spatial closure area (panel) on fisheries harvest. Fisheries harvest is relative to the optimal nonspatial management scenario

Discussion

We explored differing ways to incorporate thermal effects into a fish population and harvest model. Our goals were to explore the extent to which these temperature dependencies could drive patterns in reef fish populations and identify any potential interactions with fishing effort and spatial closures. Overall, we showed that fishing effort and spatial closure scenarios can influence the extent to which rising water temperatures affect fish populations and harvest. Incorporating spatial closures mitigated some detrimental thermal effects while still allowing for increased harvest under certain fishing effort levels.

Interactions between thermal effects, fishing effort, and spatial closures

Overall, we found that fishing effort and spatial closure scenarios can influence the extent to which rising water temperatures affect fish populations and fisheries harvest. This result was seen clearly when comparing the model versions to the baseline model. For scenarios with high fishing and small spatial closures, there were substantial differences in the fish biomass relative to the baseline model, particularly for the $r1$ and $r3$ models. These two models had the intermediate and low optimal temperatures, respectively, and thus reduced population growth rate as water temperature projections passed that optimum. Under low fishing and large spatial closure scenarios, there were smaller differences in predicted biomass between the different thermal effects model versions compared to the small spatial closure and high fishing scenarios. For the 50% spatial closure scenario, the predicted fish population biomass of each model version fell within 10% of the baseline model biomass. At the 30–50% spatial closure scenario, harvest relative to the optimal nonspatial management scenario reached higher levels than under small spatial closure scenarios (but required a higher fishing effort level to do so). Essentially, the increase in spatial closures, and corresponding spatial reduction in fishing effort, mitigated some of the detrimental thermal effects and allowed for increased harvest under certain fishing effort levels.

We observed nuance in model outcomes depending on thermal effects model version used. At low fishing effort, the r models predicted fish biomass similar to the baseline model, but at higher fishing effort levels, the r models diverged from the baseline and predicted lower biomass. The K models showed the opposite trend, where they differed more from the baseline model at low fishing effort than at high fishing effort. Generally, we found that under high fishing/low population scenarios, temperature-dependent population growth rate limited fish biomass, whereas at low fishing/high population levels, temperature-dependent carrying capacity was the limiting factor. In high fishing scenarios, a large amount of biomass was consistently removed before the population had time to grow. Thus, carrying capacity had a smaller effect because the population did not approach carrying capacity regardless of temperature. At low fishing scenarios, the temperature-dependent carrying capacity had a larger impact on biomass and harvest because the population readily approached the reduced carrying capacity. In typical logistic growth models, the intrinsic growth rate drives population dynamics at low abundance while the carrying capacity defines the maximum population size (Anderson and Seijo 2010). Because harvest reduced abundance, the intrinsic growth rate was thus a more important population parameter under increased fishing effort while carrying capacity was more relevant under low fishing.

We found that most of the thermal effects models required equivalent fishing effort in order to maximize harvest, with the exception of the $r3$ model in which a slightly reduced fishing effort maximized harvest. This finding supports claims that in some scenarios, management strategies may need to adjust to account for the effects of rising water temperature, especially in the case that the water temperature has risen past species' thermal optimum. There is a growing body of work surrounding climate-adaptive fisheries management (Pinsky and Mantua 2014; Holsman et al. 2019). Previous modeling work has also highlighted the need for fisheries regulations to adapt harvest regulations based on the impacts of rising water temperatures (Fu et al. 2013; Collie et al. 2021). However, caution should be taken when continuing to use yield-maximizing targets under climate change, which can at times lead to decreased productivity (Szuwalski et al. 2023).

A novel aspect of our work was the framework we used to simultaneously consider temperature-dependent demographic processes along with fisheries harvest and spatial closures. There has been significant previous work surrounding both thermal effects on fish populations (Table S1) and spatial closure modeling (Gerber et al. 2003). Models have been used to demonstrate how spatial closures may affect fisheries harvest (e.g., Hastings and Botsford 1999), as well as the important role of dispersal in spatial management planning (e.g., Gerber et al. 2005). Some previous work has also focused on modeling simultaneous effects of fisheries management and rising temperature, showing that higher temperatures impeded recovery of certain species, particularly those where the projected temperature surpassed the species' optima (Serpetti et al. 2017), similar to our projected results. Other work has focused on methods of incorporation of temperature-dependent bioenergetics—through consumption and respiration at an individual level—which led to lower projected fish biomass than in the baseline model (Heinichen et al. 2022). We aimed to build on previous spatial closure modeling work (White and Costello 2014; Carvalho et al. 2019) to see if and how temperature-dependent demographic processes affected modeled outcomes. Our results are similar to previous thermal effects modeling studies, as we also found that rising temperatures have the potential to decrease fish biomass and harvest. However, our methods and focus differed from previous models as we have explored two potential ways by which climate change may impact fish communities at a population level and explored how fishing effort and spatial closure can mediate these impacts.

Thermal effects on fish population parameters

Incorporating thermal effects relationships led to lower projected biomass and harvest when projected using the Insular Pacific-Hawaiian Sea Surface Temperature Anomaly Projections for the CMIP6 SSP2-4.5 scenario. These results are consistent with predictions that reef fisheries production will decline as SST increases (Jennings and Brander 2010). In our results, the extent of the biomass and harvest reduction varied depending on the formulation tested. In low levels of fishing, the K models generally led to lower projected fish biomass than the r models. This was because with no/minimal fishing, the fish population reached carrying capacity even with the reduced population growth rate as seen in the r models. The $r2$ model behaved very similarly to the baseline model because it utilized a higher optimal temperature that was already similar to the projected SST anomalies. The $r1$ and $r3$ models had lower optimal temperatures, producing a lower population growth rate, and therefore took longer to reach carrying capacity. The $K1$ (linear) model predicted the lowest fish biomass because, at anomalies within ~ 8°, the linear formulation produced a lower carrying capacity than the quadratic formulation (Fig. 1). If anomalies reached higher values (> ~ 8°), there would be a switch where the quadratic model started generating lower levels of carrying capacity than the linear model.

Virtually all organisms have a bell-shaped temperature response curve showing how growth and reproduction increase with SST until an optimal temperature is reached, after which performance will decline (Pratchett et al. 2011a, b). In general, the extent to which rising SST will have positive and negative effects on individual species depends on whether the temperatures are moving toward or away from the thermal optimum (Tewksbury et al. 2008). Increases in SST during months and seasons where temperatures are well below the optimum may increase growth and production, although there are likely to be increased risks to fish populations in seasons where SST begins to exceed the thermal optimum (Pratchett et al. 2011a, b). Current projected increases in SST of 1–3 °C will take summer maximum temperature above the range at which metabolic rate, growth, and reproduction are maximized for some reef fish species (Munday et al. 2008; Nilsson et al. 2009; Donelson et al. 2010). We used quadratic formulations where populations continued to grow until an anomaly of > 9° was reached; however, the SST anomalies we used mainly fell within 3°. If we used more conservative measures of when populations would stop growing, we would likely have seen an even stronger effect of temperature and lower projections of biomass from the r models.

There has been extensive research to understand the effects of temperature on certain species of corals (e.g., Jokiel and Coles 1977) and fish (e.g., Ospina and Mora 2004; Pratchett et al. 2015). However, understanding how these effects scale up to a population level comes with additional challenges. We used the best available data relating to SST, habitat complexity, and reef fish biomass and carrying capacity in order to estimate potential SST-K relationships and explore population-level effects on projected fish biomass and harvest. Our findings highlight that different formulations of the SST-K and SST-r relationships can yield different projections of biomass and harvest, emphasizing the need for future research to further resolve the impacts of SST on fish population parameters.

Limitations and next steps

There were several limitations to our model which suggest areas for future work. Our study focused on a theoretical population of reef fish and is not species or functional-group specific, although there is variation in the response of reef fish to fishing and climate change (Pratchett et al. 2011a, b). Future studies could focus on a specific species or functional groups and adapt the temperature responses to be specific to that group. Additionally, the fish population could be broken down into age classes to incorporate differing dispersal patterns and temperature impacts on juvenile and adult fish. Future work could also consider how somatic growth rate, size at maturity, and fecundity levels differ inside closed areas due to older spawners being present (Evans et al. 2008).

Our model could be extended to increase its spatial and temporal resolution. We represented nonspatial management broadly by varying fishing effort from zero to overfishing, rather than distinct management rules. There could be greater levels of detail included and consideration for discriminate and less discriminate gear types. To expand on the management scenarios that can be represented in this model, future work could involve simulations using a monthly time step to model seasonal closures and differentiating catch by gear type.

Although informed by data, there is uncertainty surrounding the relationships between temperature and population metrics. While we based our thermal effects relationship on the most relevant literature to our topic of interest, species-specific responses would introduce variation into these patterns (e.g., Heenan et al. 2017). We were able to address some of this uncertainty through testing multiple formulations. The uncertainty surrounding the thermal effects relationships could be reduced from additional empirically based parameterization, such as Pratchett et al.'s (2015) findings that show how the growth rate of *Acanthochromis polyacanthus* varies with deviations from an optimal temperature. In addition, our SST-K modeled relationship does not capture the time lag that occurs between increased SST and declining complexity (mortality from coral bleaching loses structure in 4–10 years; Pratchett et al. 2015).

Additionally, numerous other direct effects of climate change would be useful to incorporate into a fish population and harvest model framework, including poleward migration (distribution shifts and changes in demography and abundance; Woodworth-Jefcoats et al. 2017), decreases in species maximum sizes (Cheung et al. 2013), and physiological responses to ocean acidification and reductions in dissolved oxygen (Pratchett et al. 2015). Finally, the model could be run using multiple CMIP6 scenarios, as has been done in other modeled systems (e.g., Woodworth-Jefcoats et al. 2017). However, exploring the effects of various climate change scenarios on fish populations was outside the scope of this study, as we focused on the effects of temperature on intrinsic growth rate and carrying capacity and then expanded these relationships to explore their interactions with fisheries management scenarios.

Conclusion

Declines in fish populations due to exploitation and climate change threaten both ecosystems and food security. Because of these declines, many coastal nations are prioritizing the management of their marine resources. In this study, we presented a fish population and harvest model that explores potential climate change impacts as well as fishing effort and spatial closures, in order to better understand the interactions between multiple drivers of fish populations. Overall, we described how fishing effort and spatial closure scenarios can influence the relative importance of key processes and the extent to which rising water temperatures affect fish populations and harvest. We also showed that management strategies like spatial closures can help mitigate detrimental thermal effects without necessarily sacrificing harvest. As the interactive effects of climate change and resource exploitation continue to cause ecosystem degradation and fisheries declines, predictive models that account for multiple stressors will be essential as managers work to sustain and restore resources.

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Data availability All model code is publicly available at https://github.com/ainnesgold/sst_fisheries_2024 and archived at https://zenodo.org/doi/10.5281/zenodo.13316728.

Declarations

Competing interests The authors declare no competing interests.

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