



Fish catch management strategies: Evaluating the interplay between body size and global warming

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Abstract

Environmental temperature and body size influence the life cycle of the species, with consequences for population size. In addition, it has been reported that increased temperature can lead to a decrease in body size. In the context of a resource-stock, whose abundance is diminished by the action of an endothermic predator and also by small-scale fishing activity, we analysed a Schaefer-type fishery model that incorporates parametric variables associated with thermal performance, metabolic theory, and warming. We project the biomass of the resource in a thermal tolerance range with an increasing temperature trend obtained from current data. In the short term there could be an increase in biomass. However, over time the stock will decline rapidly, in association with the intensity of temperature increase and fishing effort.

Recommendations for Resource Managers

1. Temperature increments towards tolerance limits will generate that fish resources will eventually collapse locally. In the meantime, latitudinal variation in the physiological sensitivity of organisms will affect the outcome of the fishing effort differentially.

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2. Planning for more sustainable harvesting requires an ecophysiological understanding of both the resource and the species with which it interacts.
3. Simple models contribute to the formulation of strategies aimed to guide responsible monitoring systems, where theoretical, observational, and experimental information is highly relevant.

KEYWORDS

biomass, body size, climate change, fishery model, global warming, logistic growth

1 | INTRODUCTION

Global warming is a major concern when implementing strategies to achieve sustainable use of natural resources (Berryman & Lima, 2006; McCarty, 2001). Fisheries contribute to accomplishing global food demands and therefore appropriate harvest planning strategies must incorporate the effects of increasing temperature on resource species (Garcia, 2003). Several target species are ectothermic organisms, which are vulnerable to global warming because their body temperature depends on environmental temperature (Huey et al., 2012). This implies that warming can negatively affect the physiological performance of individuals, which may ultimately impact population size and distribution trends (Daufresne et al., 2009; Sheridan & Bickford, 2011). In addition, warming can lead to a decrease in body size due to changes in metabolic demands, oxygen supply, and changes in primary productivity (see Cheung et al., 2013; Lindmark et al., 2018; Sheridan & Bickford, 2011), which can affect the fish population measured in terms of biomass. On the other hand, latitudinal variations may increase the vulnerability of marine ectothermic organisms, where species close to the equator show lower thermal safety margins (Pinsky et al., 2019). Nevertheless, the spatial displacement of resources may not be easily followed by fisheries due to logistic constraints, meaning that local fishing activities may be restricted to harvest on resources located within the current harvesting areas (Ojea et al., 2020). As such, the productivity of marine resources are expected to undergo significant changes, and therefore, a considerable effect on the fishing small-scale fishing activity is foreseen, generating the need to create management strategies at different latitudes (Garcia, 2003; Sunday et al., 2011). Mathematical models can constitute important abstract tools that may help to elucidate a resource extraction system's general behaviour, allowing to mitigate ecological impacts resulting from global warming and economic demands (Córdova-Lepe et al., 2012; González-Olivares, 1998; May et al., 1974).

A framework to assess the effects of global warming is to relate the level of exposure to environmental change and the ability of organisms to cope with the altered conditions (Angilletta Jr, 2006; Bozinovic et al., 2016; Huey et al., 2012). A way to incorporate the impact of warming when modeling population dynamics is achieved through thermal performance curves (TPCs), which describe the performance of organisms as a function of body temperature. TPCs are unimodal functions whose main parameters are the lower and upper critical thermal limits and the optimum temperature at which performance achieve its maximum value (Huey & Stevenson, 1979; Rezende et al., 2014, 2020; Saldaña-Núñez et al., 2019).

Body size is a crucial feature that links morphology, physiology, and behaviour of species (Andersen et al., 2016; Schmidt-Nielsen & Knut, 1984) and which also affects the trophic interactions in which they are involved. From a fisheries perspective, the body size is of interest when evaluating the production of fish stocks (Boudreau & Dickie, 1989), especially in the context of warming (Cheung et al., 2013; Lorentzen, 2008). The metabolic theory of ecology (MTE) allows articulating relationships between temperature, body size, population growth rate, population density, and trophic interactions from a macroecological perspective (Brown et al., 2004; Gillooly et al., 2001). Following this theory, the mass scaled effect of temperature is represented by the Arrhenius factor $e^{-A/k \cdot \tau}$, where A is the activation energy, k is Boltzmann's constant, and τ is the temperature. Measurements of these parameters are made in Kelvin's scale (Brown et al., 2004). Results of this approach indicate a complex interaction between environmental temperature and body size on population parameters such as the intrinsic population growth rate. Nevertheless, some considerations are needed to meet physiological constraints as evidenced by TPCs (Kingsolver, 2009; Schulte et al., 2011).

The mathematical model proposed by Schaefer (1954) is a classic standing point for fisheries. It allows schematizing the growth of a natural resource-population through the differential logistic equation, where the extraction of resources represents an additional source of mortality (Schaefer, 1954). As a fishery model, the understanding is directed to evaluate biomass variations, where the returns are associated to the growth rate of the stock. Model parameters can be formulated from macroecological theory and proper relationships with current marine temperature (Assis et al., 2018; Pörtner et al., 2019), which are likely to have an impact on biomass growth rate.

In this study, we aim to integrate the effects of temperature variation resulting from ongoing climate change into a dynamic fishery model that also include macroecological elements. We extend the classical model of Schaefer (1954) incorporating MTE and TPCs to provide a simplified and synthetic way to assess the impact of global warming on fishing activities. Considering the differential impacts of warming, we also perform numerical simulations based on proposed scenarios made by the Intergovernmental Panel on Climate Change (IPCC) at different latitudes. We hope that this study will contribute to the understanding of sustainable management of marine resources.

This study is structured as follows: In Section 2 we present the general assumptions of the model, describing the growth rate of the resource, the capture rate of predators and the rate of capture by fishing. In Section 3, we describe the model that incorporates environmental temperature and body size into the logistic population growth. In Section 4 presents an analysis of the model with constant temperature and body size. In Section 5 we introduce functional expressions for all the model parameters. In Section 6 shows numerical simulations for different scenarios that consider warming to study its effects on stock size. Finally, in Section 7 we discuss our results.

2 | GENERAL ASSUMPTIONS

In the context of a resource population, that is, a stock, whose abundance is diminished by the action of a predator and also by fishing activity, we will establish some general assumptions about the types of variables involved and their rates of variation.



2.1 | Environmental temperature

Global warming is considered one of the most important anthropogenic factors altering species and ecosystem functioning (McCarty, 2001; Stenseth et al., 2002). In our modeling approach the temperature will be considered as an independent variable.

2.2 | Body size

A species attribute that has significant ecological effects is body size. This trait may show a negative relationship with warming in ectotherms due to metabolic and developmental constraints associated with the allocation of energy resources (Cheung et al., 2013; Lindmark et al., 2018; Smith et al., 1998; Vargas et al., 2017). In our modelling approach, the individual mass of the resource units will be considered (or is intended for practical purposes) as a variable that decreases over time, that is, in that time interval body size will be considered as an independent variable.

2.3 | Resource intrinsic growth rate

Isolating the resource from predation and harvesting, we will assume that environmental temperature affects resource growth rate. However, taking into account thermal physiological implications (Huey et al., 2012), the temperature will be considered to affect the intrinsic growth rate but not the component associated with the intraspecific competition. The effects of temperature will be incorporated through TPCs (Kingsolver, 2009; Schulte et al., 2011), which assume a direct relationship between body temperature and environmental temperature. The TPCs are represented by functions with an asymmetric unimodal shape biased to the left (Angilletta Jr, 2006).

Moreover, metabolic rate, body size, and temperature are linked, a relationship based on biomechanics (West et al., 1997). This theoretical relationship is supported by empirical studies (Hatton et al., 2019; Kleiber, 1932), determining that the allometric exponent is a value α in the range (2/3, 1). Consequently, several studies have proposed that intrinsic growth rate, body size and temperature are linked by a power function to the exponent $\alpha - 1$ and multiplied by the Arrhenius factor (Brown et al., 2004; West et al., 1997). In addition, it is possible to establish that the carrying capacity is also linked allometrically with body size with an exponent $-\alpha$ (Damuth, 1993). Under these considerations, intraspecific competition (intrinsic growth rate/carrying capacity) can be linked to body size.

2.4 | Capture rate in predator–prey dynamics

We will establish as a predatory model an endothermic animal, which by generating and regulating the required heat, its internal body temperature is almost independent of the environmental temperature (Huey et al., 2012). Therefore, for simplicity, we will assume that predator performance is decoupled from warming.

Body size also impacts on traits associated with foraging (Weitz & Levin, 2006). It influences relative speed, detection distance, driving time and attack success. Consequently, it is expected to play a crucial role in population dynamics (DeLong & Vasseur, 2012; Pawar et al., 2019). For

the simulations we have considered the predator to be 100 (kg). In this model, the effect of the predator influences the mortality of the resource.

2.5 | Fishing rate

A sound assumption that we will consider (for simplicity) is that the extraction per unit of time is proportional to the current population abundance (Beddington et al., 1976; May et al., 1979). The determinants of the proportionality factor are related to the fishing effort and also to the characteristics of the resources. The latter is related to the concept of catchability, which in turn depends on the fishing gear (Gulland, 1983).

In this sense, we will assume that the temperature, for the period considered, is not a relevant factor in general in the fishing effort deployed or the gear used. Moreover, this effort is not flexible; that is, remains constant over time. However, we consider that the individual mass is a variable that modifies the catchability (Munro, 1979). In this sense, we are in case of a fishery sensitive to changes in mass, by low plasticity of the fishing gear (Table 1).

3 | THE MODEL

Representing the population abundance of the resource in the time variable t through a function $N(t)$ and its variation in the period $[t, t + \Delta t]$ by ΔN , the per capita variation per unit of time is given by the following biomass balance equation:

$$\frac{1}{N} \frac{\Delta N}{\Delta t} = \left\{ \begin{matrix} \text{Intrinsic} \\ \text{Growth} \end{matrix} \right\} - \left\{ \begin{matrix} \text{Competition} \\ \text{Mortality} \end{matrix} \right\} - \left\{ \begin{matrix} \text{Predation} \\ \text{Mortality} \end{matrix} \right\} - \left\{ \begin{matrix} \text{Fishing} \\ \text{Mortality} \end{matrix} \right\}. \tag{1}$$

3.1 | Intrinsic growth rate

This rate, which we denote by r , is a function of two temperature-related variables (T_ω and T_r) corresponding with two readings of the environment temperature (τ), depending on

TABLE 1 Incorporation of temperature and body size

	Climate warming temperature	Body size mass
Resource	Yes	Yes
Growth	Intrinsic rate of growth	Intrinsic rate of growth Intraspecific competition coefficient
Predator	Not	Yes
Action		Interaction rate Death per encounter probability
Fishing	Not	Yes
Action		Capturability coefficient

Note: Specification of the impact or not at the crossing of the independent variables (temperature and individual mass) and with the dependent ones.



whether it is a short-term response (TPCs) or a longer-term one associated with reproductive processes.

The intrinsic growth rate, as a function of temperature T_ω , is assumed to be graphically representable by a TPC. Then, the definition domain of $r[\cdot]$ is determined by extreme temperatures, also called critical temperatures (minimum T_ω^m and maximum T_ω^M , respectively) and that they determine an interval $\mathcal{R} = [T_\omega^m, T_\omega^M]$, also called the thermal tolerance range. Reserving $|\cdot|$ to denote the size of an interval, we have its length is $|\mathcal{R}| = T_\omega^M - T_\omega^m$. Within \mathcal{R} is the optimal temperature, which is the temperature $T_\omega^o \in \mathcal{R}$ at which the intrinsic growth rate is optimal. In the temperature range $\mathcal{R}_\ominus = [T_\omega^m, T_\omega^o]$, an increase in the individual's body temperature results beneficial for performance since this intrinsic rate will increase. On the contrary, over the interval $\mathcal{R}_\oplus =]T_\omega^o, T_\omega^M]$, the rate shows a decrease, but as for the slope (its absolute value), it is comparatively more abrupt (bias to the left). For technical case, we assumed that $r[\cdot]$ is zero in the critical temperatures and positive within the thermal range.

In this study, we link the macroecological view and the study of TPCs modelling the intrinsic growth rate as the product of two functions. The first is T_r -dependent and mass-dependent as proposed by the metabolic theory of ecology and the second function (T_ω -dependent) is a left-skewed cubic unimodal function as presented in Saldaña-Núñez et al. (2019). So, we consider $r = r[T_r, m, T_\omega]$, given by:

$$r = r_o[T_r, m] \cdot \omega(T_\omega), \quad \omega(T_\omega) = \frac{T_\omega^o T_\omega^M - T_\omega T_\omega^o - T_\omega^m}{T_\omega^o |\mathcal{R}_\oplus| |\mathcal{R}_\ominus|}, \quad (2)$$

with m body size of the resource, $T_\omega \in \mathcal{R}$ and where the dependence on the mass variable is located at the maximum rate $r_o[T_r, m]$, which is reflected in that $\omega(T_\omega^o) = 1$ and $\omega(T_\omega) < 1$ if $T_\omega \neq T_\omega^o$. In addition, by theoretical construct $T_\omega^o = 2[\bar{T} + 1/2 \cdot \{4\bar{T}^2 - 3\hat{T}^2\}^{1/2}]/3$, where $\bar{T} = (T_\omega^m + T_\omega^M)/2$ and $\hat{T} = \sqrt{T_\omega^m \cdot T_\omega^M}$. Note that due to the mathematical structure of ω , we use temperatures measured in Kelvin. A representation of $r[T_r, m, T_\omega]$ can be seen in Figure 2.

Let us observe that the theory says that the intrinsic rate with respect to the mass has an allometric behaviour. In the representation (2), we have to

$$r_o[T_r, m] = r_o^* \cdot m^{\alpha-1} \cdot \exp\left\{\frac{A}{k} \cdot \frac{T_r - T_*}{T_r \cdot T_*}\right\}, \quad m > 0, \quad (3)$$

in which the parameter α , or allometric exponent, is called the marginal metabolic rate, when $\alpha = 3/4$ characterizes a wide variety of ectothermic species. The parameter r_o^* is independent of body mass and temperature, and T_* is the temperature from which physiological maxima are measured. The exponential is the Arrhenius factor, where A is the activation energy, k is Boltzmann's constant. These parameters are measured in Kelvin temperature scale, thus Equation (3) is valid in Kelvin scale (Brown et al., 2004; Hatton et al., 2019).

3.2 | Competition mortality

In Saldaña-Núñez et al. (2019), to express population growth, the authors use a less frequent form of the logistic equation, $N' = rN - \lambda N^2$, where λ is the parameter that indicates the intensity of intraspecific competition, which is related to the carrying capacity K through expression $K = r/\lambda$. More specifically, λ is the sum (in per capita terms) of the less number of births and the higher mortality, due to the presence of one more individual in the resource population (i.e., marginally).



Note that we are under the assumption that λ depends on mass and not on temperature. Let us observe that in the literature (Damuth, 1993; Hatton et al., 2019) it is assumed that K is proportional to $m^{-\alpha}$, then

$$\lambda[m] = \lambda_0 m^{\alpha-1} / m^{-\alpha} = \lambda_0 m^{2\alpha-1},$$

where λ_0 is a positive constant, it represents the intensity of competition when the mass is one unit.

3.3 | Predation mortality

We are assuming the action of a unique predator (or a constant in number group of a predator species) exerts the retire of prey at a rate \mathcal{P} . Thus, $\mathcal{P} = QI$, where the I is the interaction rate between this predator and the population resource, and Q is the probability that the encounter finish with the mortality of the prey resource. According to the literature (Pawar et al., 2019; Weitz & Levin, 2006), here we will consider that

$$\mathcal{P}[m_p, m] = Q(m_p/m)I(m_p, m),$$

where m_p is the mass of the predator.

3.3.1 | About $I(\cdot)$, the interaction rate

To describe the effect of the predator mass on the resource, we assume a scale hypothesis for the interaction rate (Weitz & Levin, 2006):

$$I(m_p, m) = m_p^\beta \cdot F(m_p/m),$$

where β represents the intensity of the predator mass in the interaction and the factor $F(\cdot)$, a positive value, is a scale function that describes the behaviour of the interaction rate in two cases. First, when the consumer is much smaller than the resource ($m_p \ll m$) or second when it is much larger than the resource ($m \ll m_p$). Accordingly, we consider:

- If $m_p \ll m$, interaction rate does not depend on the mass of the predator, because the predator is much smaller than the preys. For representing this fact, we define the function $F(\cdot)$ as proportional to $(m_p/m)^{-\beta}$. Under this assumption; it turns out that $I(m_p, m)$ is a magnitude proportional to m^β . That is,

$$f_0 := \lim_{\nu \rightarrow 0^+} \nu^\beta F(\nu)$$

exists and is positive (where $\nu = m_p/m$).

- If $m \ll m_p$, interaction rate does depend on the mass of the predator, since the predator is much larger than its prey. To represent this, we define $F(\cdot)$ as independent of the body sizes. Thus, with this assumption, it turns out that $I(m_p, m)$ is proportional to m_p^β . This is

$$f_\infty := \lim_{\nu \rightarrow \infty} F(\nu)$$

exists and is positive.



Summarizing, on the one hand, if $m_p \ll m$ then we have $I(m_p, m) \sim f_0 m^\beta$ and on the other extreme, if $m \ll m_p$, we must have $I(m_p, m) \sim f_\infty m_p^\beta$.

For example, when considering $F(\nu) = a/\nu^\beta + b$, some positive number a and b , whose graph is in Figure 1a, we have $\nu^\beta F(\nu) \rightarrow f_0 = a$ when $\nu \rightarrow 0^+$ y $F(\nu) \rightarrow f_\infty = b$ if $\nu \rightarrow \infty$. We get $I(m_p, m) = am^\beta + bm_p^\beta$, whose graph can be seen in Figure 1b.

3.3.2 | About $Q(\cdot)$, the probability

If there is an encounter between the predator and the resource, we assumed that the probability Q that the prey ends up being captured in such encounters is increasing concerning quotient $\nu = m_p/m$. Thus, in this case, it is expected that

$$\lim_{\nu \rightarrow 0^+} Q(\nu) = 0 \quad \text{and} \quad \lim_{\nu \rightarrow \infty} Q(\nu) = 1$$

plus $Q'(\nu) > 0$. We will also assume that its shape is sigmoid. An example of a function that can quantify this probability is $Q(\nu) = 1 - e^{-\nu^2}$, $\nu \in [0, \infty)$.

So that, about predation's mortality, notice that according to (4) we have $\mathcal{P}[m_p, m]$ equals to $Q(m_p/m)m_p^\beta F(m_p/m)$, with what we can write

$$\mathcal{P}[\nu] = m^\beta Q(\nu)\nu^\beta F(\nu), \quad \nu \geq 0,$$

and also conclude, using the previous sections, that

$$\lim_{\nu \rightarrow 0^+} \mathcal{P}[\nu] = 0 \quad \text{and} \quad \lim_{\nu \rightarrow \infty} \mathcal{P}[\nu]/\nu^\beta = f_\infty m^\beta.$$

Thus, when the mass of the predator is extreme, on the one hand, if $m_p \ll m$, then $\mathcal{P} \sim 0$, on the other, if $m_p \gg m$, then $\mathcal{P} \sim f_\infty m_p^\beta$ (independent of the resource mass).

The $\mathcal{P}[m_p, m]$ model that we will follow, from here onwards, for graphics and simulations is:

$$\mathcal{P}[m_p, m] = \left(1 - e^{-(m_p/m)^2}\right) \left[f_0 m^\beta + f_\infty m_p^\beta\right],$$

whose graphical form as a function of m (i.e., fixing m_p) is unimodal, as represented in Figure 1c.

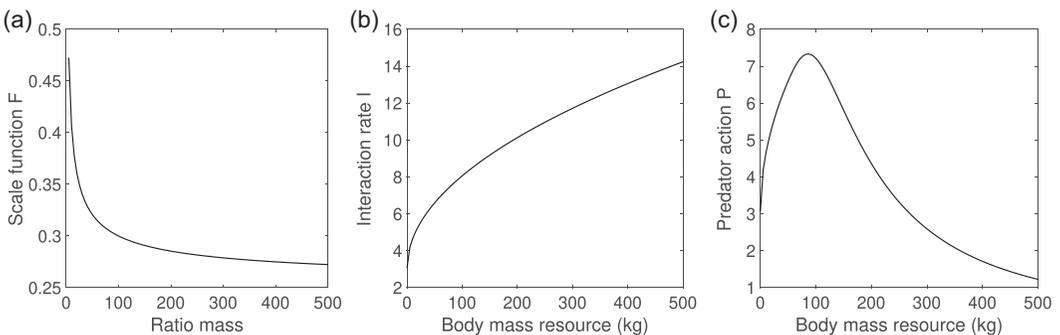


FIGURE 1 Scale, interaction rate and predator action functions. (a) $F(\cdot)$, the scale function. (b) $I(\cdot, m_p)$, the interaction rate. (c) $\mathcal{P}[\cdot, m_p]$, the predator action. Parameter values are: $f_0 = 1/2, f_\infty = 1/4, m_p = 150$ kg, $\alpha = 3/4$, and $\beta = 1/2$



3.4 | Fishing mortality

This study is framed in the modelling approach introduced in fisheries by Schaefer (Schaefer, 1954), which subtracts extraction mortality H from the natural abundance growth model, which is a linear rate regarding both: abundance and fishing-effort. As it is usual, we express this by the catch per unit effort (CPUE) hypothesis proportional to biomass, (Gulland, 1983). This is,

$$H = qEN, \quad (4)$$

where E represents the extractive effort (or fishing) parameter and q a measure of the resistance to extraction (catchability coefficient). We will assume that the input effort E is a free parameter. As for q , being related to the fishing gear, it is supposed to be dependent on the individual mass of the resource, for example, by association with size.

An important assumption is that the fishing effort deployed is uniform concerning the fishing gear; that is, the set of capture techniques and methods is rigid and specialized. In this sense, the model is applied to the extreme possibilities between artisanal arts (coastal and inland fishing) and industrial arts (external or deep-sea fishing). From the above, catchability corresponds to a measure of the efficiency of the fishing gear (which is expressed in effort). In this case, it has a concave behaviour in a neighbourhood of a mass m_o where it reaches its maximum q_o , outside this range, it must tend to zero. Without further consideration, we will assume a model of the type

$$q[m] = q_o \theta(m/m_o), \quad \text{with} \quad \theta(\mu) = \mu e^{-\mu},$$

where $\theta(\mu)$ is a unimodal and positive function what is null towards the extremes, that is, such that $\theta(\nu) \rightarrow 0$ if $\mu \rightarrow 0, \infty$. Let us note that the fishing gear can be quite rigid if it is optimised (e.g., in terms of the bending of the thread and the opening angle of the mesh at rest), to ensure some selectivity.

3.5 | The model as differential equation

Thus, taking into account in (1) the notation and the definitions introduced in the four previous sections, when considering the limit $\Delta t \rightarrow 0$, the ordinary differential equation that is deduced is given by:

$$N' = r[\tau, m]N - \lambda[m]N^2 - \underbrace{q[m]EN}_H - \underbrace{Q(m_p/m)I(m_p, m)}_p N. \quad (5)$$

We first consider the case in which body size and temperature are constant as a base situation. In the case of variable mass (individual) and global warming, Equation (5) is non-autonomous, and we will proceed mainly by performing numerical simulations and their graphs. In this case, there are most likely no steady-state solutions. In this case, it is most likely that there are no steady-state solutions. Moreover, due to global warming, temperatures are likely to reach the critical maximum temperature, which is lethal to organisms, and therefore population collapse is expected (Saldaña-Núñez et al., 2019; Rezende et al., 2014, 2020). Therefore, we focus on the behaviour in the transit period and the time horizon involved.



Therefore, we focused the attention on the behaviour in the period of transit and the time horizon involved.

4 | RESULTS WITH CONSTANT RESOURCE MASS AND TEMPERATURE

4.1 | Without fishing

Before considering fishing, an important issue regarding the dynamics of the resource is to know if the system in terms of abundance presents stability (not zero). Let's say that in its virgin state (without fishing) it maintains a type of balance on some scale. In case of constant parameters (which would represent a short-term scenario), the above means for (5) with $H = 0$, the existence of a globally stable equilibrium N^* . Thus, a starting condition is that the intrinsic growth rate of the resource is higher than the depredation rate, so that

$$N^*(T_r, m, T_\omega) = \frac{1}{\lambda[m]} \{r[T_r, m, T_\omega] - \mathcal{P}[m_p, m]\}, \quad (6)$$

has to exist and be globally stable at the same time (i.e., fulfil $(\partial_N N')(N^*) < 0$ plus uniqueness).

Let us note that if $N^*(T_*, m, T_\omega)$ exists, in terms of temperature and masses (resource and predator) is

$$N^*(T_*, m, T_\omega) = \frac{1}{\lambda_0} \left\{ \frac{r_o^* \omega(T_\omega)}{m^\alpha} - Q(\nu)[f_0 + f_\infty \nu^\beta] m^{\beta-2\alpha+1} \right\}.$$

In this regard, we have:

- If $\beta - 2\alpha + 1 = 0$, the classic case when $\alpha = 3/4$ and $\beta = 1/2$, then (6) takes the form

$$N_0^*(T_*, m, T_\omega) = \frac{1}{\lambda_0} \left\{ \frac{r_o^* \cdot \omega(T_\omega)}{m^\alpha} - Q(\nu)[f_0 + f_\infty \nu^\beta] \right\}, \quad (7)$$

and its graph can be seen in the Figure 2. Note that if $m_p \ll m$ (i.e., $\nu \sim 0$) then $N_0^*(T_*, m, T_\omega) = (1/\lambda_0)r_o^*\omega(T_\omega)/m^\alpha$, an expression that negatively correlates with m and that decreases when T_ω (within the thermal range \mathcal{R}) moves away from its optimum T_ω^o . Furthermore, note that $N_0^*(T_*, m, T_\omega^o) = r_o^*/\lambda_0 m^\alpha$. In other words, $N_0^*(T_*, m, T_\omega^o) \propto m^{-\alpha}$.

- If $\beta - 2\alpha + 1 \neq 0$, then

$$N^*(T_*, m, T_\omega) = N_0^*(T_*, m, T_\omega) + \frac{1}{\lambda_0} Q(\nu)[f_0 + f_\infty \nu^\beta] \{1 - m^{\beta-2\alpha+1}\}.$$

So if N^* exists, this is, considering a not a very large m_p , we have to:

$$N^*(T_*, m, T_\omega) > N_0^*(T_*, m, T_\omega) \quad \text{if} \quad \begin{cases} m < 1 & \text{and} & \beta - 2\alpha + 1 > 0, \\ m > 1 & \text{and} & \beta - 2\alpha + 1 < 0 \end{cases}$$

and

$$N^*(T_*, m, T_\omega) < N_0^*(T_*, m, T_\omega) \quad \text{if} \quad \begin{cases} m < 1 & \text{and} & \beta - 2\alpha + 1 < 0, \\ m > 1 & \text{and} & \beta - 2\alpha + 1 > 0. \end{cases}$$

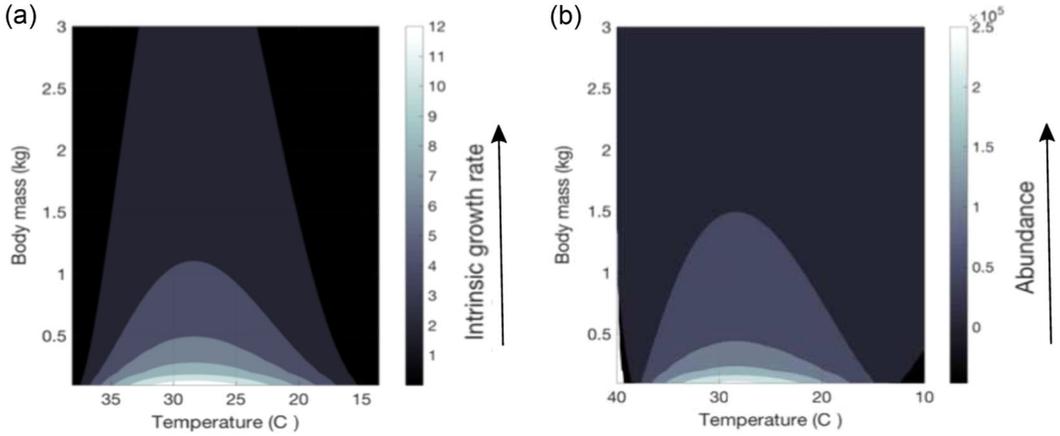


FIGURE 2 (a) Intrinsic rate of growth $r[T_*, m, T_\omega]$. (b) Globally stable equilibrium $N^*(T_*, m, T_\omega)$. (a) We observed its cubic unimodal shape as a function of temperature (i.e., fixing m at (3)), and the decreasing and convex type as a function of the mass (i.e., when setting T_ω at (2)). (b) Unimodal shape as a function of temperature (i.e., fixing the mass at (2)), and the decreasing and convex type as a function of the mass (i.e., when setting the temperature, see (3)). Parameter values are: $r_0^* = 4.2$, $\alpha = 3/4$, $T_\omega^m = 13.59^\circ\text{C}$, $T_\omega^M = 38.1^\circ\text{C}$, $T_\omega^o = 28.37^\circ\text{C}$, $f_0 = 1/2$, $f_\infty = 1/4$, $\beta = 1/2$, $m_p = 100$ kg and $\lambda_0 = 5 \times 10^{-5}$

Note that the difference in abundances $|N^* - N_0^*|$ tends to zero when $\nu \rightarrow 0$, but this difference increases if ν increases.

4.2 | With fishing

Let us observe that, considering exercised a fishing effort E , the new nonzero population equilibrium $N_*(T_*, m, T_\omega, E)$ to which it converges, in this case of constant temperature and mass, is less than the natural $N^*(T_*, m, T_\omega)$ and takes the form:

$$N_*(T_*, m, T_\omega, E) = N^*(T_*, m, T_\omega) - \frac{q[m]}{\lambda[m]}E, E \in [0, E_*], \tag{8}$$

where

$$E_*(T_*, m, T_\omega) = \frac{\lambda[m]}{q[m]}N^*(T_*, m, T_\omega) = \frac{1}{q[m]} \left\{ \frac{r_0^* \cdot \omega(T_\omega)}{m^{1-\alpha}} - Q(\nu)[f_0 m^\beta + f_\infty m_p^\beta] \right\}.$$

An effort cap that decreases with a more massive predator or with temperatures less than optimal, as expected. In case of being at the optimal temperature and mass, we have

$$E_*(T_*, m_o, T_\omega^o) = \frac{1}{q_0} \left\{ \frac{r_0^*}{m_o^{1-\alpha}} - Q(\nu)[f_0 m_o^\beta + f_\infty m_p^\beta] \right\},$$

which decreases for values of m_o higher.



Now note that sustainable production, as a function of effort (given by 4), in the range of efforts $[0, E_*]$ in which equilibrium (8) has existence, is given by:

$$H(T_*, m, T_\omega^0, E) = q[m]N_*^*(T_*, m, T_\omega^0, E)E = q[m]N_*^*(T_*, m, T_\omega^0) \left\{ 1 - \frac{q[m]E}{\lambda[m]N_*^*(\tau, m)} \right\} E, \quad (9)$$

a concave quadratic function (with respect to E). Thus, the maximum sustainable production H_{max} is obtained for (9) evaluated in the effort $E_*/2$, then

$$H_{max} = \frac{\lambda[m]N_*^*(T_*, m, T_\omega^0)^2}{4} = \frac{1}{4\lambda[m]} \left\{ r[T_*, m, T_\omega^0] - \mathcal{P}[m_p, m] \right\}^2,$$

that is to say,

$$H_{max} = \frac{1}{4\lambda_0} \left\{ \frac{r_0^*}{\sqrt{m}} - Q(\nu)[f_0 + f_\infty \nu^\beta] m^{\beta-\alpha+1/2} \right\}^2.$$

A production that decreases for larger predator masses, that increases with decreasing resource mass and that decreases for nonoptimal temperatures. Also, if $m_p \ll m$ (or if there is no depredation) and we are at the optimum temperature, we have $H_{max} = r_0^*/(4\lambda_0\sqrt{m})$. In other words, $H_{max} \propto m^{-1/2}$.

The Equation (9) shows the sustainable production. In the situation of absence of predators and in the optimal temperature it is obtained that the maximum sustainable production $H_{max} \propto m^{-1/2}$ increases if the mass of the fish decreases. The return time, T_R (Beddington et al., 1976; Beddington & May, 1977) for the logistic equation without predators and without fishing (i.e., when fishing activity ceases) is defined as: $T_R = 1/r[T_*, m, T_\omega]$. Consequently, as $r[T_*, m, T_\omega] = r_0[T_*, m]\omega(T_\omega)$ (see 2 and 3), at the optimum temperature it is obtained that: $T_R \propto m^{1-\alpha}$. As $\alpha \in (2/3, 1)$, the return time decreases when the mass of the resource decreases.

4.3 | With effort over E_*

On the other hand, if the effort exerted is above E_* , let's say a fraction ε , that is, $E = (1 + \varepsilon)E_*$, then replacing in (1), we have

$$N'/N = -\{\lambda[m]N + q[m]E_*\varepsilon\}$$

Expression, from which by direct integration, it is obtained:

$$N_\varepsilon(t) = \frac{\mathcal{E}N_0}{\lambda[m]N_0(e^{\mathcal{E}t} - 1) + \mathcal{E}e^{\mathcal{E}t}}, \quad \text{with } \mathcal{E} = q[m]E_*\varepsilon, \quad t \geq 0.$$

A function that:

- It is decreasing and tends asymptotically to zero with time, as shown in Figure 3. Note that the greater the mass, the faster the species goes to extinction.
- Setting a time t , we have that the sign of $\partial_\varepsilon N_\varepsilon$ is that of the difference $f(\mathcal{E}) = 1 - e^{-\mathcal{E}t}$ y $g(\mathcal{E}) = t\{1 + \mathcal{E}/(\lambda N_0)\}\mathcal{E}$. When comparing in the first and second derivatives, we have $f(\mathcal{E}) < g(\mathcal{E})$ if $\varepsilon > 0$. That is, as expected, $N_\varepsilon(\cdot)$ decreases when ε is greater.

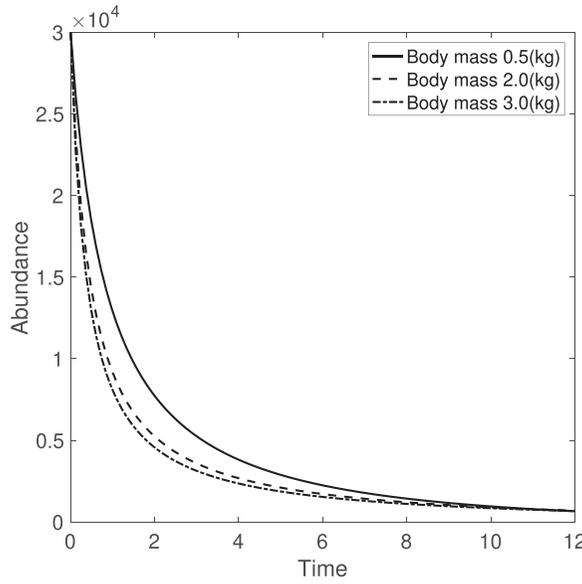


FIGURE 3 Adundance versus time with effort over E_* and different body masses. Parameter values are: $m_0 = 1.8$ kg, $m_p = 150$ kg, $T_\omega^M = 37^\circ C$, $T_\omega^m = 10^\circ C$, $T_\omega^o = 26.7^\circ C$, $N_0 = 35.000$, $\alpha = 3/4$, $\beta = 1/2$, $q_0 = 0.15$, $\varepsilon = 0.03$, $r_0 = 10$, $f_0 = 1/2$, $f_\infty = 1/4$ and $\lambda_0 = 5 \times 10^{-4}$

5 | RESULTS WITH VARIABLE TEMPERATURE AND RESOURCE MASS

5.1 | About the rise in temperature over time

In the presentation of the intrinsic growth rate, we assume that T_ω and T_r (temperatures associated with acclimatisation and reproduction, respectively) correspond to two readings of the ambient temperature (at a given latitude L) (τ_L), which affect performance. To model the temperatures described, we will use an average of these temperatures to incorporate into the main model. Thus, we have:

$$T_\chi(t) = \frac{1}{\Delta_\chi} \int_{t-\Delta_\chi}^t \tau(s) ds, \quad \chi \in \{\omega, r\}. \tag{10}$$

We mapped three locations, to incorporate future climate scenarios. Papua Province, Indonesia (latitude absolute 0.43), la Serena, Chile (latitude absolute 30.02), and Pto. Williams, Chile (latitude absolute 55.38). Using Bio-ORACLE (Assis et al., 2018), we adjust the increase in maximum ocean surface temperatures to a linear function $\tau(t) = a \cdot t + b$ adjusted over the years 2014, 2050, and 2100, as shown in Table 2. So, replacing in (10) and integrating, we have $T_\chi(\cdot) = \tau(\cdot) - a\Delta_\chi/2$, $\chi \in \{\omega, r\}$, that is, it determines a delayed effect.

In the existing literature, by analysing a large global data set of thermal tolerance limits, a functional dependence between latitude and heat and cold tolerance is obtained for ectothermic species (Sunday et al., 2019). For ectothermic species, we estimate lower and upper lethal limits as in Sunday et al. (2019) considering $T_\omega^M(L) = 38.1 - 0.24L$ and $T_\omega^m(L) = 13.59 - 0.27L$, where L is the latitude. For each latitude the thermal tolerance range will be determined by the



TABLE 2 Sea temperature trends

—	$\tau_{0.43}(t)$	$\tau_{30.02}(t)$	$\tau_{55.38}(t)$
RCP2.5	$0.0078 \cdot t + 14.6463.$	$0.0076 \cdot t + 3.812.$	$0.0056 \cdot t - 1.4973.$
RCP8.5	$0.0327 \cdot t - 35.551.$	$0.0350 \cdot t - 51.7401.$	$0.0290 \cdot t - 49.0313.$

Note: Trends obtained from the Bio-Oracle programme considering maximum ocean surface temperatures in the years 2014, 2050 and 2100 (Assis et al., 2018).

difference $T_{\omega}^M - T_{\omega}^m = R_L$ and $\tau_L(0)$ is the sea temperature 2014. In addition, with the intention of projecting T_{ω}^0 over time, we consider κ as a measure of phenotypic plasticity that modifies the temperature optimum of the species and express a linear relationship: $T_{\omega}^0(t) = \tau_L(0) + \kappa \cdot (\tau_L(t) - \tau_L(0))$. Finally, to complete the dependence of the thermal ranges on time, we use the expression for T_{ω}^M , obtained from the cubic performance curve. It is $T_{\omega}^M(t) = \left[4T_{\omega}^0(t) + R_L - \sqrt{4T_{\omega}^0(t)^2 + R_L^2} \right] / 2$ and $T_{\omega}^m(t) = T_{\omega}^M(t) - R_L$.

5.2 | About the decrease in body size over time

The decrease in body size is considered the third ecological response to global warming (Daufresne et al., 2009). Fish are born smaller and smaller. This affects their ability to move and they become easy prey for predators, making it difficult for them to survive (Cheung et al., 2013). This phenomenon corresponds to a plastic phenotypic response of organisms, which is explained by the dependence of the mass of adult individuals on the rate of individual growth and development (Ohlberger, 2013). These rates increase more rapidly with warming than growth rates, according to this, individuals raised in warmer temperatures develop a smaller size than those grown in colder temperatures (Ohlberger, 2013). To express this phenomenon, we propose an exponential model:

$$m(T_m(t)) = m(T_m(t_0)) \cdot e^{-a \cdot [T_m(t) - T_m(t_0)]}, \quad (11)$$

where $T_m(\cdot)$ is given by (10) with $\chi = m$ and a is a dimensionless proposed parameter in this study. Then, $T_m(\cdot) = \tau(\cdot) - a\Delta_m/2$.

The above equation states that body size depends on temperature (Bideault et al., 2019; Forster & Hirst, 2012), and temperature depends on time, according to the trends proposed by the IPCC (Pörtner et al., 2019). It follows from the composition of the functions that the mass is time-dependent.

6 | NUMERICAL SIMULATIONS

We show numerical simulations of the model (1), that is, solutions of (5). We consider the increase in temperature and, by (11), the decrease in body size, over time. We obtain at the three latitudes T_{ω}^M and T_{ω}^m , in this way we calculate the thermal ranges $R_{0.43} = 24.523$, $R_{30.02} = 25.41$, and $R_{55.38} = 26.17$. In addition, at these locations we extract from the data that $\tau_{0.43}(0) = 30.206^{\circ}$, $\tau_{30.02}(0) = 18.564^{\circ}$, and $\tau_{55.38}(0) = 9.444^{\circ}$. Along with this, we consider that the time required to integrate ocean temperature into the maximum intrinsic growth rate is $\Delta_r = 0661$ (year), in the performance curve it is $\Delta_{\omega} = 0.16$ (year) and in the body size it is

TABLE 3 Parameters used in the dynamic model, considering the temperature and the variable mass with respect to time

Parameter	Values
N_0	4000 (units)
L_1 absolute	0.43°
L_2 absolute	30.02°
L_3 absolute	55.38°
In $L_1: T_\omega^m / T_\omega^M$	13.472°C/38.004°C
In $L_2: T_\omega^m / T_\omega^M$	5.484°C/30.895°C
In $L_3: T_\omega^m / T_\omega^M$	-1.365°C/24.807°C
$R_{0.43} / R_{30.02} / R_{55.38}$	24.523/25.410/26.171
$\tau_{0.43}(0)$	30.206°C
$\tau_{30.02}(0)$	18.564°C
$\tau_{55.38}(0)$	9.444°C
$\Delta_\omega / \Delta_m / \Delta_r$	0.16/4.16/0.66 (years)
T_* (RCP2.6)	30. 3°C/19. 0°C/9. 7°C
T_* (RCP8.5)	30. 2°C/18. 6°C/9. 3°C
Parameter	Values
λ_0	$5 \cdot 10^{-5}$ (ad)
m_0	2.5 (kg)
m_p	100 (kg)
a	0.03 (ad)
β	0.5 (ad)
f_0	0.1 (ad)
f_∞	0.05 (ad)
q_0	0.01 (ad)
E	4.96 (effort)
r_0^*	1.5 (per capita)
k	$8.62 \cdot 10^{-5}$ (eV/K)
A	0.433 (eV)
κ	0.001 (ad)

Note: In this case it has been considered: α (Hatton et al., 2019; West et al., 1997), A and K (Brown et al., 2004) f_0, f_∞, β (Weitz & Levin, 2006), $T_\omega^M, T_\omega^m, \tau_L(0), R_L$ (Sunday et al., 2019). In the table ad indicates that it is a dimensionless parameter.

$\Delta_m = 4.16$ (year). These considerations correspond to assumptions unique to this study. It is a major simplification that reduces the applicability of the model. In addition, $T_* := T_r(0)$. Finally, we can express $T_r(t), T_\omega(t)$, and $T_m(t)$ as time-dependent, resulting in a nonautonomous Schaefer-type model. The values of the parameters used are presented in the Table 3.

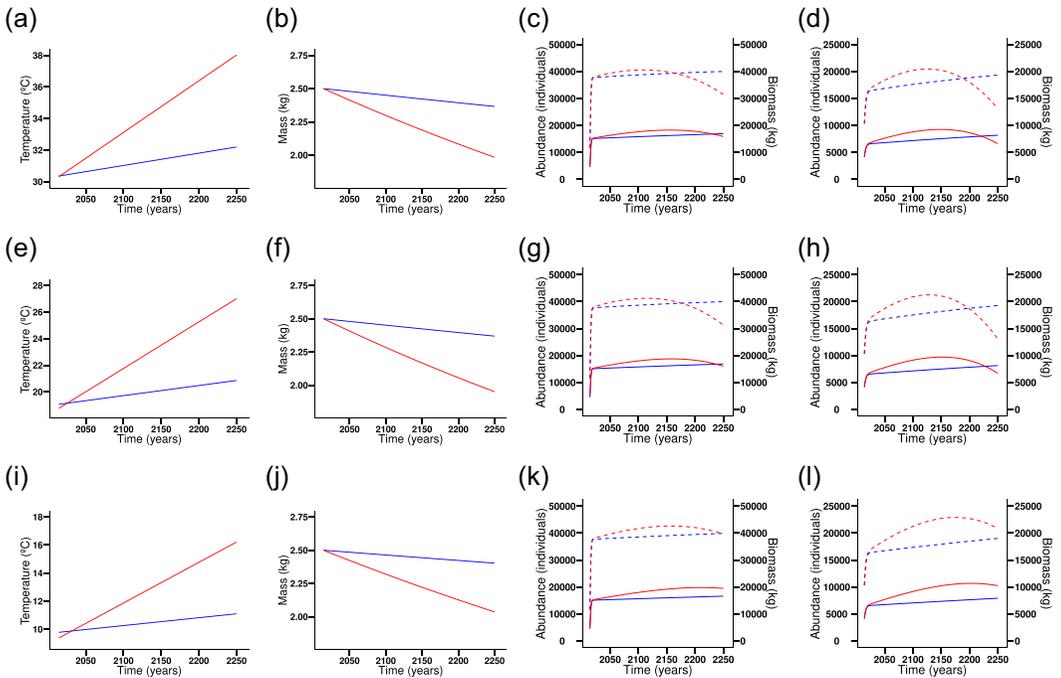


FIGURE 4 Model simulations. First row latitude 0.43, second 30.02 and third 55.38. (a), (e), and (i) Temperature increase according to RCP2.6 (blue) and RCP8.5 (red) trends. (b), (f), and (j) Mass decrease according to RCP2.6 (blue) and RCP8.5 (red) trends. (c), (g), and (k) Abundance (solid line) and biomass (segmented line) according to RCP2.6 (blue) and RCP8.5 (red) trends without predation and fishing. (d), (h), and (l) Abundance (solid line) and biomass (segmented line) according to RCP2.6 (blue) and RCP8.5 (red) trends

In the first row (Figure 4), latitude close to the equator, optimistic (RCP2.5, blue colour) and pessimistic (RCP8.5, red colour) temperature trends start at similar temperatures. Increasing temperature and decreasing body size affects the biomass of the resource (see Figure 1d). Furthermore, considering the case where the abundance of the resource is not affected by fishing and predator mortality (see Figure 4c), the decrease in body size is a factor that strongly affects the stock, generating a concave biomass curve. In the second row (Figure 4), at latitude 30.02, the temperature trends differ at the beginning and the thermal range is one Celsius higher ($R_{30.02} = 25.410$), this causes a slight change in the dynamics (see Figure 4g,h).

As for the third location, being the southernmost (latitude 55.08), the initial temperature trends differ and the thermal tolerance range is larger ($R_{55.38} = 26.17$). This indicates that the resource in this area is able to develop in a wider temperature range. Unlike species near the equator, which have the T_{ω}^o closer to the projected ambient temperature, they have a smaller thermal tolerance range. In the long run, this could be an important factor when accounting for the population, as in the pessimistic scenario the biomass drop is lower (see Figure 4l) at this latitude than at those close to the equator (see Figure 4d). Note that in the optimistic scenario the biomass trend is upward. This is due to the fact that the initial condition is lower than r_0^*/λ_0 (carrying capacity) and that during the course of time the curve representing the growth rate does not reach its optimum in the simulated time range.

Note that in all three latitudes, in the worst case climate scenario, biomass is expected to increase rapidly because the initial temperature of the simulation starts earlier and is very close



to the optimum temperature. In addition, the faster temperature increase causes the optimum temperature to be reached in a short time (rapid biomass increase). The decrease in biomass is generated because the growth rate decreases sharply between the optimum temperature and the maximum critical temperature (concavity of the biomass curve). It is important to note, that in all simulations the maximum biomass is produced considering constant fishing effort $E = 4.96$.

In Figures 4d,h,l the average biomasses differ from the biomasses obtained when assessed at time-dependent average temperatures. These consequences of nonlinear averaging are characterised by Jensen's inequality (Denny, 2017). Jensen's inequality is a mathematical property that states that the impact of thermal variation on individual physiological performance depends on the value of the mean environmental temperature relative to the temperature at which an organism reaches its maximum performance (Bozinovic & Cavieres, 2020; Estay et al., 2014). The cubic growth rate proposed by Saldaña et al. (2019) and incorporated in this study takes this property into account.

7 | DISCUSSION

The rise in temperature associated to climate change has a strong impact on the ecophysiology of organisms living in marine environments (Cheung et al., 2013). Theoretical studies and empirical evidence indicate that fish body size will be reduced as a result of warming and oxygen supply reduction (Daufresne et al., 2009; Sheridan & Bickford, 2011). A potential outcome, is that a constant effort to extract a given stock biomass would result in a greater removal of individual fishes, leading to potential fluctuations in demographic parameters that will ultimately affect the resource renewal capability.

Macroecological theory encompass established relational patterns between the concurrent effects of body mass and temperature on biological rates, which have been mostly stated by current statistical descriptions. However, the occurrence of global warming imposes the need to include a functional description of the vulnerability of organisms, which is accomplished by TPCs. This is not straightforward as a new temperature function must be imposed. As such, we included a modulator parameter that allows to differentiating the effects of temperature acting in both components of our modelling approach. If there is no fish harvesting, the effect of predation mortality is minimal (no predators), the optimal temperature for the resource (T_{ω}^0) (Equation 6) and the classical value of $\alpha = 3/4$ the macroecological pattern results from the model: $N^* \propto m^{-3/4}$ (Hatton et al., 2019). Furthermore, the maximum sustainable production $H_{max} \propto m^{-1/2}$ increases if the body size of the fish decreases. This outcome is understood as an ecological and economic problem. As the mass of species decreases, more fish can be extracted, but at the same time, the recovery of the abundance will take longer.

The effect of thermal variation on resource abundance will depend on the value of the average ambient temperature in relation to the temperature at which the intrinsic growth rate reaches its maximum (Rezende et al., 2020). If the resource stock is currently below the optimum temperature, warming trends will lead to reaching optimum temperatures, resulting in benefits for the fishing industry due to increased biomasses. However, increments in environmental temperatures above the optimum would lead to a rapid collapse of the resources.

Despite the limitations of the model, its simplified assumptions allow a deeper understanding of notions that may allow the recognition of potential resource management strategies

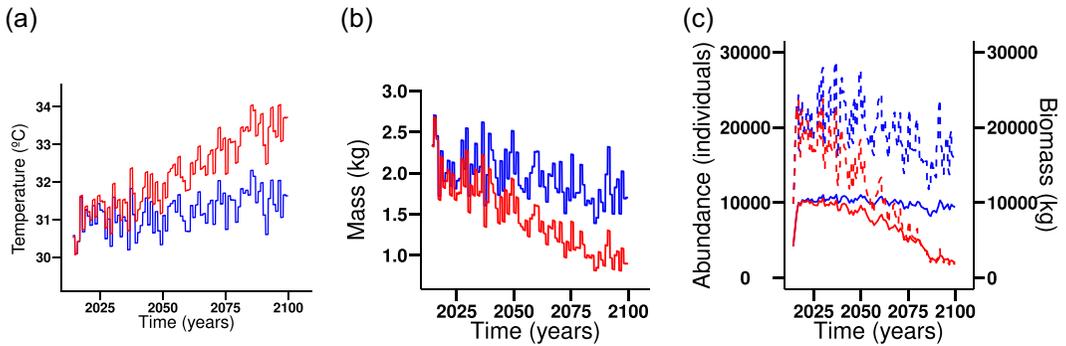


FIGURE 5 Numerical simulation considering stochastic effect on temperature (T_r , T_ω , T_m) with $\mu = 0.5$, $\sigma = 0.5$ in latitude 0.43. (a) Temperature increase according to RCP2.6 (blue) and RCP8.5 (red) trends. (b) Mass decrease according to RCP2.6 (blue) and RCP8 (red) trends. (c) Abundance (solid line) and biomass (segmented line) according to RCP2.6 (blue) and RCP8 (red) trends

(González-Olivares, 1998). In González-Olivares (1998) a modified Schaefer model, proposed by Smith (1969), is studied and analysed. The advantages of strategic models are proposed. We recognise that there are models that require a large and detailed amount of information on the species involved to accurately predict species abundance. However, a descriptive and highly unifying study (strategic models) could guide the construction of more accurate models (tactical models). The macroecological basis allows considering situations resulting from different thermal environments in a spatial context and warming trends. Many of the mechanisms used by organisms in their maintenance, survival, and reproduction can be scaled, allowing our model to be adapted to a wide variety of natural resources (Blanchard et al., 2017; Bozinovic & Cavieres, 2020). Furthermore, the effect of different warming scenarios at specific locations as proposed by the IPCC (Pörtner et al., 2019), along with specific data on thermal critical limits, can be easily evaluated (Sunday et al., 2011).

Furthermore, it is important to note that these results are subject to the uncertainties that arise in ecological systems. For example, the occurrence of stochastic temperature variation affecting the intrinsic growth rate (Borysenko & Borysenko, 2019; Levins, 1969) may have a substantial impact on the abundance and the biomass of the resource, as depicted in Figure 5. Considering environmental temperature variation may reduce the capability of forecasting trends (Estay et al., 2014).

Possible extensions of our model are to incorporate a predator whose performance and body size are affected by warming (Osmond et al., 2017) or to extend the model to a three-level food chain to assess direct and indirect effects of variations in body size and temperature (Binzer et al., 2012). Variations in the body size across developmental stages can also occur, for example, in juveniles, suggesting the study of age-structured models (Lindmark et al., 2019). In our proposal, we exemplify the complexities of modelling climate change effects proposing a link between macroecological knowledge and TPCs.

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AUTHOR CONTRIBUTIONS

William Campillay-Llanos (Corresponding Author): Conceptualization (Equal); Data curation (Equal); Formal analysis (Equal); Investigation (Lead); Methodology (Equal); Project administration (Lead); Resources (Equal); Validation (Equal); Visualization (Equal); Writing-original draft (Equal); Writing-review and editing (Equal). **Victor Saldaña-Núñez**: Data curation (Equal); Formal analysis (Equal); Investigation (Equal); Methodology (Equal); Software (Equal); Supervision (Equal); Validation (Equal); Visualization (Equal). **Fernando Córdova-Lepe**: Conceptualization (Lead); Data curation (Equal); Formal analysis (Equal); Funding acquisition (Lead); Investigation (Equal); Methodology (Equal); Project administration (Equal); Resources (Equal); Supervision (Equal); Validation (Equal); Writing-original draft (Equal); Writing-review and editing (Equal). **Felipe N. Moreno-Gómez**: Conceptualization (Equal); Data curation (Equal); Funding; acquisition (Equal); Investigation (Equal); Methodology (Equal); Project administration (Equal); Supervision (Equal); Validation (Equal); Writing-review and editing (Equal).

DATA AVAILABILITY STATEMENT

The data for the linear fit in Table 2 were obtained from the following publicly available resources: <https://www.bio-oracle.org/explore-data.php>

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