Exploring Overestimation of Harvested Populations from the Use of Single-Species Model Management

By

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A thesis submitted to the
University of Colorado Boulder
In partial fulfillment
Of the requirements to receive
Honors designation in
Environmental Studies

Defense date: April 6th, 2022

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Abstract

Harvested fish populations have dynamics that are hard to predict due to the complexity of the ecosystems in which they are found. Single-species models are used to assess the health of these populations. Single-species models ignore other environmental factors within the system, and solely focus on the harvested population, which leads to inaccurate calculations of the populations dynamics. Single-species models are used to predict the Maximum Sustainable Yield (MSY) of the population, which is the maximum catch of the population that can be sustained biologically. If managers overestimate MSY, this could unintentionally cause the depletion of the population. In this paper, we investigate whether we should expect single-species models overestimating MSY to be a general phenomenon. We use a simplified analytical model to explore the dynamics of fisheries populations, which managers wrongly assume have single-species dynamics, comparing estimated and ‘true’ MSYs. We found that there are four general cases. Two of these cases result in the manager overestimating MSY, and we argue these cases are the most common in real fisheries. Our results give a helpful insight into how we can anticipate errors when using single-species models to manage fish populations.

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Acknowledgements

I would first like to thank Matthew Burgess for giving me the opportunity to do an honors thesis and join his lab group. I am extremely grateful for this opportunity and feel lucky for being able to join his group. Matthew was extremely insightful for this paper and always made sure that I was achieving what I needed to be. I also appreciated how much support I felt from him during this process and support for what I am planning for my future. Secondly, I would like to thank Ryan Langendorf. I was grateful that he joined this project and was an immense help throughout. Ryan gave insight that I would have never thought of and was an important guide for me during this project. Lastly, I would like to thank the members of Matthews Lab group. Throughout the last two semesters I have felt a lot of support from them. Being able to talk and bounce ideas within them has been an amazing experience. I am also happy that the lab group has allowed for me to be more involved within the ENVS department. Overall, I am truly grateful for this experience, so thank you.

Introduction

Fisheries provide a vital global food source, supporting millions of coastal communities around the world. In 2018 alone, fisheries accounted for one hundred fifty tonnes of food, which is enough to feed one-hundred fifty million people for one year (FAO, 2020). Furthermore, over ten percent of the global population depends on the food that is provided from fisheries, disproportionately in developing countries (Our Ocean, 2016). Historically, fisheries have seen an increase in the amount of people that depend on them (Finegold, 2009), despite their increasing importance, many fisheries are overfished and poorly managed (Cardinale & Svedäng, 2008). In order to ensure sustainable food security, we must improve the ways in which we estimate how much catch can be sustainable.

The dynamics of fish populations have complex drivers that are difficult to directly observe thus in some cases making it hard to accurately predict how much fishing is sustainable. The maximum catch that is sustainable is known as maximum sustainable yield (MSY) and is often the target of fisheries management (Maunder, 2002). To determine the MSY of a fishery, single-species models are typically used (Skern-Mauritzen et al. 2016). A single-species model examines the population dynamics of a species without considering the rest of the ecosystem (Howell et al., 2021). From single-species models, fisheries scientists estimate the MSY, the mortality rate (called FMSY and related to fishing effort), and fish population size (BMSY) which produces the MSY. Single-species models are used to evaluate the sustainability of fisheries because they can make predictions about fish species without thorough ecosystem data and they require fitting relatively few parameters (Plagányi et al., 2014; Collie et al., 2016).

There has been criticism surrounding the use of single-species models to predict the health of fish populations. By solely using single-species models we have seen systematic issues arise, such as biases in calculations, limitations due to emphasizing the equilibrium, the fact that the models do not explore the needs of other species, and because the current models do not account for indirect effects of fishing (Quinn & Collie, 2005). However, because the data single-species are fit to come from the full ecosystem, some relevant information about the ecosystem may be indirectly accounted for by single-species models; this is called ‘abstraction’ (Burgess et al. 2017). Sometimes the ecosystem and target species properties allow single-species models to produce effective management advice, but under other conditions single-species models produce significant errors (Burgess et al. 2017).

One of the biggest issues that arises with using single-species models is when the calculated MSY is inaccurate and leads to destructive overharvesting and/or a highly misleading picture of a fishery’s catch potential. Two recent studies of Chinese fisheries illustrate the latter problem. Chinese fisheries have experienced decades of intense fishing, causing not only the depletion of the fish, but also a change in their size structure, with mostly small fish remaining (Szuwalski et al. 2017). Because larger fish eat smaller fish, the change in size structure is equivalent to a predator release for the small fish, which increased their catches. Not accounting for this, Costello et al. (2016) projected that single-species MSY management could increase Chinese fishery catches by ~1 million metric tonnes (MMT). In contrast, Szuwalski et al’s (2017) ecosystem model projected that single-species MSY management would reduce catches in the East China Sea by roughly half. The single-species model made it seem possible to rebuild predator catches without undoing the predator release that was raising prey catches. But of course, we cannot have it both ways in reality.

In this paper, we investigate whether we should expect single-species models overestimating MSY to be a general phenomenon. To do this we will use a simplified analytical model to explore the dynamics of fisheries populations and how to correctly calculate MSY. Within the model we will assume that there is continuous logistic growth within the population for analytical convenience. However, we expect that our qualitative insights will generalize to fisheries that are currently using single-species models. Given that fisheries management is likely to continue to rely on single-species models for the foreseeable future, this work will help to establish expectations regarding how severe errors might be, and what we need to do to make fisheries advice more useful.

Model

Our modeling framework assumes that there is a fish population of interest, whose dynamics are being modeled by assessment scientists assuming they function as a single-species logistic growth model, with a maximum growth rate, *r*, a carrying capacity (i.e. maximum naturally occurring population size) *K*, and a fishing mortality rate that is a function of time, *F*(*t*). The manager assumes that the dynamics of the population size, *N(t)*, varies according to the differential equation below:

(1) $\frac{dN(t)}{dt} = N(t)\left(r\left[1 - {N(t)}/{K}\right] - F(t)\right).$

We assume that *r*, *K* > 0. A sustainable harvest occurs when,

(2) $r\left[1 - {N(t)}/{K}\right] = F(t)$

which implies that the population size is not changing ($\frac{dN(t)}{dt} = 0$). The maximum sustainable harvest, MSY, occurs at the maximum value of $N(t)F(t)$, where equation (2) is satisfied. This occurs at the abundance, *N*, that maximizes $Nr[1 - {N}/{K}]$, which is *N* = *K*/2. The fishing mortality rate that produces this MSY is *F* = *r*/2 (Figure 1). MSY is given by:

(3) $\mathrm{MSY} = \frac{rK}{4}.$

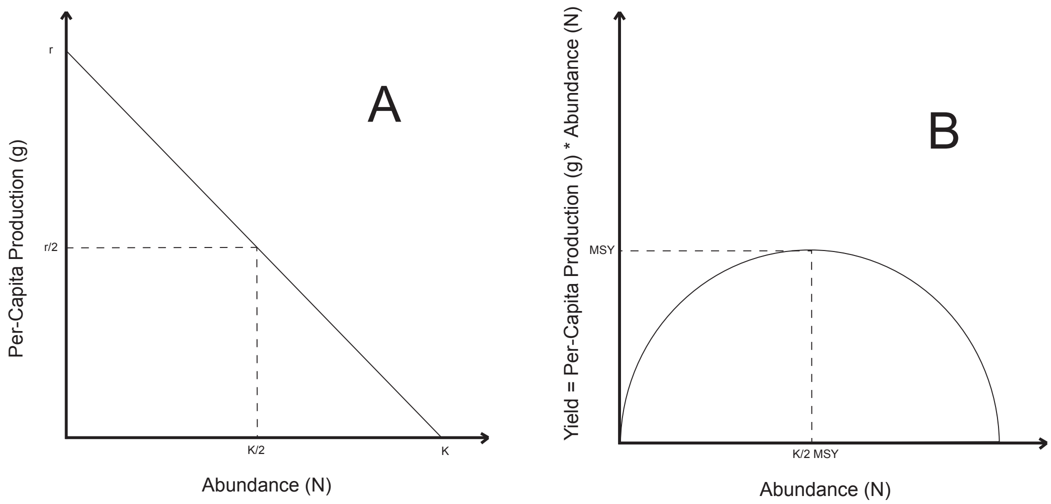

Figure 1. A shows the relationship between abundance and per-capita production, with the MSY-producing values of abundance ($N = K/2$) and fishing mortality ($F = g = r/2$) noted. **B** shows the relationship between sustainable harvest (as given by equation (2)) and abundance.

In contrast to the logistic model assumed by managers, we assume that, in reality, the fish stock's dynamics are also affected by other species and abiotic factors. Burgess et al. (2017) uses the following equation to represent the 'true' dynamics of the fish stock of interest, where $g(N(t), \boldsymbol{M}(t))$ represents the per-capita growth rate from non-fishery related factors ('per-capita production', as they call it). $\boldsymbol{M}(t)$ is a vector of other species and abiotic factors that affect the fish stock.

(4) $\frac{dN(t)}{dt} = N(t)\left(g[N(t), \boldsymbol{M}(t)] - F(t)\right)$

In this study, we use a simplified version of this model, where we assume that the 'true' dynamics can be described by a logistic equation in which r and K are time-varying instead of constant:

(5) $\frac{dN(t)}{dt} = N(t)\left(r(t)\left[1 - {N(t)}/{K(t)}\right] - F(t)\right)$

Two-species example:

To illustrate how this assumption plays out in a specific example, consider the following predator-prey system, where the predator and prey are both fished, and the prey instantaneously equilibrates to the predator's abundance (this is called 'timescale separation' in dynamic systems theory; see Burgess et al. 2017). While this is not a real-world scenario, it is a good starting point to explore the problem to be able to contextual the problem. Below are the differential equations for the population dynamics of the prey (abundance denoted *x*(*t*)) and predator (abundance denoted *p*(*t*)). We choose arbitrary parameter values, for illustrative purposes.

(6) $\frac{dx}{dt} = x(t)\ [1 - x(t) - \ .35\ p(t) - F_x(t)]$

(7) $\frac{dp}{dt} = p(t)\ [.25x(t) - \ .15 - F_p(t)]$

If the prey instantly equilibrates to the predator population, that means that we assume:

(8) $1 - x(t) - \ .35\ p(t) - F_x(t) = 0$

We can solve this equation for *x*(*t*) as a function of *p*(*t*), and insert the result into the *p*(*t*) dynamic equation in (7) above:

(9) $\frac{dp(t)}{dt} = p(t)\ \left[\left(0.1 - \ 0.25F_x(t)\right)\left(1 - \frac{p(t)}{\frac{0.1-0.25F_x(t)}{0.0875}}\right) - \ F_p(t)\right]$

We can see that equation (9) is equivalent to equation (5) with $r(t) = 0.1 - \ 0.25F_x(t)$, and $K(t) = \frac{0.1-0.25F_x(t)}{0.0875}$. If we assume that the prey's fishing mortality rate, $F_x(t)$, changes over time, then the predator's *r*(*t*) and *K*(*t*) also change over time. How they have changed over the period in which the manager collects data to estimate *r* and *K* (which they assume is constant) determine what the estimates will be. We call these estimates $\hat{r}$ and $\hat{K}$. The manager will assume that MSY is determined by $\hat{r}$ and $\hat{K}$:

(10) $\widehat{\text{MSY}} = \frac{\hat{r}\hat{K}}{4}.$

However, the values of $r(t)$ and $K(t)$ at the endpoint could be more influential in determining what sustainable catch is in reality. Thus, we can think of the 'true' MSY, at the end point in time, T, as being determined by $r(T)$ and $K(T)$:

(11) $$\text{True MSY} = \frac{r(T)K(T)}{4}.$$

Our analysis considers MSY 'overestimated' if $\widehat{\text{MSY}} > \text{True MSY}$ and underestimated if $\widehat{\text{MSY}} < \text{True MSY}$. Figure 2 illustrates this below, using the model of equations (6)-(9), over a time span of $t = 0$ to $t = T = 50$, where $F_x(t) = 0$ when $t < 25$, and $F_x(t) = 0.009(t - 25)$ when $t \geq 25$; and $F_p(t) = 0.0015t$.

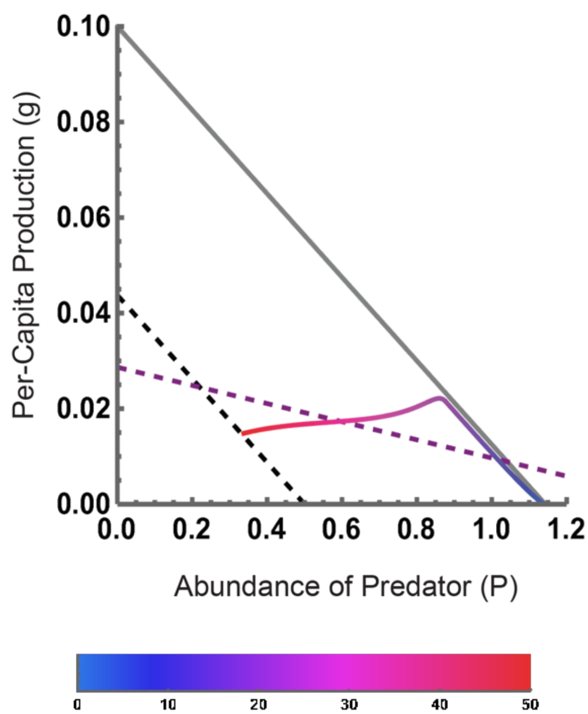

Figure 2. This figure shows how $\hat{r}$ and $\hat{K}$ are fit to the predator dynamics in the model of equations (6)-(9). The solid gray line represents the relationship between abundance, $p(t)$, and per-capita production, g, when $F_x(t) = F_x(0) = 0$. The dashed black line represents the relationship between abundance, $p(t)$, and per-capita production, g, when $F_x(t) = F_x(T)$. The curved line, that goes from blue to red, shows the true dynamics. The dashed purple line is the linear fit to these data, generating the manager's estimate of $\hat{r}$ and $\hat{K}$.

General Graphical Analysis:

Next, we graphically analyze the general case of our model, to provide general intuition into when MSY is over- or under-estimated. For simplicity, we assume that the true dynamics, in terms of abundance ($N(t)$) and per-capita production ($g(t)$) follow a straight line connecting the point {K(0), 0} to the point {N(T), g(T)} (Figure 3). In other words, we assume that:

(12) $$g(t) = \hat{r}\left[1 - \frac{N(t)}{\widehat{K}}\right], \text{ where } \widehat{K} = K(0).$$

This assumption allows us to easily calculate $\hat{r}$ and $\widehat{K}$, though Figure 2 illustrates how it is only an approximate representation of the dynamics.

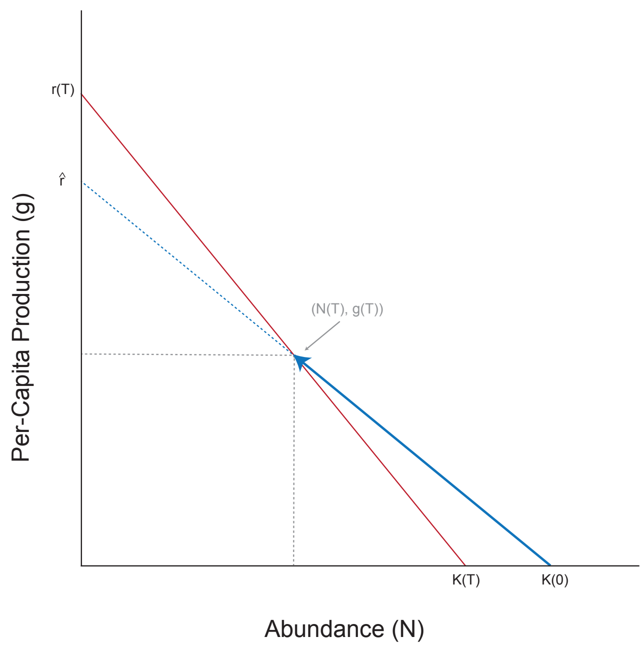

Figure 3. The general case of our model. We assume that the dynamics follow a straight line from *{K(0),0) to {N(T),g(T)}* (blue arrow). We assume that the manager traces this line to the y-axis to estimate $\hat{r}$ and sets $\widehat{K} = K(0)$ (blue dashed line). We can then compare the true and estimated MSYs via the areas under the resulting triangles, which are proportional to their respective MSY values.

We then focus on two factors: first, whether $K(t)$ (the carrying capacity) is increasing or decreasing over time; and second, whether the manager estimates that the fish stock is overfished or not. In a logistic model, a stock is overfished if $N(t) < K/2$. Therefore, we assume that the manager thinks the stock is overfished if $N(t) < K(0)/2$. We assume $N(t)$ can be perfectly observed, to simplify our analysis. Based on these two factors, there are four possible scenarios (Table 1). Our objective is to identify which of these scenarios should result in overestimating MSY, and which scenarios should result in underestimating MSY, if this can be determined.

<table>
<tr><td colspan="2" rowspan="2"></td><td colspan="2">K (T) > K (0)?
(carrying capacity increasing)</td></tr>
<tr><td>Yes</td><td>No</td></tr>
<tr><td rowspan="2">N(T) < ½ K (0)?
(overfishing perceived)</td><td>Yes</td><td>Case One</td><td>Case Two</td></tr>
<tr><td>No</td><td>Case Three</td><td>Case Four</td></tr>
</table>

Table 1. Four cases that we analyze. The rows show whether the true carrying capacity is greater than the assumed carrying capacity. The columns show whether we are over harvesting or correctly harvesting the population.

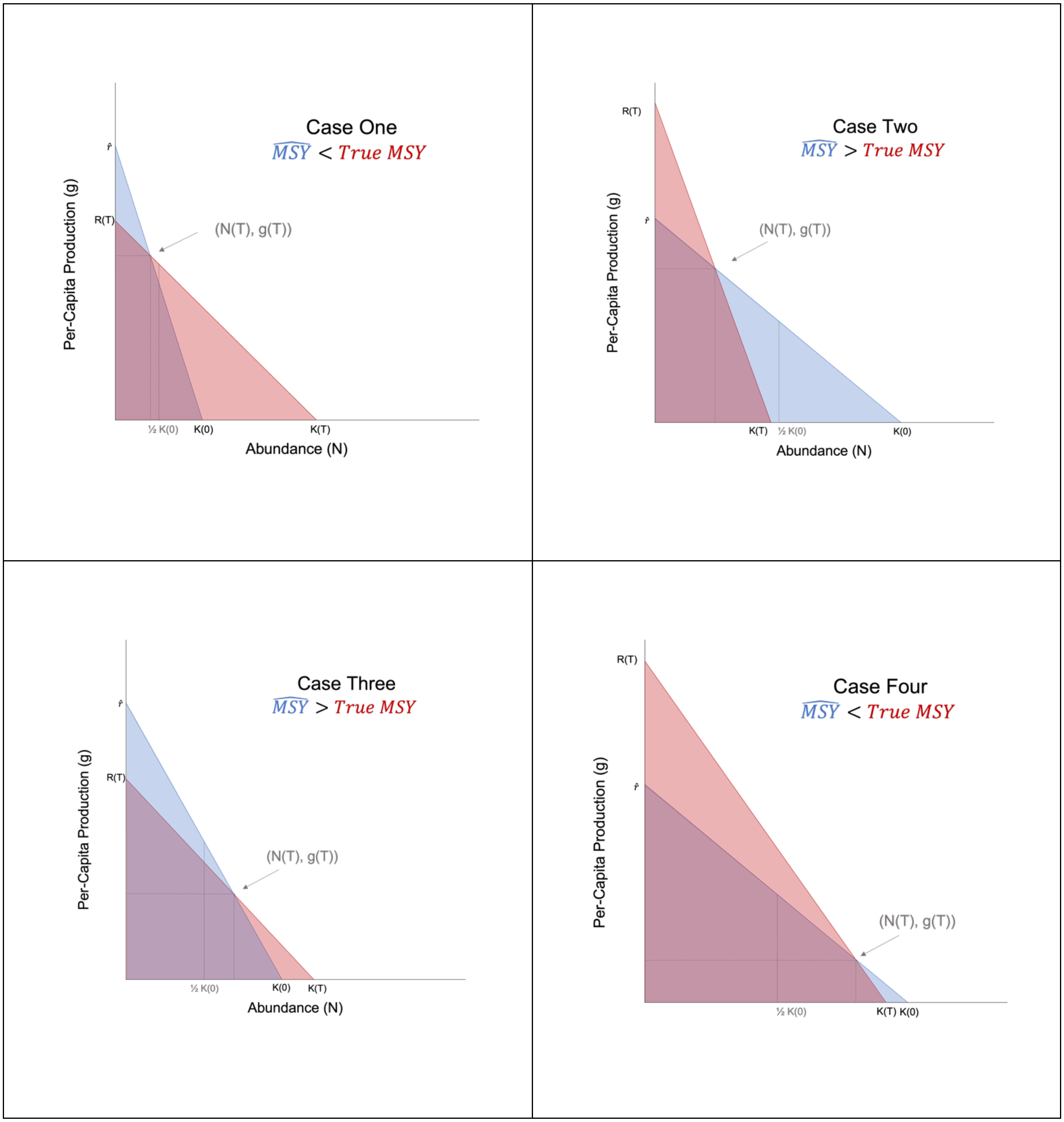

Figure 4. Panel showcases the four cases that are assumed to be found within this model. Each case shows estimated MSY in blue (which is equal to half the blue shaded area), True MSY in red (which is equal to half the red shaded area), and the intersection of the two at (*N(T), g(T))*.

Results

As Figure 3 shows, our graphical representation of the problem makes the angle C each proportional to the area of a triangle. To assess which of these triangles is larger, we compare the areas within each that are not part of the other. If the portion of the $\widehat{MSY}$ triangle that is not in the True MSY triangle is larger than the portion of the True MSY triangle that is not in the $\widehat{MSY}$ triangle, then $\widehat{MSY}$ > True MSY, and vice versa. Figure 5 illustrates how we do this for Case One (where the manager perceives overfishing, and carrying capacity is increasing).

Case One - Worked Out Example

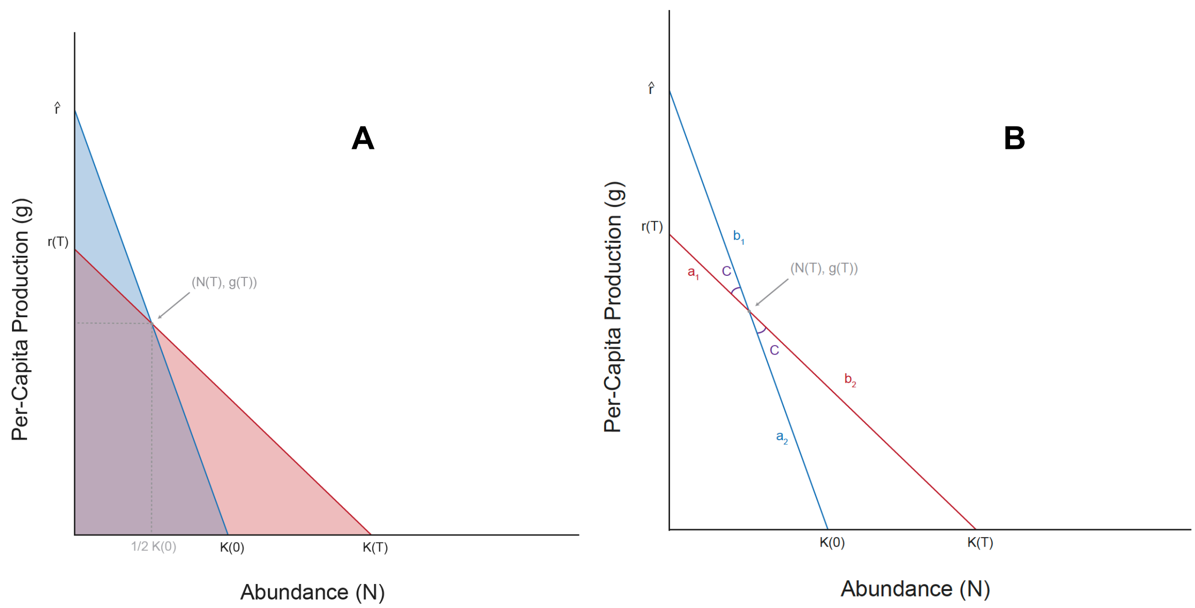

Figure 5. **A** shows what case one is assumed to look like. In this case, we assume that *N(T)* < ½ *K(0)* and that *K(T)* > *K(0).* The graphical analysis suggests that in this case we are underestimating MSY, so the estimated MSY will be less than the True MSY. **B** shows how we find the areas of the smaller triangles that determine which of the larger triangles in **A** is larger.

To determine which of these triangles is larger, we can exploit the fact that they share an angle, which we call *C*, and the following equation for the area of a triangle:

(13) $$\text{Area of Triangle} = \frac{1}{2}ab\sin C.$$

Since the angles are the same, we just need to determine which triangle has a larger product of adjacent line segments, *ab*. In other words, we are overestimating MSY ($\widehat{MSY}$ > True MSY) if $a_1b_1 > a_2b_2$, and vice-versa (Figure 5B).

We can calculate the lengths of the line segments using the Pythagorean theorem.

(14a) $a_1 = \sqrt{N(T)^2 + [r(T) - g(T)]^2}$

(14b) $b_1 = \sqrt{N(T)^2 + [\hat{r} - g(T)]^2}$

(14c) $a_2 = \sqrt{[K(0) - N(T)]^2 + g(T)^2}$

(14d) $b_2 = \sqrt{[K(T) - N(T)]^2 + g(T)^2}$

If we assume that *N*(*T*) = 1/2*K*(0), then we can simplify a_1b_1 and a_2b_2 as:

(15a) $$a_1b_1 = \left[\sqrt{\left(\frac{1}{2}K(0)\right)^2 + [r(T) - g(T)]^2}\right]\left[\sqrt{N(T)^2 + [\hat{r} - g(T)]^2}\right]$$

(15b) $$a_2b_2 = \left[\sqrt{[\frac{1}{2}K(0)]^2 + g(T)^2}\right]\left[\sqrt{[K(T) - \frac{1}{2}K(0)]^2 + g(T)^2}\right]$$

From equations (15), we can analyze the cases in Table 1. In Case One (perceived overfishing and increasing *K*), we know that $r(T) < 2g(T)$ (Figure 5A), which implies that $\sqrt{\left(\frac{1}{2}K(0)\right)^2 + [r(T) - g(T)]^2} < \sqrt{[\frac{1}{2}K(0)]^2 + g(T)^2}$. Making *N*(*T*) < 1/2*K*(0) (equations (15) assume they are equal) would only magnify this asymmetry. Because $r(T) < 2g(T)$, and we also know that $K(T) - \frac{1}{2}K(0) > N(T)$, we therefore know that $\sqrt{N(T)^2 + [\hat{r} - g(T)]^2} < \sqrt{[K(T) - \frac{1}{2}K(0)]^2 + g(T)^2}$. Putting these facts together, we know that $a_1b_1 < a_2b_2$ in Case One, which implies that $\widehat{MSY}$< True MSY in this case (Figure 4A). Using similar logic, we can show that $\widehat{MSY}$< True MSY in Case Four, and $\widehat{MSY}$> True MSY in Cases Two and Three. Figure 4 illustrates this graphically.

Discussion

Summary of main results

In this study, we used a simplified model to examine possible biases in single-species assessments of maximum sustainable yield (MSY) in fisheries. There are some real-world examples, such as in the East China sea (Szuwalski et al., 2017), where single-species models seem to overestimate MSY. Overestimation is a concern because if managers overestimate MSY, then they may believe that their fisheries can produce more food and profit than they actually can.

We explored in our model how common overestimation might be. Within the model, we investigated combinations of two specific factors: (1) whether $K(t)$ is increasing or decreasing (overestimating or underestimating), (2) whether the manager estimates that the fish stock is overfished or not (overharvesting). We chose these factors because we expect that they are at least somewhat knowable for managers.
Our model suggests that overestimation of MSY is likely to occur either when the manager estimates that the population is overfished and the population's carrying capacity is decreasing (Case Two), or when the manager estimates that the population is not overfished and the population's carrying capacity is increasing (Case Three). Table One and Panel One summaries our important findings.

Cases Two and Three, where we overestimate MSY, seem likely to be more common in real-world fisheries than Cases One and Four, where we underestimate MSY. The manager estimates that a population is overfished if it has decreased significantly in size—by more than half in a logistic model. We hypothesize that populations that face negative pressures from both fishing and other factors (Case Two) will more commonly experience significant decreases in size than populations facing positive pressures from factors outside the fishery (Case One). A real-world example of Case Two might be Gulf of Maine cod (*Gadus morhua*), which is overfished and experiencing negative pressure from climate change (Pershing et al., 2015). Similarly, we hypothesize that populations that face positive pressures from outside the fishery will more commonly not have decreased significantly in size, and therefore will more commonly not be estimated as overfished (Case Three) than populations that are facing negative pressures outside the fishery (Case Four). A real-world example of Case Three might be Gulf of Maine lobster (*Homarus americanus*), which has a booming fishery partly due to predator release from collapsing cod (Steneck & Wahle, 2013).

Limitations

Within our model, we made a few assumptions that are important to discuss. First, we assume that the manager perfectly observes growth *(g)* and population size *(N)* and fits a linear model to this relationship (logistic). We assumed this because real stock assessments are highly complicated and include data that would not be useful to our model, such as, age structure of the population (Hilborn & Walters, 1992). We also assume in our graphical model that the dynamics are perfectly linear. Real world data can be complicated and variable, this allowed for us to examine the model in a simpler way.

Secondly, we assumed that the effects of environmental factors on the fish population's growth can be adequately represented as changes in *r* and *K* in a logistic growth model. Such as, effects seen from climate change or the impacts that other species have on the observed population. In reality, environmental factors can have many different effects on population growth, including effects equivalent to changing the structure of the model, instead of only changing its parameter values.

Lastly, we assume that the population size only decreases. Some fish populations increase in size or fluctuate, of course. But, it less common to see a population that is being intensely harvested to be increasing, especially before it is assessed and managed.

Despite these assumptions, we expect our prediction, that overestimating MSY is common in single-species models, is robust. In our Case Two, the population is being depleted by both fishing and other factors, which decrease the carrying capacity. The single-species model therefore implicitly assumes that the negative effect of the other factors would reverse if fishing pressure reduced. This is why the single-species model overestimates MSY. In the Gulf of Maine cod example, the single-species model would implicitly assume that climate change reverses if fishing pressure goes down. In our Case Three, the effect of fishing on the population is being partly offset by other factors. To the single-species model, this looks like a population that is extremely resilient to fishing, and therefore could yield very high catches at very high fishing pressures. The single-species model implicitly assumes that the positive pressures on carrying capacity would increase as fishing pressure increased. This may not be true, which is why the single-species model overestimates MSY in Case Three. None of our assumptions listed above change these basic reasons behind single-species models' overestimation of MSY.

Implications

There has been recognition that the use of single-species models within fishery management has limitations, even though it is a widespread practice for practical reasons (Plagányi et al., 2014; Skern-Mauritzen et al. 2016). Our results highlight one major potential issue with single-species fishery management: overestimation of sustainable catch. Our cases can help managers understand when they might be overestimating their sustainable catches, thus facilitating management that is sustainable and planning that is realistic.

Future directions

Next, we want to test our hypothesis that Cases Two and Three are more common than Cases One and Four, using real estimates of overfishing (Costello et al., 2016) and changes in carrying capacity from climate change (Gaines et al., 2018).

Conclusion

The dynamics of harvested populations are complex and difficult to predict. Within fisheries, we see that management uses single-species models in order to predict the dynamics of the population they are harvesting. The main assessment that is used from the single-species models is Maximum Sustainable Yield (MSY) of the population, which gives how much of the species can be sustainably harvested. There are a lot of issues with solely using single-species models. Our paper examined whether we should expect single-species models overestimating MSY to be a general phenomenon, and how severe projection errors might be. We used a simplified analytical model to explore the dynamics of fisheries populations and how to correctly calculate MSY. Our results seemed to suggest that overestimating MSY is more common than underestimating it. Through our results we wanted to give a helpful insight into how we can correct our current errors when using single-species models and create a way in which we can go about sustainably harvesting these populations.

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