The effects of fishing
on the stability of a food web
under climate warming

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Effekterna av fiske på stabiliteten av en födokedja under klimatförändringar

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Abstract

Predicting the effects of fishing in a warmer environment caused by climate change requires knowledge of what trophic level is fished on, the physiological effects of temperature on fish, and how these two affect ecological interactions. Both temperature and fishing are known to affect the stability of food webs in several ways. Still, we know little of the effects on stability when fishing on different trophic levels in a warmer environment. Using a stage-structured biomass model, I analyse how fishing on adult consumers and/or predators in a warmer environment affects the stability of the community. I find that predators go extinct at a lower fishing pressure in a warmer environment while fishing on adult consumers in a warmer environment instead stabilises the community by reducing cyclic dynamics. Combined fishing on both adult consumers and predators can reduce the risk of predator extinction and negate for the negative effects of high temperature on the stability of the food web. I also find that fishing at the level corresponding to the maximum sustainable yield (MSY) of predators is unsustainable, since if the fishing pressure is raised slightly from the MSY the predator goes extinct, especially in a warmer environment. My results indicate that restricting the fishing pressure in warmer environments or fishing on the adult consumer simultaneously to avoid predator extinction might be recommended. In general, it is important to be aware of the complexity of ecological systems when managing fisheries, as climate change can result in unintuitive and unexpected results depending on what trophic level is fished.

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1. Introduction

1.1 Effects of climate change on fish food webs

The effects of climate change on fish communities and whole food webs have been studied extensively, and the predictions depend on the trophic interactions at play (Lindmark *et al.* 2019). But climate change is not the only thing that can affects food webs. Fishing, for example, can also induce effects that fully reorganise food webs and ecosystems (de Roos & Persson 2002, de Roos & Persson 2013, McCain *et al.* 2016). Fishing together with climate change can also interactively cause negative consequences to the environment (Hidalgo *et al.* 2011, Wootton *et al.* 2021). Such interactions make it difficult to predict the combined effects of several stressors on the environment (Woodward *et al.* 2010).

Increased temperature affects the metabolic rate, development rate, mortality rate, population growth rate, interactions between individuals of different populations, predation rate, biomass production, and trophic dynamics (Brown *et al.* 2004, Savage *et al.* 2004). Increased temperature can therefore have either a positive or negative effect on the population size of fish, depending on how vital rates are affected. In some geographical areas top-predator population size increases, and in some areas top-predator population size decreases (Blanchard *et al.* 2012). A theoretical study, for example, suggests that whether the top-predator population size increased or decreased with increased temperature can, for example, depend on variation in primary production (Blanchard *et al.* 2012). Higher temperature can increase stability (less cyclic dynamics) but at the same time increase the risk of extinction of predators due to starvation, contrastingly, it has also been predicted to increase the top-down control of producers by consumers (Rall *et al.* 2010, Fussman *et al.* 2014, Uszko *et al.* 2017). Several studies show that increased temperature also decreases the carrying capacity of resources (Uszko *et al.* 2017, Bernhardt *et al.* 2018). Increased temperature, therefore, has various effects on fish, their resource, and food webs.

Depending on the interactions between organisms at different trophic levels, increased temperature can, in a theoretical model, have stabilising effects or destabilising effects (Lindmark *et al.* 2019). For example, cyclic dynamics that disappear as temperature increases (Lindmark *et al.* 2019), occur only with generalist predators on both juvenile consumers and adult consumers. Alternative stable states in community composition (predator either present or extinct) occur when temperature increases, if predation is stage-specific on the juvenile consumers (Lindmark *et al.* 2019). The alternative stable states that occur when the temperature is increased are caused by emergent Allee effects, which means that if the community is bistable, the predators will either persist or go extinct depending on the initial conditions (Lindmark *et al.* 2019). The Allee effects that occur when the temperature is increased are called 'emergent' and are separate from demographic Allee effects since they are not caused by any specific model dynamic, but are instead caused by biomass overcompensation in the consumers (de Roos & Persson 2013).

Biomass overcompensation is the phenomenon that equilibrium biomass density (of a stage or of an entire population) increases rather than decreases with mortality (in the particular stage or for all). When predators predate on juvenile prey the resources per prey individual

goes up, and the growth rate of the prey increases, and they can therefore mature into adults earlier. The new adults can then produce more juveniles. The predators, therefore, promote their own survival by increasing the mortality of their prey. It is called "biomass overcompensation" since an increase in mortality leads to a greater increase in biomass than what is lost through predation (de Roos *et al.* 2007). Ontogenetic asymmetry (i.e. a difference in mass-specific rate of biomass production depending on body size and life stage) is one of the assumptions required for biomass overcompensation, ontogenetic asymmetry means that there is a difference in energetic efficiency between, for example, a juvenile and adult consumer in their ingestion of resources in relation to their energetic needs (de Roos & Persson 2013). Another requirement for biomass overcompensation is stage-specific mortality which can come from a predator, increased mortality on the predator releases the life stage from being a bottleneck (de Roos & Persson 2013). Since the temperature effects on both metabolism and intake rate are size-dependent, warming can partly shift the degree of ontogenetic asymmetry, as well as weaken predators' top-down control and thus the occurrence of biomass overcompensation.

To summarise; the effects of climate warming on the coexistence, stability, and size structure of a food web depend on the interactions between the different trophic levels (Lindmark *et al.* 2019). As temperature increases, theory suggests that the food web can either stabilise or destabilise depending on whether predators feed on juveniles or juveniles and adults (Lindmark *et al.* 2019). However, predation is not the only source of mortality that affects the stability dynamics of a food web. Also human exploitation, such as fishing, has effects on the stability of food webs (de Roos & Persson 2013, Hidalgo *et al.* 2011).

1.2 Effects of fishing on fish food webs

Fisheries contribute, both directly and indirectly, 225-240 billion $ to the global economy each year (Dyck & Sumaila 2010), and in some developing countries the economic gain from fisheries constitute a substantial proportion of the total economic gain (7 %) (Béné *et al.* 2007). Fish is also an important protein source worldwide, and especially in developing countries (FAO 2020). Furthermore, in 2017 34.2 % of all fish stocks were fished at unsustainable levels (FAO 2020). Considering these numbers, it is important to understand the implications of fishing in a warming environment to ensure a stable food supply and economy.

Fish body size commonly decreases due to fishing (Jennings & Kaiser 1998). Fishing can also cause alternative stable states in species composition by changes in predator-prey dynamics (Jennings & Kaiser 1998, Walters & Kitchell 2001, de Roos & Persson 2002). For example, species richness, fish community composition and total fish abundance changed drastically after an overfishing event on cod that led to its decline (McCain *et al.* 2016). These changes may take a long time to recover from, with only some (10-50%) previously overexploited ecosystems showing signs of recovery (Lotze *et al.* 2011). Selective removal of a specific species can cause top-down trophic cascades when predator control on the consumers decreases (Casini *et al.* 2009, Filbee-Dexter & Scheibling 2014). For example, the disappearance of north-west Atlantic cod due to exploitation has increased the abundance of

small pelagic prey like the northern shrimp (*Pandalus borealis*) and the northern snow crab (*Chionoecetes opilio*) (Frank *et al.* 2005). The effects of fishing can therefore both affect the fished species directly (Jennings & Kaiser 1998, Frank *et al.* 2005) and indirectly affect other organisms through the disappearance of their predator for example (Frank *et al.* 2005, Filbee-Dexter & Scheibling 2014, McCain *et al.* 2016).

In a lake where the size-selective top-predator brown trout (*Salmo trutta*) that preferentially feed on small juvenile fish was close to extinction due to overfishing, stunted adult consumers of Arctic charr (*Salvelinus alpinus*) were removed by fishing. This promoted the return of the predator brown trout (*Salmo trutta*) since the removal of the stunted adult consumers of Arctic charr (*Salvelinus alpinus*) promoted juvenile Arctic charr (*Salvelinus alpinus*) (Persson *et al.* 2007). The fraction of juvenile consumer fish increases when adult consumers disappear due to harvesting (de Roos *et al.* 2020). Theory suggests that increased background mortality of a juvenile-specialised predator at first leads to a slow monotonic decline in predator biomass, the relationship is however not fully monotonic as further increases in the background mortality of predators results in a collapse of the predator population, and the community has switched to the other alternative stable state, which only is comprised of consumers and the resource (de Roos & Persson 2013). The alternative stable states that occur are caused by the same ecological mechanism as in the model by Lindmark *et al.* (2019), where temperature-driven ontogenetic asymmetry leads to biomass overcompensation, which causes emergent Allee effects. High fishing mortality can therefore have detrimental effects on fish food webs by either inducing dynamics such as alternative stable states (de Roos & Persson 2002, de Roos & Persson 2013), just like the effects of temperature (Lindmark *et al.* 2019).

1.3 Combined effects of fishing and increased temperature

As the effects of fishing and climate change occur simultaneously, it is important to know what the combined effects are and if they interact (Woodward *et al.* 2010). Fishing can cause cyclic population dynamics to disappear, and climate might enhance these effects (Hidalgo *et al.* 2011). Both increased temperature and a increase in the fishing pressure decrease the body size of fish (Jennings & Kaiser 1998, Planque *et al.* 1999, Cheung *et al.* 2013). Furthermore, the combined interactive effects of increased temperature and fishing on zebrafish (*Danio rerio*) caused catastrophic effects on recruitment, and in scenarios where harvesting was size-selective the decrease in recruitment was the most severe (Wootton *et al.* 2021). Climate change and exploitation from fishing can also have interactive effects which can cause management strategies to fail (Planque *et al.* 2010). A recent study suggests that the yield of predatory fish is likely to decrease in warming waters, despite a increase in predator growth rate. The decrease in yield can be attributed to a decreased resource carrying capacity due to warming (Lindmark *et al.* 2022). The stability of fish communities, therefore, depends on both temperature and fishing, and they can also be interacting (Planque *et al.* 2010, Wootton *et al.* 2021). For example, as in the case of body size where both increased temperature and fishing decrease body size (Jennings & Kaiser 1998, Planque *et al.* 1999, Cheung *et al.* 2013), simultaneous warming and fishing can also have interacting effects on the body size of fishes (Smalås *et al.* 2020).

1.4 The knowledge gap

The effect of temperature on stability of a food web depends on the trophic interactions (Lindmark *et al.* 2019). It is also known that fishing can either cause alternative stable states (Frank *et al.* 2005, Persson *et al.* 2007, de Roos & Persson 2013, de Roos 2020) or cause limit cycles to appear or disappear (Hidalgo *et al.* 2011), depending on temperature. It is also suggested that fishing and increased temperature have interacting effects on stability and coexistence of food webs (Planque *et al.* 2010, Hidalgo *et al.* 2011, Lindmark *et al.* 2022). However, it is not known how the combined effects of fishing and increased temperature on stability (alternative stable states, cyclic dynamics and extinctions) depend on the feeding interactions between predator and prey and what trophic level is fished on. This limits the ability to predict the effects of different fishing strategies on food webs during climate change.

1.5 Research question

How does fishing on adult consumers and/or predatory fishes affect stability and size-structure of a food web in an environment which is warmer due to climate change? To answer this question, I analysed the stability (alternative stable states, extinctions and cyclicity) and size-structure in a food web where size-selective predators feed exclusively on juvenile consumer fish.

1.6 Hypotheses

Since both fishing (de Roos & Persson 2013) and increased temperature (Lindmark *et al.* 2019) can induce emergent Allee effects, I expect that fishing on the predators in a warmer environment will further reduce the stability of the food web by inducing a switch in alternative stable states at a lower fishing pressure (such that the predator goes extinct). I expect this due to the effects of temperature on metabolism, mortality rate and other vital rates, and since the temperature effects depend on size (Brown *et al.* 2004, Savage *et al.* 2004).

Since fishing on adult consumers can cause cyclic dynamics to appear (Persson *et al.* 2007), and increases in temperature has been shown to reduce cyclic dynamics (Hidalgo *et al.* 2011) I therefore hypothesise that fishing on adult consumers could lead to cyclic dynamics, that disappear when in a warmer environment.

I expect that fishing on both adult consumers and predators could make the community more resistant to a shift in alternative stable state due to the extinction of the predator, since removal of adult consumers promotes juvenile consumers (Persson et al. 2007 and de Roos 2020), which means more food for the predator. In a warmer environment there will still be a positive effect of fishing on both adult consumers and predators, but due to the effects of temperature on metabolism, mortality rate and other vital rates (Brown *et al.* 2004, Savage *et al.* 2004) and the resources carrying capacity (Blanchard *et al.* 2012), the positive effects will not be as pronounced.

2. Methods

2.1 Model dynamics

This study uses a modified version of the generic stage-structured biomass model from Lindmark *et al.* (2019), which is derived from de Roos *et al.* (2007) and de Roos & Persson (2013) and was modified to be temperature dependent. The modelling study by Lindmark *et al.* (2019) uses both a generic and an empirical stage-structured biomass model. The generic model is simpler than the empirical model, because it only uses one variable q to determine whether the juvenile consumers or adult consumers are competitively superior (de Roos *et al.* 2008). In this study I modified that model to investigate the effects of fishing.

The generic stage-structured biomass model has three trophic levels; resource, consumers, and predators, where the consumers are split into juvenile consumers and adult consumers (Lindmark *et al.* 2019). The average body size of adults and predators are set to 0.0001 *g* and 0.01 *g* respectively. These average body sizes are used to calculate the consumer and predator mass-specific ingestion rate $M_{C,P}$, consumer and predator mass-specific maintenance rate $T_{C,P}$ and juvenile, adult and predator background mortality $\mu_{J,A,P}$. While the average body sizes of adults and predators are smaller than any typical fish, the importance lies in the ratio between the body sizes. Therefore, the average body size of predators is 100 times the average body size of adult consumers (Peters & Wassenberg 1983).

2.2 Temperature dependence

Just like in Lindmark *et al.* (2019), to achieve temperature dependence a few select rates and variables were scaled with a Boltzmann-Arrhenius function which is scaled to the reference temperature of $19°C$ ($292.15K$). I used this form of the Boltzmann-Arrhenius function:

$$r_Y = e^{\frac{E_Y(T-T_0)}{kTT_0}}$$

$E_Y[eV]$ is the activation energy of Y (Appendix 1, Table A3), $T[K]$ is the current temperature, $T_0[K]$ the reference temperature of $19°C$ ($292.15K$) and $k[eVK^{-1}]$ is the Boltzmann constant (Gillooly *et al.* 2001). The parameters and functions (Y) that are temperature dependent are resource turnover rate (ρ), maximum resource density (R_{max}), maintenance rate ($T_{C,P}$), maximum intake rate ($M_{C,P}$) and background mortality rate ($\mu_{C,P}$) (Lindmark *et al.* 2019).

2.3 Model and equations

The state variables for biomass density $g\ m^{-3}$ of resources, juvenile consumers, adult consumers and predators are R, J, A, and P respectively (equations 1-4):

$$\frac{dR}{dt} = G(R,T) - w_J(R,T)J - w_A(R,T)A \tag{1}$$

$$\frac{dJ}{dt} = v_A^+(R,T)A - \gamma(v_J^+, d_J, T)J + v_J(R,T)J - d_J(P,T)J \tag{2}$$

$$\frac{dA}{dt} = \gamma(v_J^+, d_J, T)J + (v_A(R,T) - v_A^+(R,T))A - d_A(T)A - f_A A \tag{3}$$

$$\frac{dP}{dt} = (v_P(J,T) - \mu_P r_\mu)P - f_P P \tag{4}$$
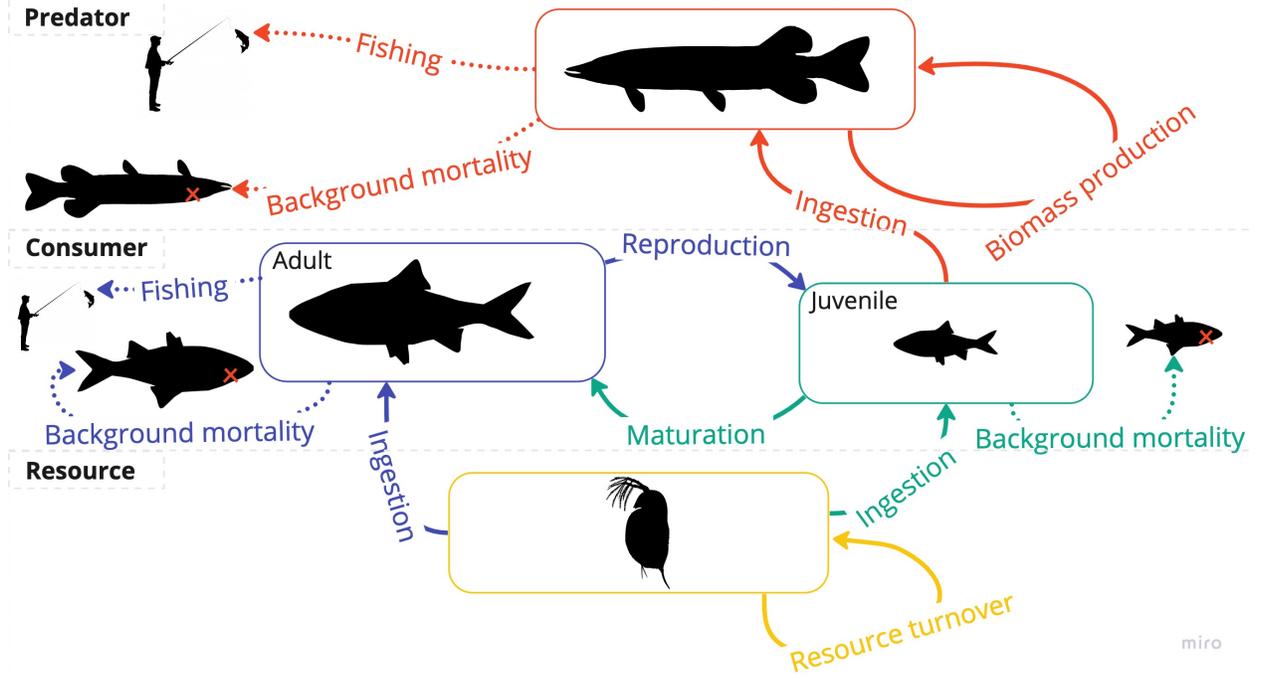
Figure 1. Flowchart of biomass of the stage-structured biomass models three trophic levels; Predator, Consumer and Resource. Here represented as northern pike (Esox lucius), common roach (Rutilus rutilus) and daphnia (Daphnia spp.). The consumer trophic level is split into juvenile consumers and adult consumers. The predators feed on the juvenile consumers. The predators and/or adult consumers are fished on. All vital rates other than fishing on adult consumers and predators are temperature dependent. The northern pike, common roach and daphnia silhouette are from Phylopic (http://phylopic.org/), and the fisherman silhouette from PublicDomainPictures (http://PublicDomainPictures.net).

Resource biomass density (R) increases with semichemostat dynamics:

$$G(R,T) = \rho r_\rho (R_{max} r_{R_{max}} - R)$$

ρ is the turnover rate and R_{max} the resources maximum biomass obtained without consumers (de Roos & Persson 2013), and $r_{R_{max}}$ is the temperature-dependence of maximum resource biomass (Lindmark *et al.* 2019).

Mass-specific foraging of the resource by juvenile and adult consumers respectively are set by:

$$w_J(R,T) = M_C r_M \frac{R}{(H_C + R)}$$

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and

$$w_A(R,T) = qM_C r_M \frac{R}{(H_C + R)}$$

Ingestion by the consumers follows a type II functional response as a function of the resource biomass density R, where M_C is the mass-specific maximum ingestion rate and r_M is the temperature-dependence of ingestion. The ingestion rate of resources has a maximum, when R goes to infinity the expression $\frac{R}{(H_C+R)}$ goes to 1. Therefore, when R is goes to infinity, the consumers ingestion rate is M_C and qM_C respectively. H_C is the half-saturation point, at this resource biomass density the ingestion rate of the consumers is half of its maximum value (Yodzis & Innes 1992). The difference between juvenile and adult foraging is set phenomenologically by the factor q, which determines the ratio of adult to juvenile ingestion of the resource (de Roos & Persson 2013).

Juvenile and adult consumer biomass increases by the terms for net biomass production:

$$v_A(R,T) = \sigma_C w_A(R) - T_C r_T$$

and

$$v_J(R,T) = \sigma_C w_J(R) - T_C r_T$$

where σ_C is the conversion efficiency from the ingested resource ($w_{J,A}(R,T)$) to production of new biomass. It decreases by the energy (in terms of biomass) required for maintenance T_C (Yodzis & Innes 1992). Juvenile biomass also increases by the adults reproduction $v_A^+(R,T)$ which is $v_A(R,T)$ but restricted to positive values, and juvenile biomass decreases through maturation ($\gamma(v_J^+, d_J, T)$), which is a function of $v_J^+(R,T)$ and $d_J(P,T)$. Consumers stop growing in biomass once they reach maturity, all of v_A goes into reproduction through v_A^+. The effect of using the $v_{J,A}^+$ notation is that as long as juvenile and adult net production is positive; there is growth, maturation and high fecundity (de Roos & Persson 2013).

The mortality rate for juvenile consumers follows a type II functional response, due to the predators type II functional response, described as:

$$d_J(P,T) = \mu_J r_\mu + M_P r_M \frac{P}{H_P + J}$$

M_P and H_P are the predators' mass-specific maximum ingestion rate and ingestion half-saturation prey density (de Roos & Persson 2013).

And the mortality rate of adult consumers is:

$$d_A(T) = \mu_A r_\mu$$

Both adults and juveniles have a background mortality rate $\mu_{J,A}$ that is temperature-dependent, according to r_μ.

Juveniles mature to adults according to:

$$\gamma(v_J^+, d_J, T) = (v_J^+(R,T) - d_J(P,T))/(1 - z^{(1 - \frac{d_J(P,T)}{v_J^+(R,T)})})$$

The juvenile maturation rate increases with $v_J^+(R,T)$ and decreases with $d_J(P,T)$. That is, a high and positive net biomass production of juveniles means that more juveniles will mature to adults whereas if $d_J(P,T)$ is high only a small fraction will survive to continue to the adult stage (de Roos & Persson 2013). The term:

$$1 - z^{(1 - \frac{d_J(P,T)}{v_J^+(R,T)})}$$

adjusts for the ratio between size at birth and size at maturation z, when the size difference between new-borns and adults is large, z decreases which in turn decreases the maturation rate because the probability of making it to adulthood will be lower (de Roos & Persson 2013).

The predator biomass density changes with the following function:

$$\frac{dP}{dt} = (v_P(J,T) - \mu_P r_\mu)P$$

where μ_P is the predator per-capita mortality and $v_P(J,T)$ is the net biomass production of predators:

$$v_P(J,T) = \sigma_P M_P r_M \frac{J}{H_P + J} - T_P r_T$$

The net biomass production of predators depends on the ingestion of juvenile prey and thus has a type II functional response. σ_P is the conversion efficiency of the predators. As before, net biomass production is the difference between ingested energy and maintenance T_P, both of which depend on temperature. M_P and H_P are the predators' mass-specific maximum ingestion rate and ingestion half-saturation prey density (de Roos & Persson 2013). The predators are specialised on the juvenile consumers, hence $v_P(J,T)$ only contains the term J for juvenile consumers, and not A for adult consumers.

Finally, to investigate the effects of fishing on the stability of the food web, the terms:

$$f_A A$$

and

$$f_P P$$

for fishing pressure on adult consumers and predators are added. Fishing pressure has a linear relationship with the biomass densities of adult consumers and predators (A and P).

The yield of either adult consumers or predators are obtained by multiplying the fishing pressure ($f_A A$ or $f_P P$) with the equilibrium biomass density (A or P):

$$f_A A * A$$

and

$$f_P P * P$$

A flowchart of the temperature-dependent stage-structured biomass model with added fishing is presented in figure 1.

2.4 Analyses

Equilibrium biomass densities and bifurcations were analysed using the MATLAB (MATLAB 2022) package MATCONT GUI (Dhooge *et al.* 2008) to look for the effects of fishing on stability (alternative stable states, cyclicity and extinctions) and size-structure in a warmer climate. Bifurcation analysis is conducted by testing for the effects on the equilibrium biomass densities by changing the value of a parameter, in this case $f_{A,P}$. During the computation of the bifurcation curve MATCONT GUI (Dhooge *et al.* 2008) gives information on changes of the dynamics of the system and at what values they occurred at. For example, if the system goes fixed points to cycles (Hopf point) or if the system switches from one alternative stable state to another (Limit point).

To analyse for the effects of fishing on stability (alternative stable states, cyclicity and extinctions) and size-structure in a warmer climate three temperatures were chosen. From Lindmark *et al.* (2019) the temperatures of $21°C$ ($294.15K$) and $24°C$ ($297.15K$) were selected because between these temperatures a switch between two alternative stable states occurs. The final temperature of $18°C$ ($291.15K$) was selected because increased temperature combined with increased fishing pressure can either cause limit cycles to appear or disappear (Hidalgo *et al.* 2011), and the model by Lindmark *et al.* (2019) exhibits cycles at lower temperatures when predation is not size-selective. In all computations, juveniles are competitively superior to the adults (the adult to juvenile consumer ingestion ratio $q = 0.5$), and the juvenile to adult consumer size ratio z is set to 0.01.

At each of these three temperatures ($18°C$, $21°C$ and $24°C$), equilibrium biomass densities of the state variables (R, J, A, and P) were obtained through time integrations. Next, bifurcation analysis was conducted at each temperature by increasing the fishing pressures of f_A and f_P separately, which gives us how the equilibrium biomass density of each state variable (R, J, A, and P) changes as either the fishing pressure on adult consumers (f_A) or predators (f_P) changes. There are three possible ways in which the equilibrium of the system can change, it can reach a Hopf bifurcation point where the system goes from fixed equilibrium points to limit cycles (biomass densities of the state variables display a cyclic behaviour). The system can also reach a limit point, which tells us at what parameter value the system switches from one alternative stable state to another. Finally, the system can reach a branch point, which tells us at what parameter value one of the populations of the

food web goes extinct (a state variable goes to zero). After identifying how the equilibrium of the food web changes with the two parameters f_A and f_P separately, these results were used to understand the behaviour of the system when both the adult and predator are fished on simultaneously.

To investigate the effects of simultaneous increase of two parameters (in this case f_A and f_P), two-parameter bifurcation analysis was conducted from the same points of interests as previously, hopf points, limit points and branch points. I, for example, selected a limit point, which tells us how the food web goes from one alternative stable state to another, at a particular value of f_P and when f_A is zero and use MATCONT (Dhooge *et al.* 2008) to determine this for a wide range of values of the two parameters. I then constructed a landscape of all possible combinations of values of the two parameters (f_P and f_A), which tells us where the alternative stable state occurs. The same procedure was also done for Hopf points and branch points. This finally gives us at what combinations of the two parameters (f_A and f_P) where there are cyclic dynamics, at what parameter values the system switches between two alternative stable states and when the community is bistable. A distinguishing difference between the two alternative stable states could be that one of the populations of the food web goes from being present to going extinct.

Minimum and maximum biomass values of limit cycles were calculated by running time integrations at different parameter values until the system reaches equilibrium.

To track how different rates vary in the bifurcation analysis, I specified User functions in MATCONT (Dhooge *et al.* 2008) for each rate.

R version 4.1.2 (R Core Team 2021) and the R packages R.matlab (Bengtsson 2022) and tidyverse (Wickham *et al.* 2019) was used to plot the figures. The R package knitr (Xie 2021) was used to produce the tables in Appendix. Model files, instructions for viewing and implementing the model in MATCONT, and R-scripts to reproduce the figures with simulated data have been deposited on https://github.com/gabrielnordstrom/Fishing_Temperature. The model code for MATCONT can also be found in the Appendix, under "Model code for MATCONT".

3. Results

Fishing in a warmer climate has different effects depending on what trophic level (adult consumers or predators) is fished on and if several trophic levels are fished at the same time (figure 1, 3 and 5).

3.1 The fishing pressure where predators go extinct is lower at higher temperatures

Fishing on predators (f_P) causes food webs to switch to an alternative stable state, where the predator has gone extinct and cannot re-invade despite lowered fishing pressure, and the composition of the consumer population has changed drastically (figure 2).

In an environment with a higher temperature the fishing pressure (f_P) where the alternative stable state occurs is lower (figure 2e-h). This means that it takes less fishing on the predator in a warmer environment for the predator to go extinct (figure 2e-h). At $24°C$ and at low f_P values the resource-consumer-predator community is always in a bistable state (dashed black line region of figure 2a-d). The community is bistable if at the same fishing pressure (f_P) the community can either go to the alternative stable state where the predators are present or the one where the predators are extinct, depending on the initial biomass density levels. At $18°C$ however, the community can experience biomass density levels that are not bistable at low enough fishing pressures (full line region in figure 2e-h). Increased fishing pressure on the predator (f_P) causes the predator biomass to decrease and eventually go extinct (figure 2d and h). Decreases in predator biomass cause juvenile (figure 2b and f) and adult (figure 2c and g) consumers to increase. Increases in consumer biomass lead to increases in their ingestion rate of the resource, which decreases the resources' equilibrium biomass density. The ratio of adult consumer to juvenile consumer equilibrium biomass density is tripled when the predator goes extinct, compared to when predators are present, at both $18°C$ and $24°C$ (Appendix, figure A5). This means that when present, predators control the ratio of adult to juvenile consumers by feeding on the juvenile consumers, but if the predators go extinct due to fishing the control disappears, which causes the adult consumer biomass to explode.

The predator population collapses at a lower fishing pressure at $24°C$ ($297.15K$) compared to at $18°C$ ($291.15K$) because warming decreases the predators' net biomass production rate ($v_P(J, A)$) (Appendix, figure A4). Since the predator's only source of mortality in the absence of fishing is their background mortality μ_P (equation 4 in methods) which is constant, the fishing pressure on the predators (f_P) where the predators go extinct depends entirely on the net biomass production rate of the predators ($v_P(J, A)$). The net biomass production rate of the predators ($v_P(J, A)$) is the highest at $19°C$ ($292.15K$), and at temperatures both lower and higher than $19°C$ ($292.15K$) the predator net biomass production rate($v_P(J, A)$) decreases. The net biomass production rate decreases faster at temperatures above $19°C$ ($292.15K$), compared to at temperatures below $19°C$ ($292.15K$) (Appendix, figure A4).

Warming of the environment affects the regulation of the consumer population. The lowest of maturation rate and the reproduction rate constitute the bottleneck of the consumer population. The limiting factor for population growth switches from reproduction to maturation when the predator goes extinct (figure 3). When the predator is extinct, the difference

between maturation and reproduction rate is larger in the warm environment than in the cold, meaning that competition in the adult consumer stage is stronger in a warmer environment (Appendix, figure A15). Without fishing, a high predator biomass density can control the consumer population by inducing a high mortality in the juvenile consumers which leads to a higher reproduction rate that promotes the biomass density of its prey, the juvenile consumers. As the predator biomass density decreases due to fishing its control on the consumer population also weans, leading to a decrease in reproduction rate and an increase in maturation rate (figure 3). When the predators are extinct, the regulation of the consumer population switches to a state where it instead is limited by a high maturation rate. The switch in what rate (maturation rate or reproduction rate) limits the consumer population when the predator is present or extinct due to fishing (figure 3) is caused by biomass overcompensation in response to juvenile consumer mortality.

With no predation on the juvenile consumers, the consumer population is limited by a low reproduction rate due to the adult consumers being competitively inferior to the juvenile consumers ($q = 0.5$, Appendix Table A1). When the predators are extinct the per biomass maturation rate is high, which also means that the competition amongst the adult consumers is high (Appendix, figure A15). The adult consumers are therefore outcompeted by themselves and the juvenile consumers when the resource biomass density is low (figure 1a & d), the per biomass reproduction rate is therefore low. In a warmer environment, the difference between the population level maturation rate and reproduction rate is higher which means that as the environment heats a slightly greater ratio of adult consumers to juvenile consumers is observed (Appendix, figure A5). A greater density of adult consumers, therefore, means that the adult consumers experience stronger competition in their life stage (Appendix, figure A15b). Adult consumers therefore experience greater adverse effects than juvenile consumers, in a warmer environment.

At the higher temperature of $24°C$, the fishing pressure (f_P) where predators can invade is zero. This means that for the food web to be successfully restored by either immigration or stocking of predators the fishing activity needs to stop entirely (figure 2a-d), and the immigration or stocking needs to increase the predator biomass density to the level at the red line for it to succeed. At $18°C$ the fishing pressure (f_P) where predators can invade and restore the food web is larger than zero (figure 2e-h). Fishing on predators can therefore cause alternative stable states where the predator either is present or extinct and it takes less fishing before the predators go extinct when the environment is warmer (figure 2).

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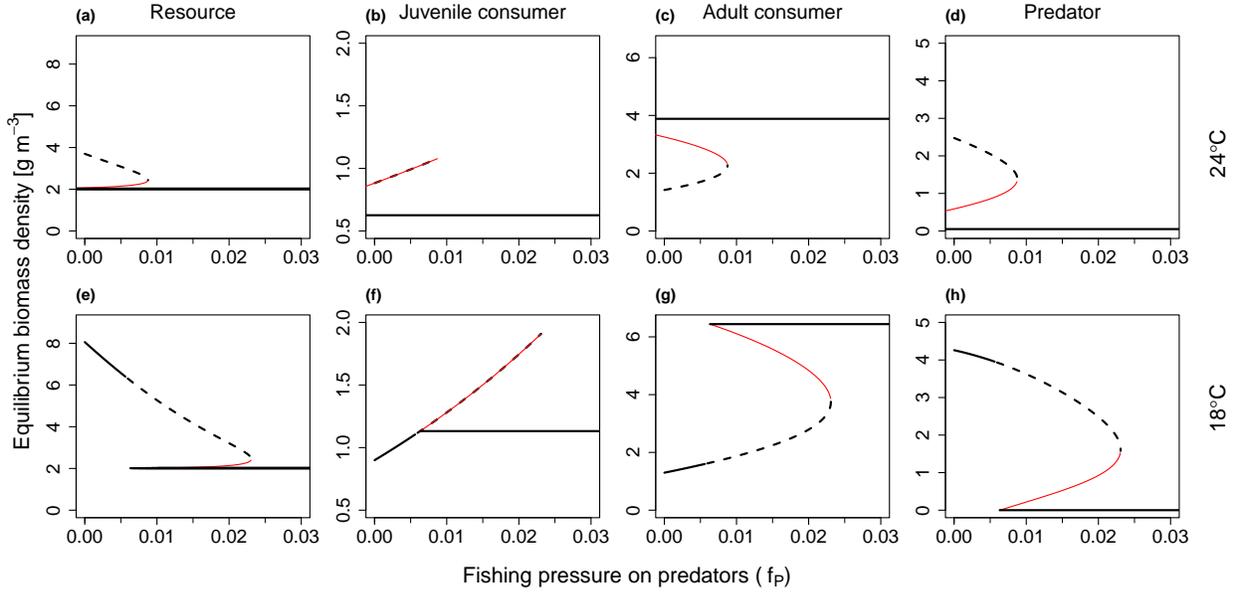
Figure 2. Equilibrium biomass densities of the resource (a and e), juvenile consumer (b and f), adult consumer (c and g) and predator (d and h) as a function of fishing pressure on the predator (f_P) at two temperatures 18°C (e-h) and 24°C (a-d). Black lines (full and dashed) are stable equilibria while red lines annotate unstable equilibria that connect the two stable regions between the unstable region. Alternative stable states occur between fishing pressures on the predator (f_P) of ~ 0.005 and 0.0225 at 18°C (e-h), and at fishing pressures on the predator (f_P) of ~ 0 and 0.01 at 24°C (a-d). As the fishing pressure on the predator (f_P) increases it causes the resource to decrease (a and e), juvenile consumer to at first increase but at the alternative stable state to crash to a lower level (although higher than at zero f_P) (b and f), the adult consumer increases (c and g) and the predator decreases to eventual extinction (d and h). At the alternative stable state all biomass densities stabilise and stop changing with further increases in f_P, and all other than the predator are non-zero (d and h). Predators can therefore handle less targeted fishing at higher temperatures before the predator population goes extinct. All parameters have default values (Appendix, Table A1 & A3).

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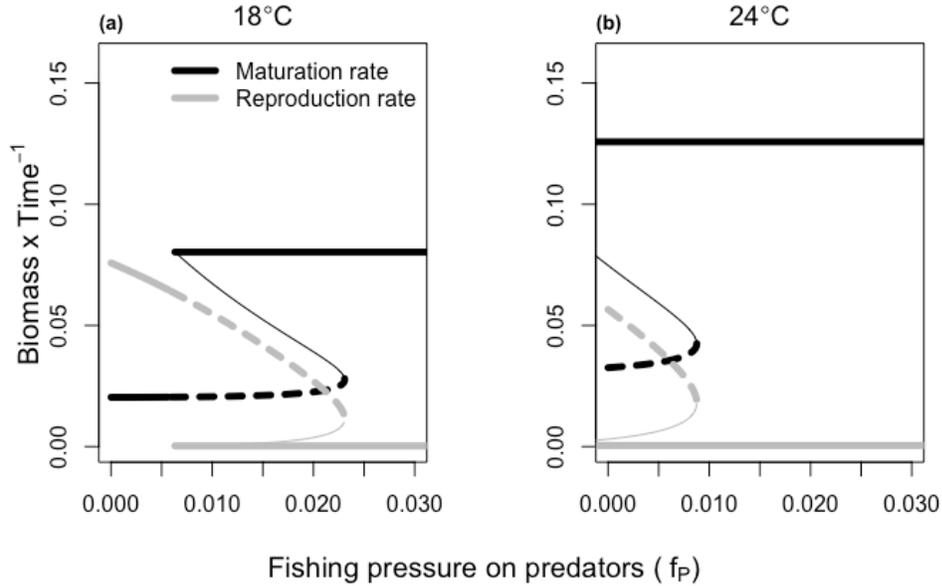
Figure 3. Population level maturation and reproductive rate changes as the fishing pressure on the predator (f_P) increases at 18°C (a) and 24°C (b). The consumer population goes from being limited by a low maturation rate to a low reproduction rate when the predators are not getting fished on compared to when the predators have gone extinct. When predators are present at high enough biomass densities, they can control the consumer population by inducing a high reproduction rate, the population then becomes dominated by juvenile consumers. In a warmer environment the difference between maturation and reproduction is larger, adult consumers therefore experience a higher competition due to increased biomass densities, at higher temperatures. All parameters have default values (Appendix, Table A1 & A3).

3.2 Fishing on adult consumers causes limit cycles, but only at lower temperatures

As the fishing pressure on the adult consumer (f_A) increases it either causes limit cycles to start and then later on stop (figure 4e-h) or has no effect on the stability (does not induce limit cycles) of the food web (figure 4a-d), depending on the temperature of the environment (figure 4). At 18°C increased fishing pressure on the adult consumer (f_A) leads to limit cycles between fishing pressure on the adult consumer (f_A) of ~ 0.05 and ~ 0.45, with a maximum of the limit cycles amplitude at ~ 0.10 f_A. At 24°C increased f_A does not cause limit cycles to start. Generally, at both temperatures when f_A is increased the adult consumer equilibrium biomass density will decrease due to higher mortality (figure 4c and g), the decrease in adult consumer equilibrium biomass density causes the resource biomass density to increase due to decreased consumption of the resource (figure 4a and e). The juvenile consumer's equilibrium biomass density is constant with increasing f_A (figure 4b and f) and predator equilibrium biomass density decreases (figure 4d and h). While the resource, juvenile consumer, and predator biomass density decrease with temperature (figure 4), adult consumer biomass density increases with temperature (Figures 4c and g). Adult consumers do not go extinct when f_A is 1 since there is always a supply of new adult

consumer biomass from the juvenile consumer stage through maturation. The origin of the limit cycles at $18°C$ is coupled to the dynamics between the predator and its prey, the juvenile consumers, as when the predators are extinct there are no limit cycles at either $18°C$ or $24°C$ (Appendix, figure A10). The predator and juvenile consumer biomass densities oscillate out of phase with approximately 1/4 of a cycle (Appendix, figure A8), which is characteristic of predator-prey cycles.

The predator-prey cycles between the juvenile consumers and predators at $18°C$ between fishing pressures of ~ 0.05 and ~ 0.45 starts as the fishing pressure on the adult consumers increases (f_A), due to a lower level of competition in the consumer population as the adult consumer biomass decreases. As adult consumer biomass density decreases due to fishing (f_A), the juvenile consumer net energy production rate (Appendix, figure A7) goes up. A faster production of juvenile consumers eventually generates predator-prey cycles since a faster production of juvenile consumers also means a higher ingestion rate for the predators (Appendix, figure A9a). The juvenile consumer and predator equilibrium biomass densities start to oscillate over time due to the overshoot in juvenile consumer equilibrium biomass density. juvenile consumers do not continue to grow indefinitely as higher densities of the juvenile consumer also mean more food for their predators and a faster ingestion rate (Appendix, figure A6). Higher densities of juvenile consumer biomass at the same time cause the intake rate of predators to increase (Appendix, figure A6), and the net energy production rate is unable to compensate for the increased mortality due to predation (Appendix, figure A6), which causes the juvenile consumer biomass density to decrease (Appendix, figure A6). Predator intake rate, therefore, crashes (Appendix, figure A6) due to lower juvenile consumer biomass densities (Appendix, figure A6).
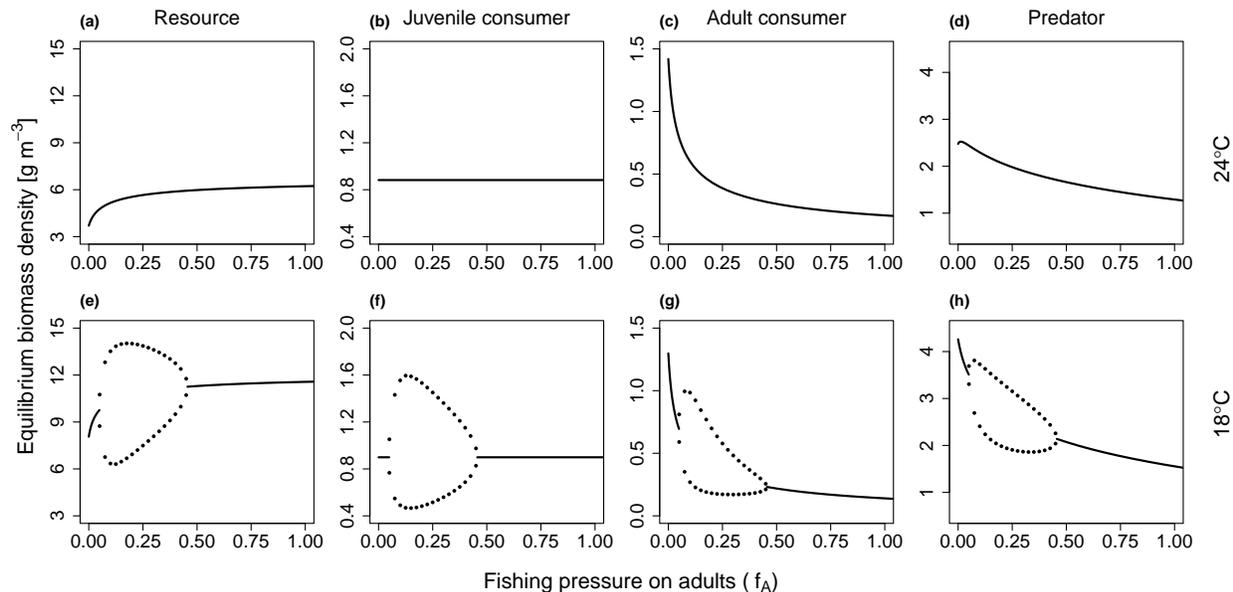
Figure 4. Equilibrium biomass densities of the resource (a and e), juvenile consumer (b and f), adult consumer (c and g) and predator (d and h) as a function of fishing pressure on the adult consumer (f_A) at the two temperatures $18°C$ (e-h) and $24°C$ (a-d). Maximum and minimum densities of limit cycles are shown with points (e-h). At the lower temperature of $18°C$ (e-h), but

not 24°C (a-d), does increased fishing pressure on the adult consumer (f_A) cause limit cycles to emerge while further increased fishing pressure causes them to disappear (e-h). The limit cycles at 18°C occurs between fishing pressures on the adult consumer (f_A) of ~ 0.05 and 0.45. Increased fishing pressure on the adult consumer (f_A) causes the resource equilibrium biomass densities to increase (a and e), juvenile consumer equilibrium biomass density is constant (b and f), adult consumer equilibrium biomass density decreases (c and g) and predator biomass density decreases (d and h). Though initially at 24°C the equilibrium biomass density increases at low f_A values, but as f_A continues to increase the predator equilibrium biomass density start decreasing (d). All parameters have default values (Appendix, Table A1 & A3).

3.3 The yield either increases or decreases when the environment warms up

The yield of predator biomass density has a hump-shaped relationship with the fishing pressure (f_P) at both 18°C and 24°C (figure 5a) when the fishing pressure reaches the point where the predator goes extinct ($f_P \approx 0.01$ at 24°C and $f_P \approx 0.0225$ at 24°C) the yield goes to zero (figure 5a). Due to the yield having a hump-shaped relationship with the fishing pressure (f_P), which is also shifted to the right in the graph, it means that the fishing pressure corresponding to maximum sustainable yield (MSY) is dangerously close to fishing pressures where the predator goes extinct. At 18°C the MSY occurs at ~ 82 percent of the fishing pressure which results in extinction (blue diamond in figure 5a), at 18°C however the MSY occurs at a fishing pressure which is ~ 94 percent of the fishing pressure which results in extinction (red diamond in figure 5a). This means that if the predators are fished at the fishing pressure corresponding to the MSY the risk of extinction will be much larger, if in a warmer environment.

The yield of adult consumers on the other hand increases monotonically with the fishing pressure on the adult consumers (f_A) (figure 5b). At 18°C the yield of adult consumers also oscillates when the fishing pressure on the adult consumers is between 0.05 and 0.45 (dotted part of the blue line in figure 5b) because of the population cycles. Another difference compared to the yield of predators is that the yield is higher at 24°C compared to 18°C. This means that it depends on what trophic level is fished on to know what effects a warmer climate has on the yield of fish.
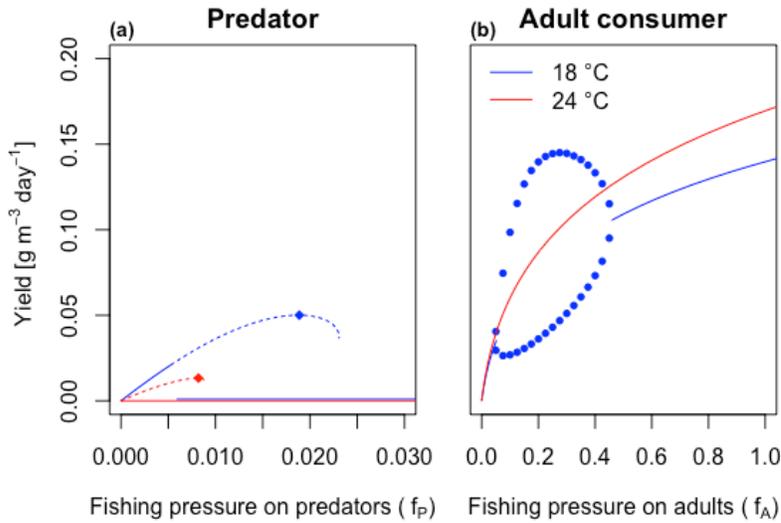
Figure 5. The yield of predators (a) and adult consumers (b) as a function of the fishing pressure on predators (f_P) (a) and fishing pressure on adult consumers (f_A) at 18°C (blue line) and 24°C (red line) when fishing at the equilibrium. The maximum sustainable yield (MSY) when fishing on predators (a) is lower at high temperatures than at low temperatures. The community is also in a bistable state (dashed lines) at the fishing pressure on predators (f_P) which corresponds to the MSY, which means that depending on the initial conditions the community will either be in a state where predators are present or extinct. At a temperature of 24°C (red line) the MSY occurs at a fishing pressure which is 94 percent of the fishing pressure on predators (f_P) which results in predator extinction (red diamond in a). At the lower temperature of 18°C the MSY occurs at a fishing pressure on the predator (f_P) which is ~ 82 percent of the fishing pressure which results in predator extinction (blue diamond in a). The yield when fishing on adult consumers (f_A) increases monotonically (b). At the temperature of 18°C (blue line) the yield is smaller than at 24°C. The yield also oscillates between fishing pressures on the adult consumer (f_A) of ~ 0.05 and ~ 0.45 at 18°C, maximum and minimum yields during the cycles are shown with points (blue dots in b). All parameters have default values (Appendix, Table A1 & A3).

Fishing on adult consumers (f_A) therefore leads to limit cycles which appear and disappear, at low temperatures (figure 4) and fishing on predators (f_P) results in alternative stable states where the predator goes extinct (figure 2). Higher temperature means that the predator goes extinct at lower fishing pressure levels (figure 2). And the effects of increased temperature on the yield depends on what trophic level is fished on (figure 5). But how does simultaneous fishing on both adult consumers (f_A) and predators (f_P) affect the stability and size-structure of the food web? And what are the effects of temperature?

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3.4 Fishing on the adult consumers gives the opportunity to fish more on the predators

It is possible to fish more of the predators (f_P) before the predators go extinct if there is a simultaneous increase in fishing pressure on the adult consumers (f_A). A further increase in the fishing pressure on the adult consumers does however mean that the predators will go extinct at a lower fishing pressure, evident by the hump-shaped outline of the consumer-resource region (predator is extinct) (dark orange area in figure 6). In a warmer environment, the predators are also at a higher risk of extinction, evident by a larger consumer-resource region (predator is extinct) (dark orange area in figure 6). The community can also be bistable which means that depending on the initial conditions the predator can either go extinct or survive, this bistable region is larger at higher temperatures which means that the predator population is at a higher risk of collapse in a warmer environment (light orange area in figure 6). The predators are also at constant risk of extinction in a warm environment without fishing on the adult consumers (figure 6b). It is more beneficial to fish on both the adult consumer and predator in a warmer environment in terms of stability since the community will not be bistable when fishing on only the predators. It is also possible to compensate for the negative effects of temperature on stability by fishing on both the adult consumer and predator, so that the fishing pressure can be as high as in a colder environment without risking predator extinction.

Combined fishing on the adult consumer (f_A) and predator (f_P) leads to increased juvenile consumer biomass density, which benefits the predators (Appendix, figure A11). When only predators are fished on (f_P), the juvenile consumer's net energy production rate decreases (Appendix, figure A13) due to the effects that a lower level of predator biomass density has on competition in the consumer population. A lower net biomass production rate for juvenile consumers will also result in a lower juvenile consumer equilibrium biomass density. The juvenile consumer's net biomass production rate with simultaneous fishing on both adult consumers and predators has the opposite response to fishing since the competition in the consumers is lessened when adult consumer biomass density is removed when they are fished on (f_A) (Appendix, figure A12). However further increases in f_A decrease the juvenile consumer equilibrium biomass density as the adult consumers have passed a biomass density threshold where their reproduction decreases, which results in less biomass of juvenile consumers (Appendix, figure A11b, and d). This in turn means that the predators will go extinct at a lower level of f_P at 1 f_A than at ~ 0.3 f_A (18°C) or ~ 0.5 f_A (24°C) (figure 6a and b).

3.5 Cyclic dynamics can be removed by simultaneous fishing on the predators

The food web experiences limit cycles at different combinations of f_A and f_P, the limit cycle region goes from ~ 0.05 to ~ 0.45 f_A just like when the fishing pressure on adult consumers (f_A) is increased on its own (figure 4e-h). But depending on the current fishing pressure (f_A) in this interval, the food web continues to oscillate as the fishing pressure on the predator (f_P) increases. The maximum fishing pressure (f_P), which still results in limit cycles is at

f_P of ~ 0.04 and f_A of ~ 0.10 (figure 6a) which corresponds to where the amplitude of the limit cycles is the largest when the fishing pressure on adult consumers (f_A) is increased on its own (figure 4e-h).
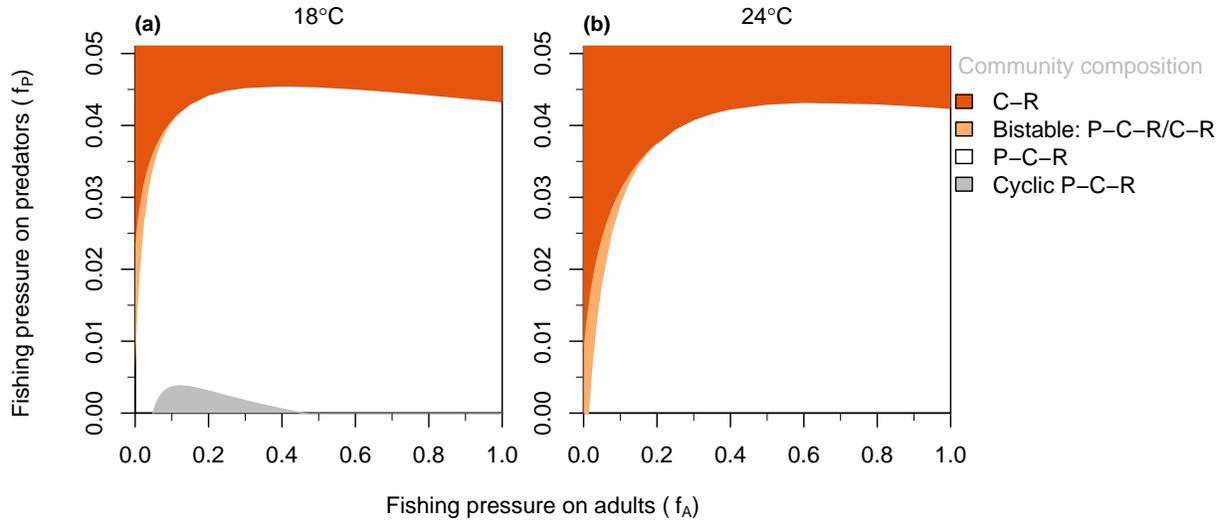
Figure 6. Community composition of the food web at 18°C (a) and 24°C (b) with a fishing pressure on both adult consumers (f_A) and predators (f_P). Gray notates stable limit cycles; orange is the area where the predator goes extinct and light orange is the bistable region where predators either go extinct or survive depending on the initial conditions. The point at which the predators go extinct (orange area) due to the fishing pressure on the predators (f_P) moves up when the fishing pressure on adult consumers (f_A) increases simultaneously, at both 18°C and 24°C (a and b). At a certain point however, the predators stop to gain an advantage with increased fishing on the adult consumers (f_A) and reaches a maximum, as the fishing pressure on the adult consumer (f_A) continues to increase the predator go extinct unless f_P decreases (a and b). The bistable area is larger at 24°C than at 18°C (a and b), and at zero f_A the predators are always vulnerable and at risk of extinction (b). At 18°C the community experiences limit cycles starting at ~ 0.05 f_A, it continues to oscillate as f_P increases and eventually reaches a top at ~ 0.10 f_A and ~ 0.004 f_P, this point corresponds with the f_A value in figure 2e-h where the amplitude is the greatest. All parameters have default values (Appendix, Table A1 & A3).

4. Discussion

Here I show, using a stage-structured biomass model, that the effects of fishing on stability (alternative stable states, cyclic dynamics, and extinctions) of aquatic food webs depend on what life-stage and trophic-level is fished on and the temperature of the environment. Fishing on the predator (f_P) in a warmer environment causes a switch to an alternative stable state (predator goes extinct) at a lower fishing pressure. Fishing on the adult consumer on the other hand (f_A) causes cycles in the population densities, but not in the warmer environment. The community is re-stabilised (cycles disappear) when fishing pressure on the adult consumer (f_A) increases. Combined fishing on both adult consumers (f_A) and predators (f_P) gives the possibility to fish more on predators without causing them to go extinct. Simultaneous fishing in a warmer environment can thus counteract the negative effects on stability caused by climate change. These results are consistent with the findings of previous studies, but it would be necessary to, for example, conduct experiments to determine whether they are valid.

My study corroborates the findings of previous modelling studies suggesting that predators do worse in a warmer environment (Rall *et al.* 2010, Fussman *et al.* 2014, Lindmark *et al.* 2019). I show, just like in Rall *et al.* (2010) and Fussman *et al.* (2014), that temperature can have stabilising effects by removing cyclic behaviour. In my study however, cycles only appear when the fishing pressure on the adult consumers increases and they disappear without an increase in temperature, when the fishing pressure is increased further. Compared to Rall *et al.* (2010) and Fussman *et al.* (2014), which focuses on the effects of temperature, this study only looks at a few select temperatures and focuses more of the effect of fishing. This study also differs from Rall *et al.* (2010) and Fussman *et al.* (2014) as it investigates a food web with several trophic levels, stage-structured consumers, and stage-specific predation. The results I present add new knowledge in the field since my model show the effects of fishing in a warmer environment on several trophic-levels, and not only fishing on the predator stage.

4.1 Fishing on predators in a warmer environment

There is evidence of alternative stable states in the wild due to overfishing. In a lake where the top-predator had collapsed the predator was able to recover when large prey fish were removed, which promoted small prey fishes (Persson *et al.* 2007). This is similar to my results: adult consumers benefit the most from predator extinction when the predator feeds exclusively on juvenile consumers. Furthermore, juvenile consumer biomass increases when adult consumers are fished on. However, the latter is not true for all levels of fishing mortality, as the effect of mortality on adult consumer biomass is hump-shaped when predators are extinct. If the adult consumers were fished, invasion either through immigration or stocking would be more successful, just as in Persson *et al.* (2007). It is however unclear what effects increased temperature would have, as Persson *et al.* (2007) did not investigate the effects of temperature in their study on lake Takvatnet. I show that in a warmer climate, it would take less fishing on the predator to revert lake Takvatnet once again to a consumer-resource state, and that for the predators to successfully invade through immigration or stocking is

harder in a warmer environment as the fishing pressure would need to be decreased further.

The predators can handle less fishing in a warmer environment due to the negative effects that high temperature has on the predator's net biomass production rate. When the environment gets warmer the net energy production rate of the predators decreases, in part due to the direct effects of temperature, and in part due to indirect effects of temperature on the other trophic levels. Similarly, Blanchard *et al.* (2012) showed that, whether increased temperature either increases or decreases the production of fish depends on the effects that temperature has on the production of the resource, phytoplankton. In areas where the production of the resource was below its optimal temperature, the production of predators increased when the temperature of the environment rose. Conversely, in areas where the resource production had already passed the optimum temperature (due to a higher mean temperature), the production of predators decreased (Blanchard *et al.* 2012). Furthermore, Lindmark *et al.* (2022) shows that even though the growth rate of larger fish increases with temperature, the yield will not be larger when the resources' carrying capacity decreases with temperature (Lindmark *et al.* 2022). Both these studies show the importance of studying several trophic levels, especially the resource. And whether the production of fish will increase or decrease with temperature depends on if the current temperature is below or above the resource's optimum temperature. My research adds to our understanding of communities with stage-specific predation and biomass overcompensation, in which the negative effects of warming on the resource can cause the predator to risk sudden collapse (to the alternative stable state where they are extinct), and that the predator becomes extinct at lower fishing pressure in a warmer environment.

4.2 Fishing on adult consumers in a warmer environment

When the fishing pressure on the adult consumer increases it results in population cycles (which disappear with further increases in the fishing pressure), but not in a warmer environment. The exact model mechanism for why the cycles only appear when the temperature of the environment is low remain unclear. However, since there are no population cycles at either low or high temperatures when the predator is extinct, it suggests that the interaction between the predator and its prey controls the cyclic dynamics. Here, the population level intake rate of the predator ($d_J(P)P$) and net biomass production rate of the juvenile consumers ($v_J(R)$) oscillate out of phase with each other by 1/4 of a cycle. Juvenile consumer and predator biomass density then oscillate, also out or phase by 1/4 of a cycle. This is characteristic of classic predator-prey cycles. In another type of stage-structured biomass model (which displays the mechanism of emergent facilitation), it has been observed that predator-prey cycles can emerge due to interactions between the resource and consumer when the predator feeds on the competitively superior consumer (de Roos & Persson 2013). Therefore, the cyclic dynamics at low temperatures are likely due to the combination of the type of predator-prey interactions and the ontogenetic asymmetry.

Cyclic dynamics only emerge at low temperatures ($18°C$) and not at higher temperatures ($21°C$ and $24°C$). This could be due to that the resource decreases in equilibrium biomass density over temperature. A lower resource biomass density means that competition between

juvenile and adult consumers increases. Increased competition might therefore lead to a lower predator ingestion rate and therefore no cyclic dynamics. A decreased resource biomass density due to increased temperature might therefore be the reason why I do not observe cyclic dynamics in a warmer environment.

Reduced cyclic behaviour in a warmer environment could mean that the community also might be more stable in response to stochastic processes (in either the environment or demography) resulting in the extinction of species. Another effect of increasing temperature is that while the biomass of the resource, juvenile consumer, and predators decreases, the biomass of the adult consumer increases. Climate change may therefore reduce cyclic dynamics in aquatic communities, which ultimately means that the community becomes more stable both due to fewer cycles and a smaller risk of extinction due to stochasticity during the cycles.

4.3 Fishing on both adult consumers and predators in a warmer environment

When fishing on both predators and adult consumers in a warmer environment, it is possible to increase the fishing pressure further without the predator going extinct (due to lack of bistable region). This compensates for the negative effects on the stability of the food web caused by increased temperature. This is possible since an increased fishing pressure on adult consumers increases the juvenile consumer equilibrium biomass density. Since the persistence of the predators only depends on the net biomass production rate of the predators ($v_P(J)$) (mortality among the predators is constant), which is dependent on the predator biomass density, the juvenile consumers, it means that a higher juvenile consumer equilibrium biomass density means that the predators will be able to handle a higher fishing pressure before going extinct. However, if the adult consumers are exploited maximally the persistence ability of the predators is decreased, which is due to the juvenile consumer equilibrium biomass density (and net energy production rate of the juvenile consumers ($v_J(P)$) decreases when the adult consumer is exploited maximally. Previous modelling studies show that increased temperature has negative impacts on fisheries (Blanchard *et al.* 2012, Lindmark *et al.* 2022), but I show that the negative effects of temperature on stability can be negated through simultaneous fishing on several trophic-levels.

4.4 Yield

The maximum sustainable yield (MSY) when fishing on predators is lower in a warmer environment. The MSY is also closer to the fishing pressure where the predators go extinct (94% at $24°C$ and 82% at $18°C$). This means that a slight increase in the fishing pressure from where the highest yield is obtained (the MSY) results in extinction. The MSY also occurs at a fishing pressure where the community is bistable, both in cold and warmer environments. This means that it is more unsustainable to fish at the MSY in a warmer environment, and the yield obtained will be lower. This follows the same pattern as in a modelling study by Lindmark *et al.* (2022), where the yield decreased in a warmer environment due to the

negative effects on the resources carrying capacity. It is therefore less sustainable to fish at the MSY in a warmer environment.

The yield of adult consumers is however larger in a warmer environment since adult equilibrium biomass density increases with temperature. However, when the predators are extinct, there is no increase in adult consumer equilibrium biomass density in a warmer climate. This means that there is a mechanism in which the predators are involved in that increases the yield of adult consumers when the predators are present. Predators are therefore necessary to maximise the yield in a warmer climate. In colder environments, the yield oscillates at certain fishing pressures, though the mean yield will be comparable to when there are no cyclic dynamics. Therefore, in a warmer environment, there is an increase in the yield of adult consumers, and the yield does not oscillate.

The yield of predators when adult consumers are fished simultaneously is projected to increase compared to when only predators are fished. This is because the predators indirectly profit from the exploitation on adult consumers because the juvenile consumer biomass increases. In a warmer environment, it is also possible to negate the risk of predator extinction due to increased temperature by joint exploitation. The yield of the adult consumer could also increase through joint exploitation of the predators since the adult consumers profit from less predation on the juvenile consumers. The yield might also benefit from an increase in temperature since the yield of adult consumers increases in a warmer environment. The predators should however not be fished to extinction since the adult consumers (and therefore the yield of them) profit from the predators being present. Therefore, joint fishing on both predators and adult consumers is projected to increase the yield, but whether the total yield of both would increase or decrease in a warmer environment is still unclear.

What these results show is that a holistic view is needed for sustainable fisheries, and not view fish as a resource that can simply be harvested. Since the effects of fishing differs substantially based on what trophic level is fished on, and that temperature can either cause the yield to either increase or decrease, fisheries need to consider the whole ecosystem, as suggested by Pikitch *et al.* (2004).

4.5 Management implications

My results can have implications for stocking and fishing in warmer environments. In single-species models which display Allee effects the bistable equilibrium acts as a threshold, which separates population growth from population decrease by the population either being above or below that bistable point. This is not the case in stage-structured models in which emergent Allee effects occur, as the biomass density can decrease even above this threshold. The initial biomass density, therefore, needs to be substantially higher than the level at the bistable equilibrium, for the predators not to go extinct (de Roos & Persson 2013). A common management practice of fisheries is to stock fish into waters to increase population sizes (Arlinghaus *et al.* 2016). If the purpose is to stock predators into a stable consumer-resource community to reverse the alternative stable state, there is a challenge in knowing where the threshold for successful stocking is. This makes it a costly venture to increase the chance of success, as major stocking would be needed. In colder waters, it might therefore

be recommended to lower the fishing pressure below the bistable area. In warmer waters, however, that is not an option as the modelled predator-consumer-resource community is always bistable. However, stocking is a management practice that does not always succeed. Stocking can, for example, be fraught with high mortality rates due to predation (Ivasauskas & Bettoli 2011). Stocked fish can also have physiological, behavioural and genetic problems due to being raised in captivity (Pedersen *et al.* 2008, Urke *et al.* 2013, Attard *et al.* 2022). Stocking might therefore fail, even if a sufficient biomass of fish is introduced.

My results also suggest to be restrictive of what fishing pressure is allowed at higher temperatures, as there is a risk of extinction of the predators due to stochastic events even at low fishing pressures. The predators can go extinct due to stochastic events if the predator biomass density momentarily passes below the threshold for persistence, even when the predator is not fished on. Meanwhile, at low temperatures, the resource-consumer-predator community is stable at low fishing pressures. Therefore, at lower temperatures, the possibility of "staying safe" to avoid predator extinction exists. The MSY of predators also occurs in this bistable region, both in colder and warmer environments. Even though the yield is maximised, fishing at fishing pressure corresponding to the MSY is risky due to the bistable nature of the food web. My model shows that lowering the fishing pressure is likely better (especially in a warmer environment), as the costs of reversing the alternative stable state exceed the benefits of achieving the maximal yield. Previous studies have predicted a decrease in either yield (Lindmark *et al.* 2022), a change in the production rate of top predators (Blanchard *et al.* 2012), or a change in the potential catch (Cheung *et al.* 2010) due to climate warming. My results show the problem of managing fisheries in a warmer climate since a resource-consumer-predator community is always bistable. Not only might the yield, and production rate of top predators or potential catch be lower (Cheung *et al.* 2010, Blanchard *et al.* 2012, Lindmark *et al.* 2022), but I show that the population of predators risks sudden extinction due to factors which might be hard to predict.

Fishing on the adult consumer in the range when the community is cyclic when in a colder environment, leads to an increased risk of extinction when the biomasses are at their lowest due to stochasticity. A previous study that studied the impacts of fishing on both an age-structured model and a stage-structured model, which was similar to the model I used but without a predator stage, found that irrespectively of the model used that equal harvesting rates on the juvenile consumer and adult consumer were a preferred strategy both for conservation and yield (Lundström *et al.* 2019). It might therefore be recommended to also fish on the juvenile consumers. Though since Lundström *et al.* (2019) neither had a predator stage present nor tested for the effects of increased temperature, more research would be needed if equal harvesting on the juvenile consumers and adult consumers was to be recommended.

My results suggest fishing on both the adult consumer and the predators, to be able to increase the fishing pressure on the predator, especially in a warmer environment since the predators go extinct at a lower fishing pressure. Another positive effect of fishing on adult consumers and predators when in a warmer environment is that it is possible to avoid a bistable community. In a warmer environment, it might therefore be a recommended strategy since it not only means that the community is not in a bistable state, like previously mentioned, but also since the yield could increase.

Recommendations on management strategies however must be made in the light that the model I have used is very general. This is because the model is parametrised on zooplankton whose average body sizes are significantly smaller than fish. The model is also not parametrised on any specific sets of species and is instead parametrised on averages. This makes the model applicable to no specific food web, but also applicable to a wide set of food webs due to its generality. However, when this model was tested against a similar less general model parametrised on a set of fish species and daphnia, the models behaved in the same way (Lindmark *et al.* 2019). Recommendations might therefore be reliable if the same result is expected in a model parametrised on fish. It is still however a simple model compared to the complexity of food webs in nature.

4.6 Future research

Ontogenetic diet shifts are prevalent in both marine, freshwater, and terrestrial ecosystems (Thunell *et al.* 2021). Therefore, it would be interesting to see what effects fishing has in a warmer environment on other types of stage-structured biomass models with different interactions in the food web and different food web structure. In a model which exhibits ontogenetic diet shifts (juvenile predators eat resource, adult predators eat consumer) the effects of warming results in a collapse of the predator population but due to another mechanism (Thunell *et al.* 2021). It would be interesting to see what effects fishing has on both predators and consumers in this model in combination with increased temperature.

The Boltzmann-Arrhenius function was used for temperature dependence of vital rates, which is suitable for maintenance and mortality rates. However, the relationship between ingestion rate and temperature is humped shaped, which means that it has an optimum (Englund *et al.* 2011). To use the Boltzmann-Arrhenius function for temperature dependence of ingestion is therefore only suitable at temperatures below the optimum (Englund *et al.* 2011, Uszko *et al.* 2017). It would therefore be interesting to investigate the effects on how temperature dependence was implemented. It is however complicated to add a hump-shaped relationship of ingestion rate to temperature since assumptions must be made of the location along the temperature scale where the optima reside, which adds complexity (Dee *et al.* 2020). If, however a hump-shaped response to temperature for the predator's ingestion rate is implemented, depending on what temperature is set to the optimal temperature it will have different effects on the predator and community. As the temperature increases towards the optimum it will result in a higher ingestion rate of juvenile consumers, this would mean that the strength of the biomass overcompensation increases. On the other hand, when the temperature has already passed the optimum the strength of biomass overcompensation would weaken, and predators would eventually be unable to control the consumer population, which results in predator extinction. However, the fact that other vital rates are also being affected by temperature at the same time has to be taken into consideration, which complicates the predictions of what a hump-shaped response to increased temperature of the predator's ingestion rate would result in.

4.7 Conclusion

I found that even a simple stage-structured model can have unexpected and unintuitive community-level responses due to fishing in a warmer environment, depending on what trophic level is fished on. This means that to know what effects fishing will have in a warmer environment it is both important to know what trophic level it inhabits and how it interacts within the food web. I also found that fishing at the fishing pressure corresponding to the maximum sustainable yield of predators is not a sustainable management strategy, especially in warmer environments, due to several risks of extinction. In general, my results suggest being restrictive of fishing on predators in a warmer environment due to extinction risks, and fishing at both the adult consumer and predator to decrease the risks of extinction and to increase the yield in a warmer environment. I would say that independent of the structure of the food web, it is important to be aware of the complexity of natural systems when managing fish populations for exploitation - especially as the climate warms up.

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Popular Science Summary

One of the biggest concerns currently facing both humans and nature, particularly fish, is climate change. However, humans are also a threat to marine life through fishing, which is causing damage that marine life may never be able to recover from. I have looked into what happens when fishing in warmer waters as a result of climate change. I demonstrate that fishing in a warmer climate can have unexpected and counter-intuitive impacts depending on whether adult consumer fish or predators are targeted, and that targeting both adult consumer fish and predators results in even more surprising outcomes.

The extinction of the predators did not occur gradually; rather, it happened suddenly, seemingly out of nowhere, and the predators went extinct, even though their population size appeared to be stable. I discovered that predator fish may withstand less fishing in a warmer environment before they go extinct. Following the extinction of the predators, the prey population exploded as a result of there being no predators. Additionally, I discovered that maximising the yield of predators in a warmer environment is more unsustainable. On the other hand, when adult consumers are targeted for fishing, I discovered that a warmer environment stabilizes the community and boosts the yield. This indicates that there are entirely distinct effects on both the stability and yield depending on whether adult consumers or predators are fished in a warmer environment.

To prevent the extinction of predators, I thus advise against overfishing them in warmer climates. In a warmer habitat, it might also be advised to fish for both adult consumers and predators since the risk of predator extinction may be reduced even further while maintaining a good yield. It might even be a good strategy to switch to fishing on adult consumers in a warmer environment, since both stability and yield increase.

I investigated this using a model that included resources, juvenile consumers, adult consumers, and predators. At three different temperatures, the effects of fishing on adult consumers and/or predators were explored.

My findings add new understanding on the effects of fishing in warmer environments, and perhaps even a glimpse into the future.

Acknoledgements

Appendix

Tables

Table A1. Parameter values at 19°C (de Roos & Persson 2013)

Parameter	Value	Unit	Description
k	$8.61733326e^{-5}$	eVK^{-1}	Boltzmann's constant
Resource			
ρ	0.1	day^{-1}	Resource turnover rate
R_{max}	18	$g\,m^{-3}$	Resource maximum biomass density
Consumer			
W_A	0.0001	g	Average adult consumer body size
M_C	$0.1W_A^{-0.25}$	day^{-1}	Mass-specific maximum ingestion rate
H_C	3	$g\,m^{-3}$	Ingestion half-saturation resource density
q	0.5	$-$	Adult-juvenile consumer ingestion ratio
T_C	$0.01W_A^{-0.25}$	day^{-1}	Mass-sepcific maintenance rate
σ_C	0.5	$-$	Conversion efficiency
z	0.01	$-$	New born-adult consumer size ratio
μ_J	$0.0015W_A^{-0.25}$	day^{-1}	Juvenile background mortality
μ_A	$0.0015W_A^{-0.25}$	day^{-1}	Adult background mortality
f_A	$0.0 - 1.0$	$-$	Adult fishing pressure
Predator			
W_P	0.01	g	Average predator body size
M_P	$0.1W_A^{-0.25}$	day^{-1}	Mass-specific maximum ingestion rate
H_P	3	$g\,m^{-3}$	Ingestion half-saturation prey density
T_P	$0.01W_A^{-0.25}$	day^{-1}	Mass-sepcific maintenance rate
σ_P	0.5	$-$	Conversion efficiency
μ_P	$0.0015W_P^{-0.25}$	day^{-1}	Predator background mortality
f_P	$0.0 - 1.0$	$-$	Predator fishing pressure

Table A2. Functions of the stage-structured biomass model, based on the stage-structured predator-prey biomass model (de Roos & Persson 2013), with temperature dependence (Lindmark et al. 2019)

Function	Expression	Description
$G(R,T)$	$\rho r_\rho (R_{max} r_{R_{max}} - R)$	Intrinsic resource turnover
$w_J(R,T)$	$M_C r_M \frac{R}{(H_C+R)}$	Resource intake by juveniles
$w_A(R,T)$	$q M_C r_M \frac{R}{(H_C+R)}$	Resource intake by adults
$v_J(R,T)$	$\sigma_C w_J R - T_C r_T$	Net energy production of juveniles
$v_A(R,T)$	$\sigma_C w_A R - T_C r_T$	Net energy production of adults
$d_J(P,T)$	$\mu_J r_\mu + M_P r_M \frac{P}{H_P+J}$	Mortality rates of juveniles
$d_A(T)$	$\mu_A r_\mu$	Mortality rates of adults
$\gamma(v_J^+, d_J, T)$	$(v_J^+(R,T) - d_J(P,T))/(1 - z^{(1-\frac{d_J(P,T)}{v_J^+(R,T)})})$	Maturation rate of juveniles
$v_P(J,T)$	$\sigma_P M_P r_\mu \frac{J}{H_P+J} - T_P r_T$	Net energy production of predators

Table A3. Values of temperature dependence (Savage et al. 2004, Ohlberger et al. 2011, Ohlberger et al. 2012, Lindmark et al. 2018)

Parameter	Value	Unit	Description
E_ρ	0.43	eV	Activation energy of resource turnover rate
$E_{R_{max}}$	-0.43	eV	Activation energy of maximum resource density
$E_{T_{C,P}}$	0.594	eV	Activation energy of maintenance
$E_{M_{C,P}}$	0.594	eV	Activation energy of maximum intake rate
$E_{\mu_{C,P}}$	0.45	eV	Activation energy of mortality

Figures
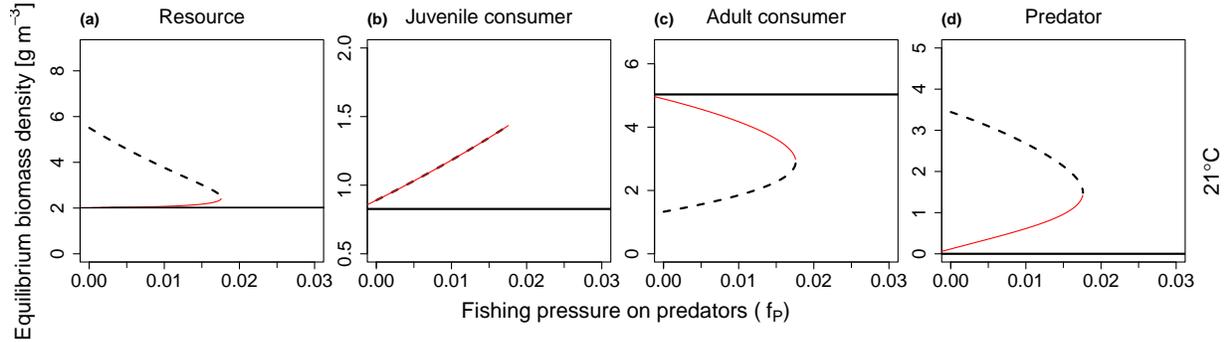
Figure A1. Equilibrium biomass densities of the resource (a), juvenile consumer (b), adult consumer (c) and predator (d) as a function of fishing pressure on the predator (f_P) at the intermediate temperature of $21°C$. Black lines (full and dashed) are stable equilibria while red lines annotate unstable equilibria that connect the two stable regions between the unstable region. Alternative stable states occur between fishing pressures on the predator (f_P) of ~ of 0 and 0.015 at the intermediate temperature of $21°C$ (a-d). As the fishing pressure on the predator (f_P) increases it causes the resource to decrease (a), juvenile consumer to at first increase but at the alternative stable state to crash to a lower level (although higher than at zero f_P) (b), the adult consumer increases (c) and the predator decreases to eventual extinction (d). At the alternative stable state all biomass densities stabilise and stop changing with further increases in f_P, and all other than the predator are non-zero (a, b and c). Predators can therefore handle less fishing on themselves at higher temperatures before the predator population goes extinct. All parameters have default values (Appendix, Table A1 & A3). The figure for the temperatures of $18°C$ and $24°C$ can be seen in figure 1.
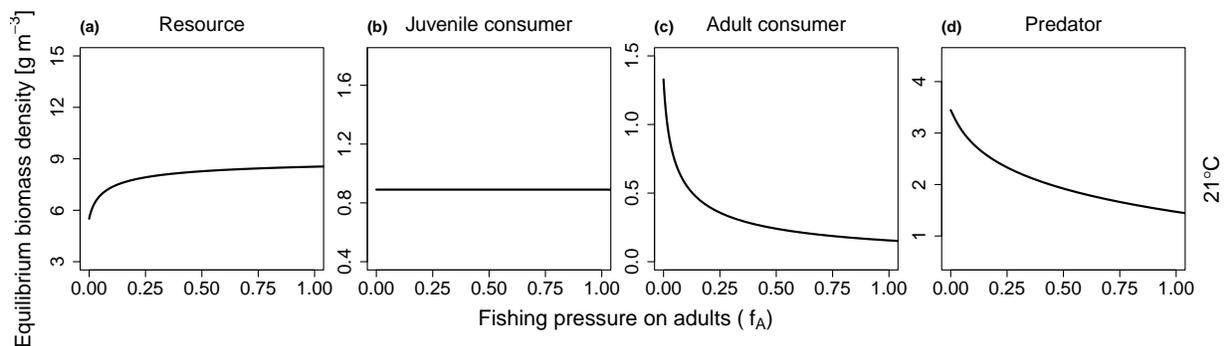
Figure A2. Equilibrium biomass densities of the resource (a), juvenile consumer (b), adult consumer (c) and predator (d) as a function of fishing pressure on the adult consumer (f_A) at the intermediate temperature of $21°C$ (a-d). At $21°C$ increased fishing pressure on the adult consumer (f_A) does not cause limit cycles to emerge (a-d). Increased fishing pressure on the adult consumer (f_A) causes the equilibrium biomass densities of resources to increase (a), juvenile consumer equilibrium biomass density is constant (b), adult consumer equilibrium biomass density decreases (c) and predator biomass density decreases (d), though initially at $21°C$ the equilibrium biomass density increases at low f_A values, but as f_A continues to increase the equilibrium biomass density of predators start decreasing (d). All parameters have default values (Appendix, Table A1 & A3). The figure for the

21°C
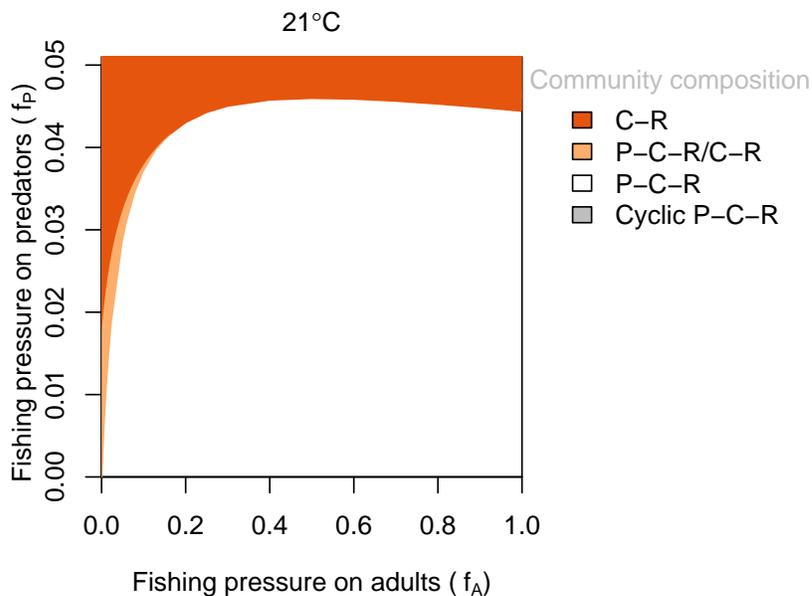
Figure A3. Community composition of the food web at the intermediate temperature of $21°C$ with a fishing pressure on both adult consumers (f_A) and predators (f_P). Gray notates stable limit cycles, orange is the area where the predator goes extinct and light orange is the bistable region where predators either go extinct or survive depending on the initial conditions. The point at which the predators goes extinct (orange area) due to the fishing pressure on the predators (f_P) moves up when the fishing pressure on adult consumers (f_A) increases simultaneously. At a certain point however the predators stop to gain an advantage with increased fishing on the adult consumers (f_A) and reaches a maximum, as the fishing pressure on the adult consumer (f_A) continues to increase the predator will go extinct unless f_P decreases. At zero f_A the predators are always vulnerable and at risk of extinction. All parameters have default values (Appendix, Table A1 & A3). The figure for the temperatures of $18°C$ and $24°C$ can be seen in figure 5.
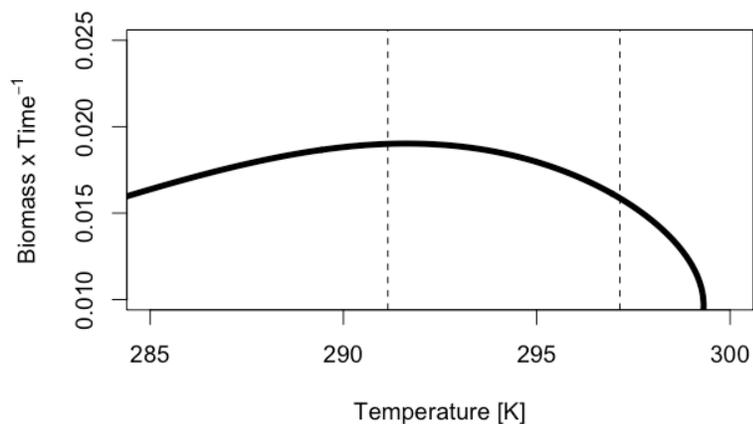
Figure A4. Population level net energy production rate of the predators $(v_P(J, A))$ as a function of temperature. The two dashed vertical lines are the temperatures of $18°C$ $(292.15K)$ and $24°C$ $(297.15K)$. The predators net energy production rate has a maximum at $19°C$ $(292.15K)$. As temperature either increases or decreases from $19°C$, the rate decreases. The rate at which the net energy production rate decreases is higher when the temperature increases than decreases. An equal shift in temperature $(\pm 3°C$ for example) into either a warmer or a colder environment therefore has different effects, as the net energy production will be higher at the lower temperature. All parameters have default values (Appendix, Table A1 & A3).
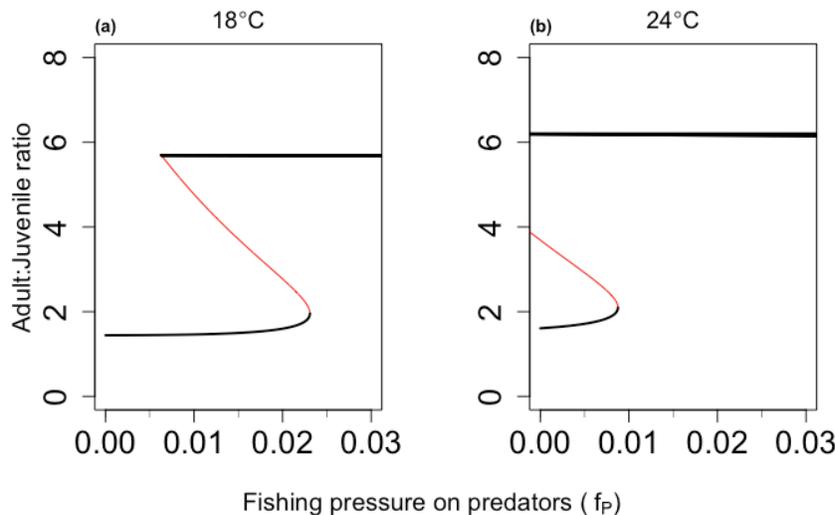
Figure A5. The ratio of adult consumer to juvenile consumer equilibrium biomass density as a function of the fishing pressure on the predator (f_P) at $18°C$ and $24°C$. At both temperatures there is a shift between two alternative stable states (black line), which is connected via an unstable equilibria (red line). At $18°C$ the ratio of adult consumers to juvenile consumers switches from 2 times to 6 times the adult consumer to juvenile consumer equilibrium biomass density between when the predator is not fished on $(f_P = 0)$ to when the predator is extinct (a). At $24°C$ the same pattern emerges, the ratio is 6 times the adult consumer to juvenile consumer equilibrium biomass density when the predator has gone extinct (b). All parameters have default values (Appendix, Table A1 & A3).
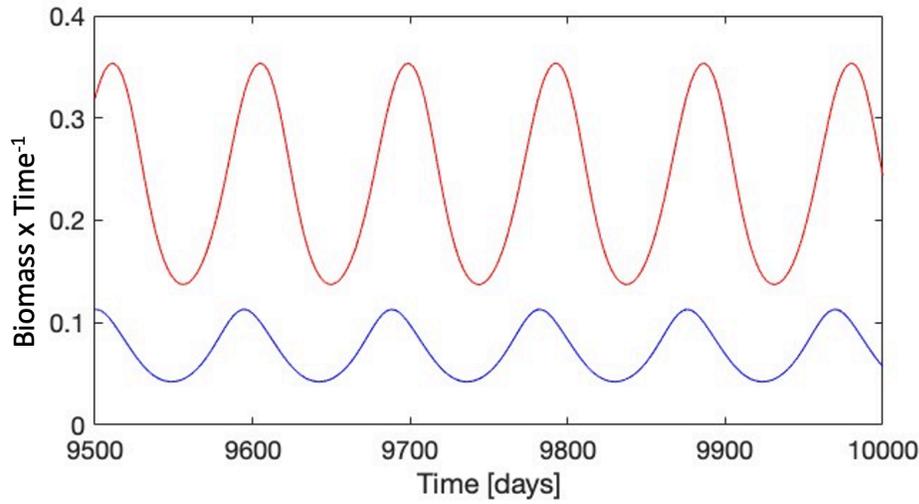
Figure A6. Population level predator intake rate $\frac{d_J(P)}{P}$ (blue) and juvenile consumer net energy production rate $v_J(R)$ (red) over time at equilibrium. The two rates oscillate with each other out of phase by ~ 1/4 a cycle. When the juvenile consumer net energy production rate increases a lagged response emerges where the predator intake rate also increases, the juvenile consumers net energy production rate then reaches a maximum, just before the predator intake rate does as well. The juvenile consumer net energy production rate and predator intake rate (albeit at a later time step) decreases from the maximum. $f_A = 0.1$ and $T = 18°C$, all other parameters have default values (Appendix, Table A1 & A3).
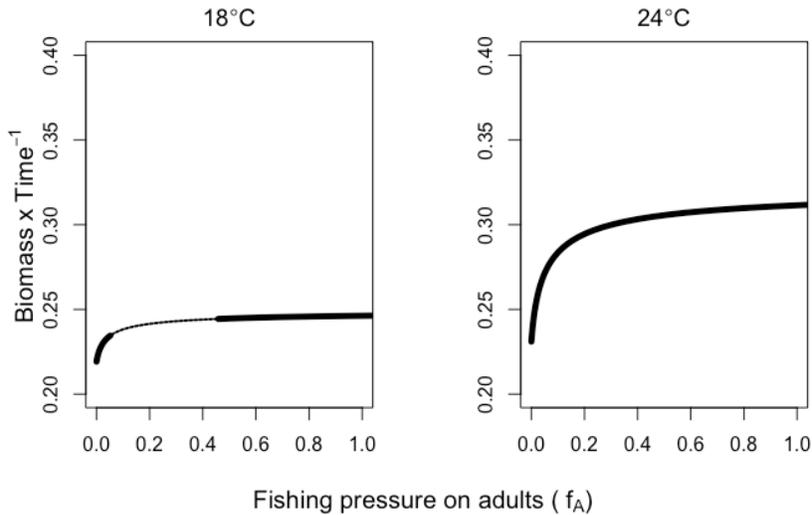
Figure A7. Population level net energy production rate of the juvenile consumers $(v_J(R))$ as a function of the fishing pressure on the adult consumer (f_A) at $18°C$ (a) and $24°C$ (b). The juvenile consumers net energy production rate increases with increased fishing pressure on the adult consumer (f_A) but reaches a plateau when $f_A \approx 0.4$ at $18°C$ and at $24°C$ the rate increases slower but does not reach a plateau. All parameters have default values (Appendix, Table A1 & A3).
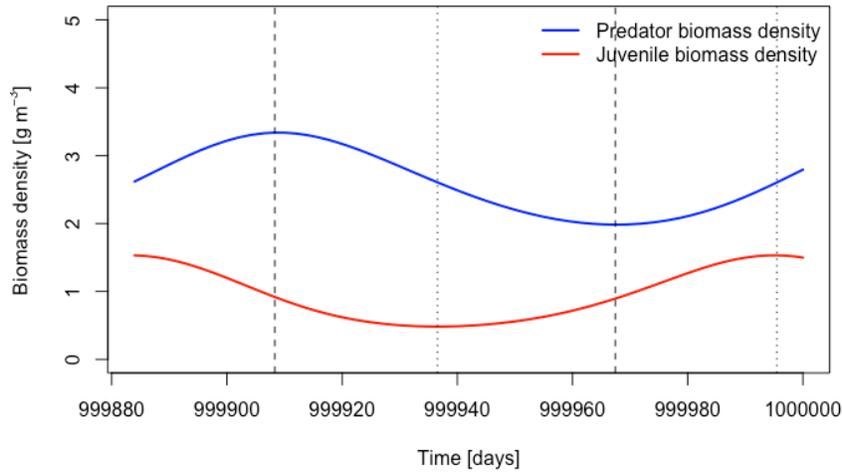
Figure A8. Biomass densities of juvenile consumers (red) and predators (blue) at equilibrium, the two biomass densities oscillate out of phase by ~ 1/4 of a turn with each other. The two vertical dotted lines vertical indicate the maximum and minimum biomass densities of the juvenile consumer and the two vertical dashed lines indicate the maximum and minimum biomass densities of the predator. $f_A = 0.1$ and $T = 18°C$, all other parameters have default values (Appendix, Table A1 & A3).
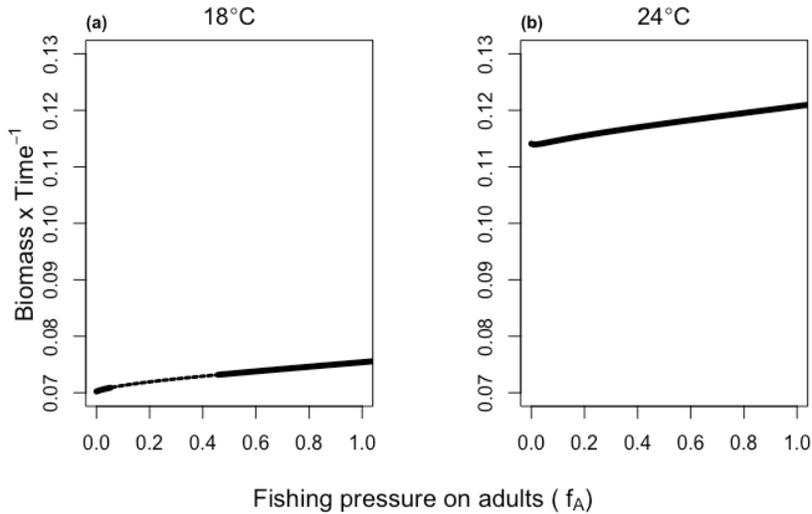
Figure A9. Population level intake rate of the predator as a function of the fishing pressure on the adult consumer (f_A) at $18°C$ and $24°C$. At both temperatures a almost linear increase in the predators intake rate as the fishing pressure on the adult consumer increases. At $18°C$ the intake rate increases exponentially in the beginning (a). At $24°C$ the intake rate decreases at first at very small fishing pressures on the adult consumer (f_A) and then starts to increase (b). The intake rate is higher at $24°C$ but increases at the same rate with fishing pressure (f_A) as at $18°C$ (a and b). All parameters have default values (Appendix, Table A1 & A3).

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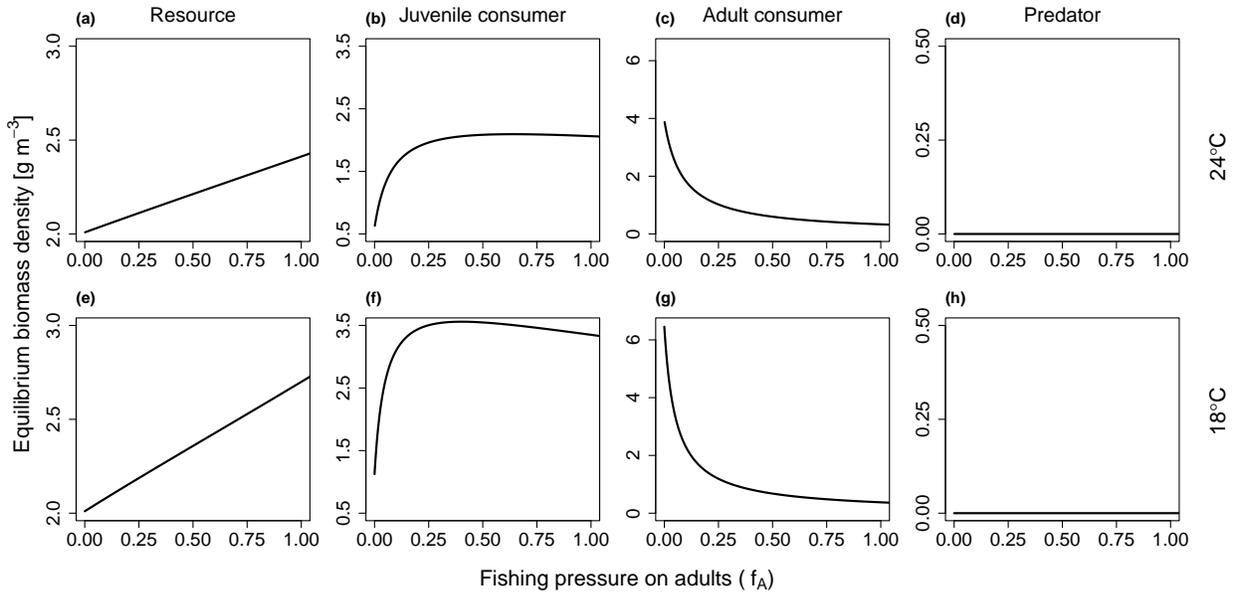
Figure A10. Equilibrium biomass of resources (a and e), juvenile consumers (b and f), adult consumers (c and g) and predators (d and h) as a function of fishing pressure on the adult consumers (f_A) at the two temperatures of $18°C$ (e-h) and $24°C$ (a-b). Compared to when predators are present (figure 3), increases in fishing pressure on the adult consumer (f_A) does not cause limit cycles to appear or disappear at either of the two temperatures, which suggests that the limit cycles that occur when predators are present are due to dynamics between the predator and its prey, the juvenile consumer. All parameters have default values (Appendix, Table A1 & A3).
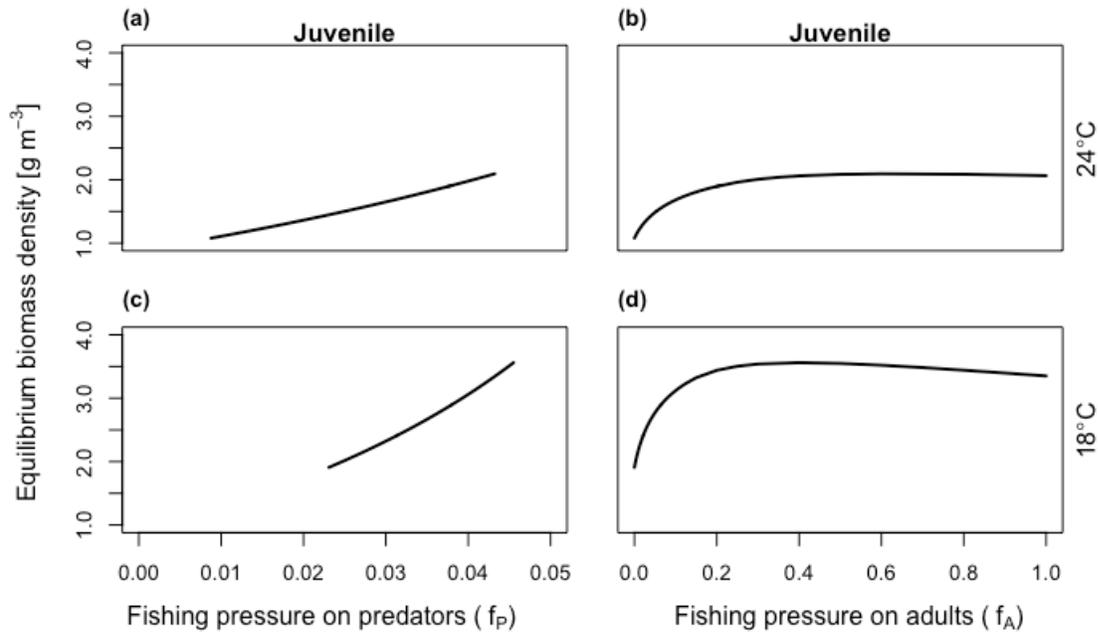
Figure A11. Juvenile consumer equilibrium biomass density as a function of simultaneous fishing

on the adult consumer (f_A) (b and d) and predator (f_P) (a and c) at 18°C (c and d) and 24°C (a and b). The juvenile consumers equilibrium biomass density increases with both f_A and f_P (a-d), however an optimum fishing pressure of both f_A and f_P exists where the juvenile consumers equilibrium biomass density has a maximum at both 18°C (c and d) and 24°C (a and b). All parameters have default values (Appendix, Table A1 & A3).
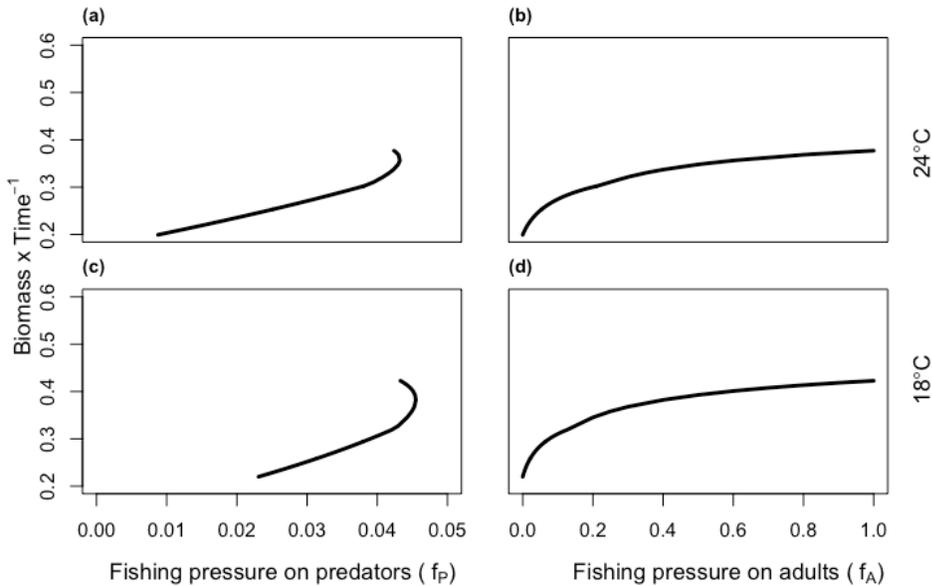
Figure A12. The population level net energy production rate of juvenile consumers ($v_J(R)$) as a function of fishing pressure on both the adult consumer (f_A) (b and d) and predator (f_P) (a and c) at 18°C (c and d) and 24°C (a and b). The juvenile consumers net energy production rate increases with increased fishing pressure on both predators (f_P) (a and c) and adult consumers (f_A) (b and d) at both 18°C (c and d) and 24°C (a and b). The net energy production rate is higher at 18°C (c and d). The increase in net energy production rate results in higher juvenile consumer biomass densities, which is why the predators can handle a higher fishing pressure on themselves (f_P) with simultaneous fishing on the adult consumers f_A. All parameters have default values (Appendix, Table A1 & A3).
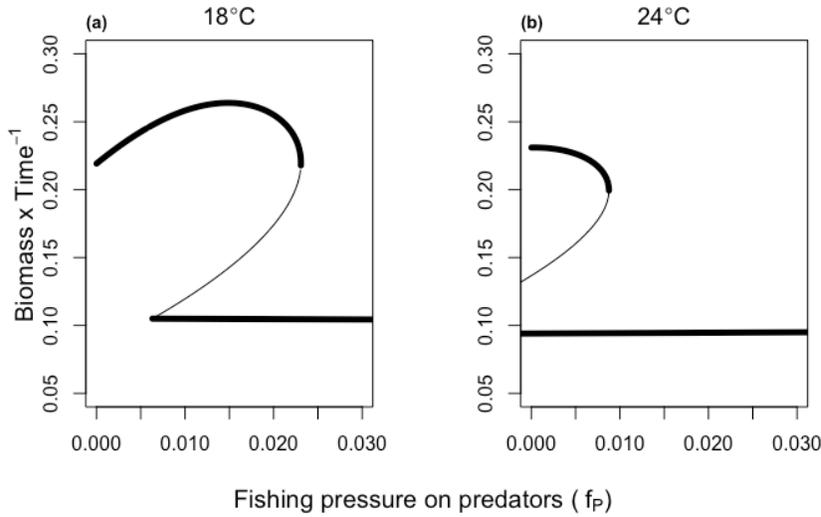
Figure A13. The population level net energy production of juvenile consumers $(v_J(R))$ as a function of fishing pressure on the predator (f_P) at $18°C$ (a) and $24°C$ (b) (Thick black lines indicate stable equilibria and thin black lines indicate unstable equilibria). The juvenile consumers net energy production rate decreases as the fishing pressure on the predator (f_P) increases and an eventual collapse when the predator goes extinct, the net energy production rate when predators are present and extinct are roughly the same at both $18°C$ (a) and $24°C$ (b). All parameters have default values (Appendix, Table A1 & A3).
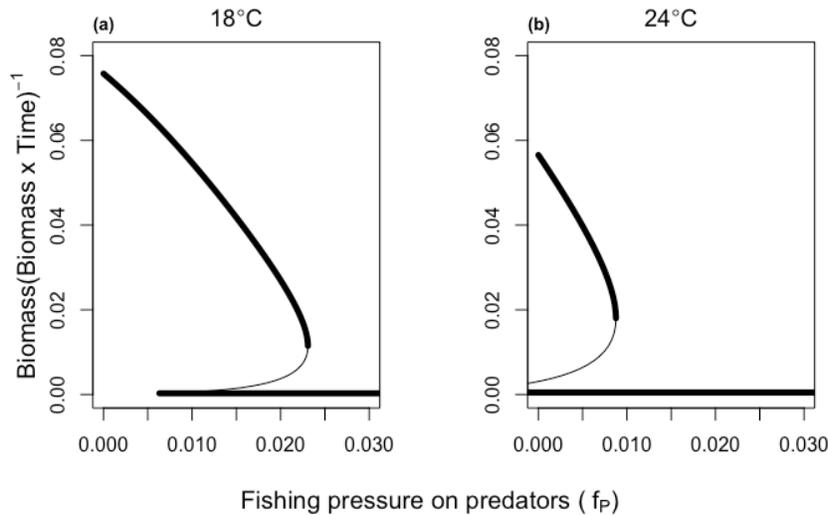
Figure A14. Mass-specific net energy production rate of the adult consumers $(v_A(R))$ as a function of the fishing pressure on the predator (f_P) at $18°C$ (a) and $24°C$ (b) (Thick black lines indicate stable equilibria and thin black lines indicate unstable equilibria). The mass-specific net energy production rate of the adult consumers decreases at both $18°C$ (a) and $24°C$ (b) and at the alternative stable state when the predators are extinct, the rates at $18°C$ (a) and $24°C$ (b) crash to levels close to zero. The mass-specific net energy production rate of the adult consumers is higher at $18°C$ (a) than at $24°C$.

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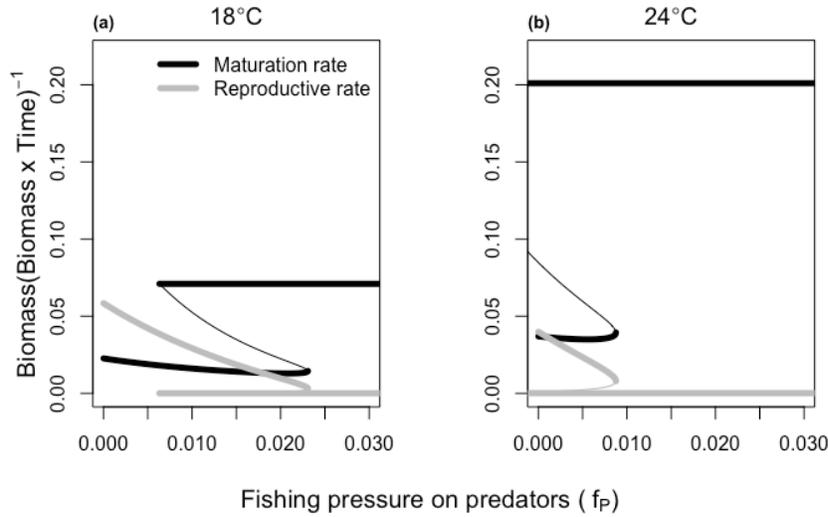
Figure A15. Mass-specific maturation and reproductive rate changes as the fishing pressure on the predator (f_P) increases at 18°C (a) and 24°C (b) (Thick lines indicate stable equilibria and thin lines indicate unstable equilibria). As the fishing pressure on the predator increases both the mass-specific maturation rate and reproduction rate decreases. When the predator goes extinct and there is a switch in alternative stable states, there is also a switch where the mass-specific maturation rate becomes larger than the mass-specific reproduction rate. In a warmer environment the difference between the mass-specific maturation rate and reproduction rate is larger, when the predators are extinct (b). All parameters have default values (Appendix, Table A1 & A3).

Model code for MATCONT

Name: TF_Main_generic

Coordinates: Rs, Cj, Ca, P

Parameters: E_rdel,T,T0,k,E_K,E_m,E_i,E_u,del,K,H_c,q,sig_c,sig_p,phi,H_p,z,f_Ca,f_P

r_del=exp((E_rdel*(T-T0))/(k*T*T0))
r_K=exp((E_K*(T-T0))/(k*T*T0))
r_m=exp((E_m*(T-T0))/(k*T*T0))
r_i=exp((E_i*(T-T0))/(k*T*T0))
r_u=exp((E_u*(T-T0))/(k*T*T0))

G=del*r_del*(K*r_K-Rs)

M_c=0.1*0.0001.^-0.25

w_Cj=M_c*r_i*Rs/(H_c+Rs)
w_Ca=q*M_c*r_i*Rs/(H_c+Rs)

M_p=0.1*0.01.^-0.25
T_p=0.01*0.01.^-0.25
T_c=0.01*0.0001.^-0.25

Nu_Cj=sig_c*w_Cj-T_c*r_m
Nu_Ca=sig_c*w_Ca-T_c*r_m
Nu_P=(sig_p*M_p*((phi*Cj+(1-phi)*Ca)/(H_p+phi*Cj+(1-phi)*Ca)))-T_p*r_m

u_j=0.0015*0.0001.^-0.25
u_a=0.0015*0.0001.^-0.25
u_P=0.0015*0.01.^-0.25

u_Cj=u_j*r_u+((M_p*r_i*phi*P)/(H_p+phi*Cj+(1-phi)*Ca))
u_Ca=u_a*r_u+((M_p*r_i*(1-phi)*P)/(H_p+phi*Cj+(1-phi)*Ca))

if(Nu_Ca>0), Nu_p_Ca=Nu_Ca; else ;Nu_p_Ca=0; end
if(Nu_Cj>0), Nu_p_Cj=Nu_Cj; else ;Nu_p_Cj=0; end

mat_rate=(Nu_p_Cj-u_Cj)/(1-z^(1-(u_Cj/Nu_p_Cj)))

Rs'=G-w_Cj*Cj-w_Ca*Ca
Cj'=Nu_p_Ca*Ca-mat_rate*Cj+Nu_Cj*Cj-u_Cj*Cj
Ca'=mat_rate*Cj+(Nu_Ca-Nu_p_Ca)*Ca-u_Ca*Ca-f_Ca*Ca
P'=(Nu_P-u_P*r_u)*P-f_P*P

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