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Spare the young fish? Maybe not. An age-structured predator-prey analysis*

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Abstract

This study presents a bioeconomic, age-structured, multi-fleet, predator-prey model. By solving the model for a range of scenarios and parameter values, we show that preferred selectivity and optimal harvesting change with the levels of predation and predation-weight conversion rates. While the model reproduces insight from age-structured single-species and biomass predator-prey models, it also shows that positive scaling of age-specific predation coefficients can shift the preferred selection pattern towards smaller predator individuals and increase the overall fishing pressure for the predator. This involves sacrificing utilization of predator growth potential to achieve better utilization of prey growth potential, both at an individual level and at the stock level. In addition, it involves sacrificing predator harvest efficiency to achieve better prey harvest efficiency. The model also shows that positive scaling of predation-weight conversion rates can counteract the abovementioned. To the best of our knowledge, this represents novel findings. The findings are important because they bring awareness to why managers should think twice before changing gear restrictions in direction of targeting bigger fish on basis of single-species analyses, in which selectivity studies are common. Moreover, they display the usefulness and value of age-structured multi-species modeling, which has received limited attention in the bioeconomic literature so far, as opposed to age-structured single-species modeling and biomass multi-species modeling.

JEL classification: Q2, Q22, Q28

Keywords: Age-structure, Predator-prey, Optimal harvesting, Selectivity

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Introduction

The importance of taking a holistic ecosystem view on bioeconomic modeling and marine management has been acknowledged for several decades (Larkin, 1996). The usefulness of single-species models should not be underestimated, but under many circumstances results become different, and offer more insight, when more than one species is included, which in turn can improve system understanding and management (Brekke & Moxnes, 2003; Ekerhovd & Steinshamn, 2017).

A first step toward ecosystem modeling is to replace traditional single-species models with models including two, or more, species. The most common types of multi-species models are arguably two-species predator-prey models based on extensions and variations of the Lotka-Volterra equations. Numerous articles investigating such models have appeared over the last five to six decades, focusing on mathematical, biological, and economic aspects.

Within mathematics and theoretical biology, there is a large literature on mathematical aspects of predator-prey population models, and new studies keep coming. Kar & Chakraborty (2010), Li et al. (2017), Liu et al. (2018), and Wikan & Kristensen (2019) represent some recent ones.

In the bioeconomic literature, variations of the predator-prey model outlined in the first (1976) edition of Colin Clark’s iconic book “Mathematical Bioeconomics” (2010) are quite common. Among the bioeconomic population model papers, we will mention Hannesson (1983) and Flåten & Stollery (1996). Hannesson was one of the first to point out the importance of the relative price-relationship between the species, and he also pointed out that some of the conventional wisdom based on single-species models, does not apply to models with more than one species. Notably, that subsidizing fishing (of the predator) may sometimes be optimal; an increased discount rate may imply an increase in the optimal standing stock; higher price and/or lower cost of effort may increase the standing stock. Flåten & Stollery (1996) investigate economic losses related to reduced harvesting of the prey due to increased predator stock.

Age-structured predator-prey models are also quite common in the mathematical and biological literature. Smith and Mead (1974), Gurtin & Levine (1979), Cushing & Saleem (1982), Li (1990), and Wikan (2001, 2017) study phenomena like the existence and stability of equilibria, bifurcation, and chaos. In the biological literature age-structured multi-species simulation models have been used to analyze the consequences of various predetermined policies (Goto et al., 2021; Tjelmeland & Bogstad, 1998).

In the bioeconomic literature, the number of age-structured studies with more than one species are limited. Fister & Lenhart (2006) were among the first to propose a bioeconomic age-structured multi-species model. This is a fairly theoretical study where the emphasis is on the existence and uniqueness of optimal control combinations. Nieminen et al. (2015) apply a bioeconomic age-structured multi-species model to assess the cod, herring, and sprat fisheries in the Baltic Sea under different environmental conditions. Bertram & Quaas (2017) apply an age-structured multi-species model to Baltic Sea fisheries where they include the value of biodiversity in their objective function. Voss et al. (2022) also present an age-structured multi-species model for cod, herring, and sprat in the Baltic. They focus on the differences between maximizing sustainable and economic yield in an age-structured multi-species setting. Skonhøft & Friberg (2021) use an age-structured model to study predation on terrestrial stocks (both wild and livestock) by carnivorous predators like wolf.

Several of the abovementioned age-structured predator-prey studies only consider age-structure for one of the fish-stocks, while keeping the other fish-stock biomass-structured – Voss et al. (2022) is a notable exception. In this paper we use a bioeconomic predator-prey model, where both the predator and prey are represented by full-blown age-structured models. This is necessary as the purpose of the study is to analyze how optimal selectivity and harvesting change in response to changes in the absolute and relative strength of age-specific biological interactions, as well as changes in the relative prices.

There has been a significant focus on optimal selectivity in bioeconomic age-structured single-species studies (e.g., Bang & Steinshamn, 2022; Diekert et al., 2010; Helgesen et al., 2018; Reed, 1980; Skonhøft et al., 2012). However, the role of selectivity in bioeconomic age-structured multi-species settings is an under-researched topic. To the best of our knowledge, Voss et al. (2022) is the only bioeconomic age-structured multi-species study that touches upon the topic, and there are

still many knowledge gaps to cover. Considering the importance of gear selectivity and regulations in modern fisheries, which is a key motivator for the single-species studies on the topic, this is surprising and highlights the need for more studies on the topic.

We look at two biological interactions. Firstly, we focus on the effects of two different versions of the predation profile, namely one where predation is proportional to the size/age of the predator, and one where the predation pressure increases more than proportionally with size/age. The rationale behind the latter is that larger fish swim longer and can cover a larger area in their search for food than smaller fish. Moreover, large predator fish tend to base more of their food consumption on prey fish than small predator fish—at least that is the case for cod and capelin (Holt et al., 2019).

Secondly, we investigate two age profiles for the conversion factor between prey and predator. One is uniform conversion after a certain predator age, the other is decreasing conversion after a certain predator age where it is assumed that the metabolism decreases with age down to a certain level. Also, for older fish, more of the energy go to spawning products and not to growth.

It is quite intuitive and demonstrated formally by Hannesson (1983) and others, that the relative price between predator and prey may have important implications for the optimal harvest pattern and stock levels. Therefore, as a sensitivity analysis, we also check how the results change when we move from a high-valued predator and a low-valued prey, such as cod-capelin, to the opposite.

Methods

We develop a deterministic, age-structured, multi-fleet, predator-prey optimization model. The model considers a sole owner who manages two fleets and two interacting commercial fish stocks—one fleet targets a predator stock and another targets a prey stock. The model considers two types of species interactions—predator-induced predation mortality for the prey, and predation-weight conversion for the predator.

Regarding the use of terminology, we distinguish between two types of natural mortality, natural mortality induced by the predator in the model, and other natural mortality. In the following, we simply refer to the two types of natural mortality as predation mortality and natural mortality, respectively, in which natural mortality should be understood as natural mortality excluding predation mortality.

Figure 1 provides a high-level overview of the model. The biological sub-model describes the processes of natural mortality, predation mortality, growth, maturation, and recruitment, while the economic sub-model describes fishing effort, and costs, revenue, and profits associated with harvest. The harvest functions bridge the biological and economic dimensions.

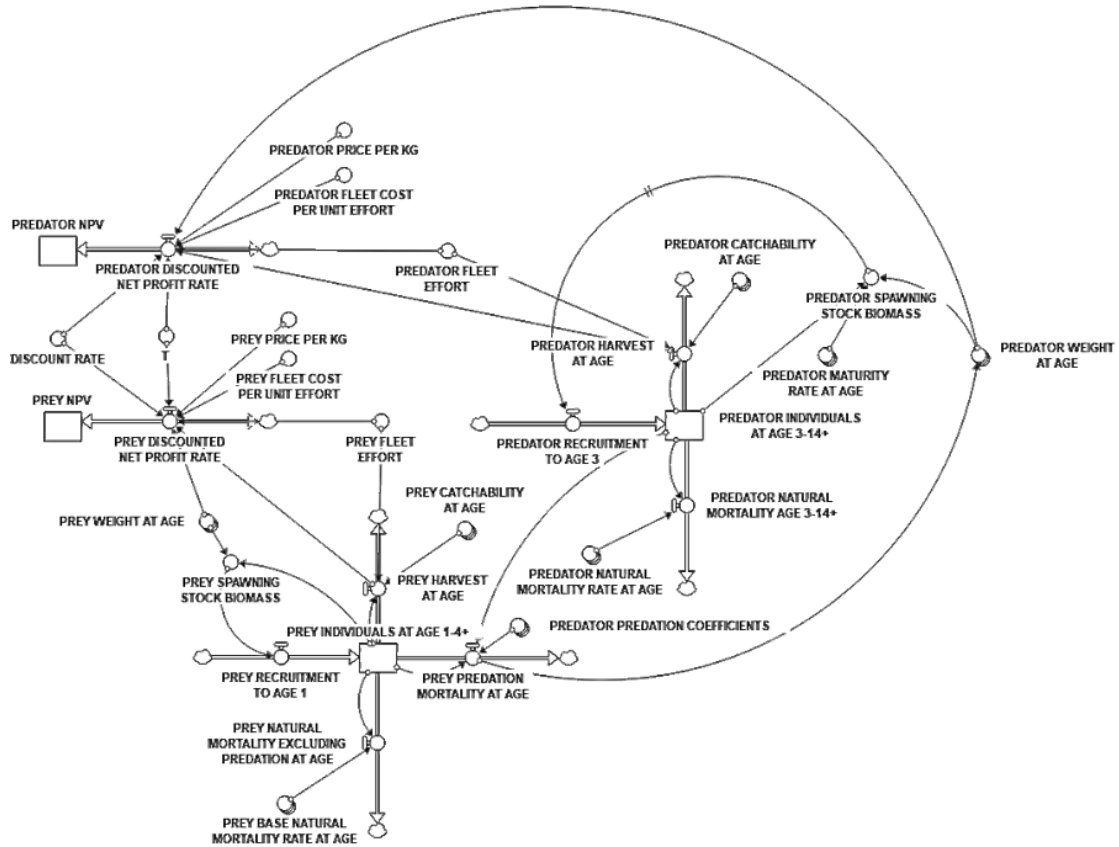


Figure 1: Simplified high-level stock and flow model overview

The modeled system structure and parameterization are inspired by cod and capelin in the North-East Arctic ecosystem, in which cod exists as the predator, and capelin exists as the prey. However, the model is intended for more encompassing conceptual and theoretical investigations. So, while the model is built on inspiration from cod and capelin, and while the analysis considers some scenarios that are directly relevant for cod and capelin, the model is also used to explore scenarios that are less relevant for cod and capelin, and more relevant for other predator-prey cases, e.g., cod and shrimp. The abstractions from the cod-capelin case particularly apply to various investigations regarding the relative price of predator to prey. Overall, the inspiration from cod and capelin is used more as a point of departure and for sensible grounding of the model, rather than being meant as an applied practical study of said fisheries.

Model parameters, variables, and equations

The model comprises a range of sets, parameters, variables, and equations. Table 1 gives an overview of all sets, parameters, and variables, while Table 2 gives a full overview of the model objectives, control variables, and equations. Tables 5-19 in the Appendix give a full overview of the employed parameter values and initial values.

Table 1: Model sets, parameters, and variables

Set	Description	Units
t	t represents time	Years
a	Predator age groups	Years
i	Prey age groups	Years
Parameter	Description	Units
T	T represents the end of the time horizon	Years
r	Discount rate	Dimensionless / Year
P_{pred}	Price per kilogram predator	NOK / kilogram
P_{prey}	Price per kilogram prey	NOK / kilogram
$q_{pred,a}$	Predator fleet catchability at age a	Predator harvest number of individuals in thousands / Predator effort * Predator number of individuals in thousands
$q_{prey,i}$	Prey fleet catchability at age i	Prey harvest number of individuals in thousands / Prey effort * Prey number of individuals in thousands
C_{pred}	Predator fleet cost per unit effort	NOK / Predator effort
C_{prey}	Prey fleet cost per unit effort	NOK / Prey effort
α_{pred}	Predator Beverton-Holt recruitment parameter	-
α_{prey}	Prey Beverton-Holt recruitment parameter	-
β_{pred}	Predator Beverton-Holt recruitment parameter	-
β_{prey}	Prey Beverton-Holt recruitment parameter	-
$M_{pred,a}$	Predator natural mortality at age i	Dimensionless / Year
$P_{pred,a,i}$	Predation coefficients for predators at age a for prey at age i	Kilogram / Predator Individual
$M_{prey,i}$	Prey natural mortality at age i (excluding predation mortality)	Dimensionless / Year
$w_{pred,a}$	Predator exogenous growth at age	Kilogram / Predator Individual
Υ_a	Predator-prey weight conversion factor at age a	Dimensionless
$W_{prey,i}$	Prey weight at age i	Kilogram / Predator Individual
$u_{pred,a}$	Predator maturity rate at age a	Dimensionless
$u_{prey,i}$	Prey maturity rate at age i	Dimensionless
SC_p	Predation scaling factor (used to scale predation up and down)	Dimensionless
SC_w	Predator-prey weight conversion scaling factor (used to scale conversion up and down)	Dimensionless
Variable	Description	Units
E_{pred}	Predator fleet effort	Predator fleet fishing days / Year
E_{prey}	Prey fleet effort	Prey fleet fishing days / Year
$Y_{pred,a,t}$	Harvest number of predator individuals from age group a at time t	Predator harvest number of individuals in thousands / Year
$Y_{prey,i,t}$	Harvest number of prey individuals from age group i at time t	Prey harvest number of individuals in thousands / Year
$R_{pred,t}$	Predator recruitment at time t	Predator number of individuals in thousands / Year
$R_{prey,t}$	Prey recruitment at time t	Prey number of individuals in thousands / Year
$N_{pred,a,t}$	Predator number of individuals in age group a at time t	Predator number of individuals in thousands
$N_{prey,i,t}$	Prey number of individuals in age group i at time t	Predator number of individuals in thousands
$\lambda_{prey,i,t}$	Prey predation mortality at age i	Dimensionless / Year
$Q_{pred,a,t}$	Predator prey biomass consumption at age a at time t	Kilogram/Predator Individual
$W_{pred,a,t}$	Predator weight at age a at time t	Kilogram/Predator Individual
$SSB_{pred,t}$	Predator spawning stock biomass at time t	Thousand tons
$SSB_{prey,t}$	Prey spawning stock biomass at time t	Thousand tons

Table 2: Objective, control variables, and model equations

Description	Objective/Control Variables/Equation	Eq. no.
Objective	$\max \sum_{t=1}^T e^{-rt} \left(P_{pred} \sum_{a=3}^{14} y_{pred,a,t} W_{pred,a,t} + P_{prey} \sum_{i=1}^4 y_{prey,i,t} W_{prey,i,t} - C_{predator} E_{predator} - C_{prey} E_{prey} \right)$	(1)
Control variables	E_{pred}, E_{prey}	(2)
Harvest Predator	$y_{pred,a,t} = \frac{q_{pred,a} E_{pred}}{q_{pred,a} E_{pred} + M_{pred,a}} N_{pred,a,t} (1 - e^{-(q_{pred,a} E_{pred} + M_{pred,a})})$	(3)
Harvest Prey	$y_{prey,i,t} = \frac{q_{prey,i} E_{prey}}{q_{prey,i} E_{prey} + M_{prey,i} + \lambda_{prey,i,t}} N_{prey,i,t} (1 - e^{-(q_{prey,i} E_{prey} + M_{prey,i} + \lambda_{prey,i,t})})$	(4)
Recruitment	$R_{pred,t} = \frac{\alpha_{pred} SSB_{pred,t-3}}{\beta_{pred} + SSB_{pred,t-3}}$	(5)
Predator population dynamics	Age 4-13 $N_{pred,a+1,t+1} = N_{pred,a,t} e^{-(M_{pred,a,t} + q_{pred,a} E_{pred})}$ Age 14+ $N_{pred,14+,t+1} = N_{pred,13,t} e^{-(M_{pred,13,t} + q_{pred,13} E_{pred})} + N_{pred,14+,t} e^{-(M_{pred,14+,t} + q_{pred,14+,t} E_{pred})}$	(6) (7)
Recruitment,	$R_{prey,t} = \frac{\alpha_{prey} SSB_{prey,t-1}}{\beta_{prey} + SSB_{prey,t-1}}$	(8)
Prey population dynamics	Age 1 Age 2-3 $N_{prey,i+1,t+1} = N_{prey,i,t} e^{-(q_{prey,i} E_{prey} + M_{prey,i} + \lambda_{prey,i,t})}$ Age 4+ $N_{prey,4+,t+1} = N_{3,t} e^{-(q_{prey,3} E_{prey} + M_{prey,3} + \lambda_{prey,3,t})} + N_{4+,t} e^{-(q_{prey,4+} E_{prey} + M_{prey,4+} + \lambda_{prey,4+,t})}$	(9) (10)
Predator weight	$W_{pred,a,t} = w_{pred,a}$	(11)
Predator prey biomass consum.	$W_{pred,a,t} = W_{pred,a-1,t-1} + SC_w \Upsilon_{a-1} \hat{\phi}_{pred,a-1,t-1} + w_{pred,a}$ $\varphi_{pred,a,t} = \sum_{i=1}^4 \frac{SC_p P_{pred,a,i} N_{pred,a,t}}{q_{prey,i} E_{prey,t} + M_{prey,i} + \lambda_{prey,i,t}} N_{prey,i,t} (1 - e^{-(q_{prey,i} E_{prey,t} + M_{prey,i,t} + \lambda_{prey,i,t})}) W_{prey,i}$	(12)
Predation mortality	$\lambda_{prey,i,t} = \sum_{a=3}^{14} SC_p \hat{\phi}_{pred,a,t} N_{pred,a,t}$	(13)
Predator SSB	$SB_{pred,t} = \sum_{a=3}^{14} v_{pred,a} N_{pred,a,t} W_{pred,a,t}$	(14)
Prey SSB	$SSB_{prey,t} = \sum_{i=1}^4 v_{prey,i} N_{prey,i,t} W_{prey,i}$	(15)

The sole owner’s objective is to maximize the net present value of harvest (eq. 1 in Table 2) from the two fish stocks with respect to the effort of the two fleets (eq. 2 in Table 2) subject to the system (eq. 3-15 in Table 2). The control variables are restricted such that $E_t = E_{t+1}$ for both fleets in all periods $t=0, 1, \dots, T-1$. These control constraints enforce steady-state fishing schemes, which is what we focus on.

The harvest by each fleet from each age group in each stock is determined by classical Baranov catch equations, i.e., the harvest by each fleet from each age group in each fish stock is a function of effort and the number of individuals in each age group (eq. 3-4 in Table 2) (Baranov, 1918). Harvest is density-dependent and increases linearly by the size of the stock—that is, catch per unit effort-wise, there are benefits to having access to and maintaining abundant fish stocks.

Inspired by state-of-the-art modeling of North-East Arctic cod, the predator stock is split into 12 age groups, ranging from age group 3 to age group 14+, in which the first age group represents all individuals that are three years of age, while the last represents all individuals that are 14 years and older (Diekert et al., 2010; ICES, 2021; Kovalev & Bogstad, 2005). Similarly, inspired by state-of-the-art modeling of capelin, the prey stock is split into four age groups, ranging from age group 1 to age group 4+ (ICES, 2021).

The predator and prey individuals are both subject to natural mortality. In this model, both species are commercial, and thus also subject to fishing mortality (eq. 6-7 and 9-10 in Table 2). In addition, the prey is subject to predation mortality, which is separate from other natural mortality in the model (eq. 9-10 in Table 2).

The natural mortality rates are considered exogenous and constant. Bang & Steinshamn (2022) show that assumptions of exogenous natural mortality rates can lead to significant overestimation of the biological and economic potential of fish stocks, which makes it clear why such factors should be considered endogenously in models that are intended for applied and practical analysis. However, the focus in this study is more conceptual and theoretical than practical, and we choose to treat these factors exogenously to allow clear focus on the objectives of this study, which encompass the effects of predation, predation-weight conversion, and relative prices on optimal harvesting schemes and preferred selectivity.

The number of prey individuals that die from predation is determined by age-specific predation coefficients, the number of predator individuals at age, and the number of prey individuals at age (eq. 13 in Table 2). For intuition, the reader can think of the predator as a competing fishing fleet consisting of several vessel groups (age groups), each with its own efficiency and selection pattern in harvesting the prey (predation coefficients), and an employed effort (number of predator individuals at age). The predation functions have the same structure as the harvest functions, but as opposed to harvest, the predation functions generate no direct value for the fishing industry. The choice of density-dependent predation functions is motivated by the fact that cod has been shown to shift to alternative prey such as amphipods and krill when the capelin stock is low (Dalpadado et al., 2001; Holt et al., 2019)—i.e., when less capelin is available, cod is more likely to base more of its food consumption on alternative prey.

The weight at age for the predator in the current year is determined by the weight at age of that cohort in the previous year, predation-weight conversion rates, the biomass consumption of prey per predator individual, and an exogenous growth factor (eq. 11 in Table 2). It is well-known that predator species can have reduced feeding levels and smaller growth rates when the prey stock is at low levels, and vice versa (Gjøsæter et al., 2009; Holt et al., 2019; Mehl & Sunnanå, 1991).

The weight at age for the prey is assumed exogenous and constant. Like assumptions of exogenous natural mortality, this assumption can lead to overestimation of the biological and economic potential (Bang & Steinshamn, 2022). However, again, our intention here is not to provide accurate estimates on the biological and economic potential of either stock, but rather to provide a conceptual, theoretical, and broader contribution. As such, the simplification can be well-defended.

The recruitment to the predator and prey stocks are determined by Beverton-Holt recruitment functions, i.e., the recruitment to each stock is a concave function of spawning stock biomass (SSB), with positive horizontal asymptotes (eq. 5 and 8 in Table 2) (Beverton & Holt, 1957). The spawning stock biomass is calculated according to eq. 14 and 15 in Table 2.

The following subsection gives necessary insight to the numerical specification of the model. The

reader is referred to tables 5-19 in the Appendix for a full description of the numerical specification of the model.

Model scenarios

This study focuses on how preferred selectivity and optimal harvesting change in response to changes in the absolute and relative strength of age-specific biological interactions, as well as changes in relative prices. To acquire the desired insight, the model is solved for 8 scenarios with 72 different combinations of scaling values that determine the strengths of the predator-prey interactions (ref. eq. 11-13 in Table 2) . In total, 576 runs are conducted to produce the results.

The scenarios apply various combinations of settings (modes) regarding the predator fleet selection pattern, predation coefficients, predation-weight conversion rates, and relative price of predator to prey. Table 3 gives an overview of the scenarios including the applied combination of modes, while Figure 2 shows the selectivity, predation, and conversion modes referred to in Table 3. Table 4 gives an overview of the applied scaling values.

Table 3: Overview of model scenarios

Scenario	Selectivity mode	Predation mode	Conversion mode	Relative price (P_{pred}/P_{prey})
1	1	1	1	1
2	2	1	1	1
3	1	2	2	1
4	2	2	2	1
5	1	2	2	1.5
6	2	2	2	1.5
7	1	2	2	0.66
8	2	2	2	0.66

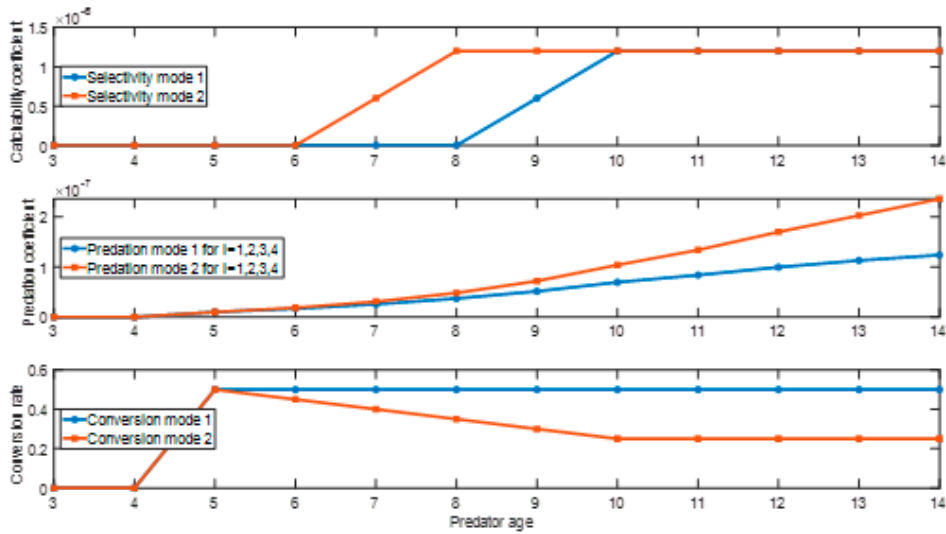


Figure 2: Selectivity, predation, and conversion modes. Selectivity coefficient values. ‘Spare the young’ (selectivity mode 1) and ‘Take them early’ (selectivity mode 2). Baseline predation coefficients (scaling factor = 1). Size-proportional (predation mode 1) and size-disproportional predation (predation mode 2). Baseline predation-weight conversion rates (scaling factor = 0.5). Uniform conversion rates (conversion mode 1) and non-uniform conversion rates (conversion mode 2)

With reference to the predator fleet selectivity modes (top plot in Figure 2), we apply one mode where the selection pattern is such that young fish are spared for future harvest. In age-structured

single-species models, this is often optimal even though it may come at a cost in terms of reduced catch per unit effort and cost (Bang & Steinshamn, 2022; Diekert et al., 2010; Helgesen et al., 2018; Kovalev & Bogstad, 2005; Reed, 1980; Skonhoft & Friberg, 2021). In the second selectivity mode, the selection pattern is shifted such that younger individuals are targeted.

Regarding the predation modes (middle plot in Figure 2), we apply one mode where the predation coefficients are increasing proportionally with base weight at age, which is defined by the weight functions when the predation-weight conversion is set to zero (eq. 11). In the second predation mode, the predation coefficients are increasing disproportionately with base weight at age such that, e.g., a 5 kg predator consumes more than twice the amount of prey when compared to a 2.5 kg predator, *ceteris paribus*. Mehl (1986) states, “With increasing predator length fish prey become more and more important. For sizegroup 20-39 cm fish were the major prey in 2/3 of the investigated areas and periods. while for cod \geq 60 cm fish always were the dominating prey category. And with increasing predator length the size and importance of larger fish prey increased gradually”. Based on this, we conclude that the second mode is more realistic than the first. However, it is still interesting to consider the difference between the two.

Regarding the predation modes, note that within each predator age group, the predation coefficients are uniform for $i=1,2,3,4$ for all age groups—that is, a predator of age a has the same selectivity on prey of age 1 as prey of age 2, etc. This assumption is made for simplicity. In the real world, a predator of age 3 may for example have a higher selectivity for prey of age 1 than prey of age 4, while a predator of age 10 may have a higher selectivity for prey of age 4 than of age 1. Considering the latter part of the above quote from Mehl (1986), it is reasonable to think that large predators prefer larger prey than small predators.

For the predation-weight conversion rates, we apply one mode where the predation-weight conversion rates are uniform, and another where the predation-weight conversion rates are decreasing with age before stabilizing at a constant level (bottom plot in Figure 2). For each of the eight scenarios in Table 3, the optimization model is solved for 72 combinations of strengths in predation and predation-weight conversion rates. The strengths are determined by the product of baseline values multiplied by scaling values, in accordance with eq. 11-13 in Table 2. The combinations of scaling values used are displayed in Table 4.

Table 4: Overview of combinations of scaling values for use in solving each scenario

Combinations of scaling factors for use in solving each scenario								
Conversion Scaling Factor								
0, 0								
0, 0.1								
0, 0.2								
0, 0.3								
0, 0.4								
0, 0.5								
0, 0.6								
0, 0.7								
0.5, 0								
0.5, 0.1								
0.5, 0.2								
0.5, 0.3								
0.5, 0.4								
0.5, 0.5								
0.5, 0.6								
0.5, 0.7								
1, 0								
1, 0.2								
1, 0.2								
1, 0.3								
1, 0.4								
1, 0.5								
1, 0.6								
1, 0.7								
1.5, 0								
1.5, 0.2								
1.5, 0.2								
1.5, 0.3								
1.5, 0.4								
1.5, 0.5								
1.5, 0.6								
1.5, 0.7								
2, 0								
2, 0.2								
2, 0.2								
2, 0.3								
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4, 0.7								

Solution approach

The model has been set up in MS Excel, and a combination of VBA programming and the GRG Nonlinear solving method have been used to solve the 576 optimization problems to generate the results. The model can be accessed through one of the author’s github repository (link will be provided if the paper is accepted).

The GRG Nonlinear solver is designed for problems with nonlinear objectives and/or nonlinear constraints (Lasdon et al., 1974; Microsoft, 2021). The solver uses values within the spreadsheet model for its initial search for an optimum and considers small changes in the control variables to

improve the objective. In this way, when the goal is to maximize, the solver climbs “uphill” until it reaches an optimal solution. This search procedure may get stuck on locally optimal solutions. Thus, to ensure that we report results that are de facto globally optimal, we have solved the problems several times with different initial search values for the control variables. Using this procedure, we observe that the solver converges towards the same solutions regardless of initial search values. The observation from the repetitive solving procedure goes a long way in validating the global optimality of the results.

Results and discussion

The model scenarios are designed to study how preferred selectivity and optimal harvesting respond to changes in the strength of two predator-prey interactions, namely predation mortality and predation-weight conversion, and to changes in the relative price of predator to prey. The main results are summarized in Figure 3-7 below. In this section, we go systematically through the results.

Figure 3 shows the results from scenarios 1 and 2 in Table 3. That is, the scenarios with predation coefficients that increase proportionally to base predator weights at age, and with uniform predation-weight conversion rates (ref. Figure 2).

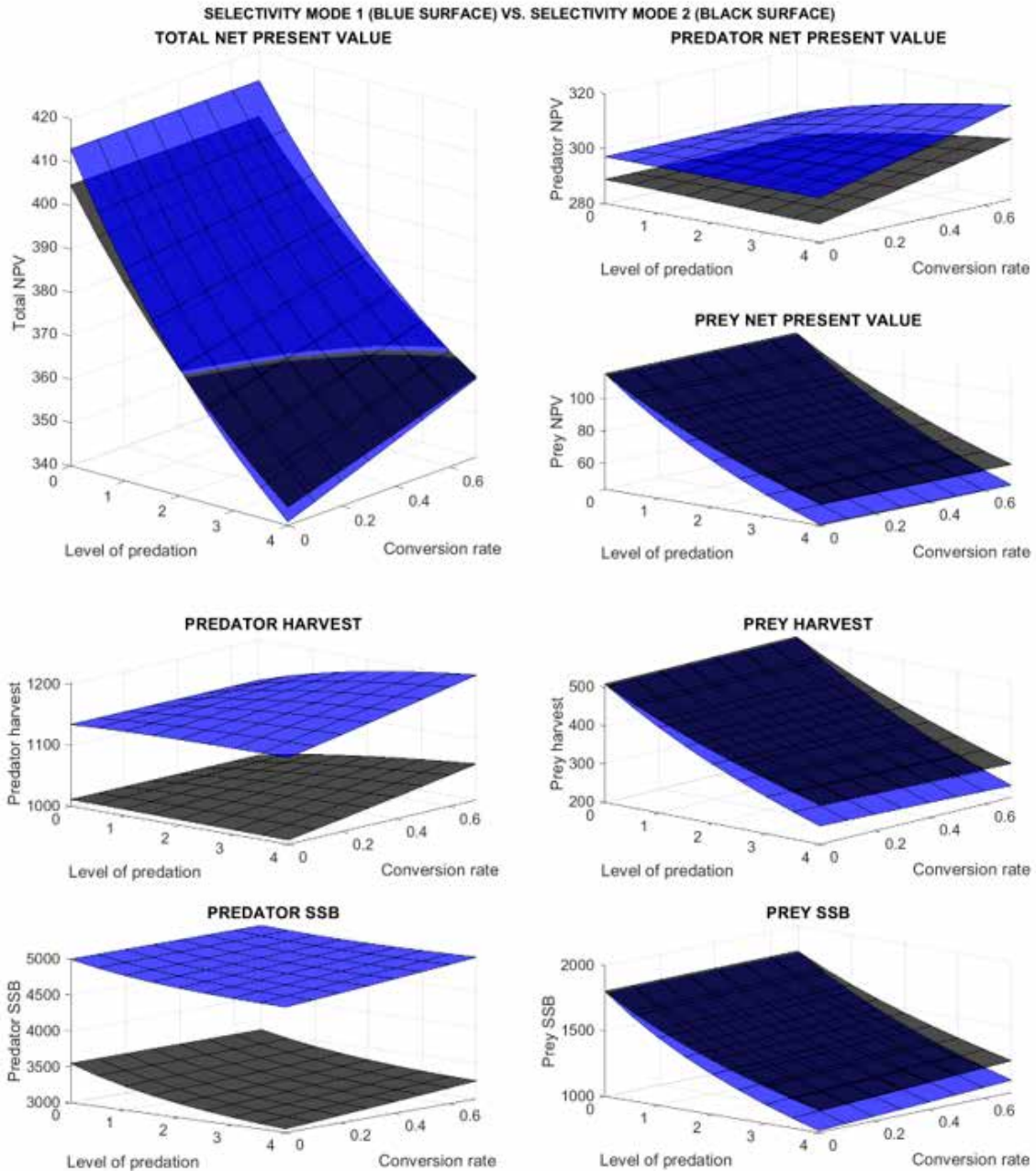


Figure 3: Key results from scenarios 1 and 2

First, consider the top left plot in Figure 3. This part of the figure gives high-level, but also key novel insight. Starting with zero predation and zero predation-weight conversion, the plot shows that the sole owner prefers selectivity mode 1—that is, the selectivity mode where young predator fish are spared for future harvest such that the individual predator growth potential is better utilized. This result is aligned with existing theory and research (Bang & Steinshamn, 2022; Diekert et al., 2010; Helgesen et al., 2018; Reed, 1980; Skonhøft et al., 2012). However, as predation increases (right-wards movement on the axis labeled ‘Level of predation’, which is defined by the scaling factor SC_P), the net benefit of applying selectivity mode 1 shrinks relative to the alternative selectivity mode 2, where smaller predator individuals are also targeted (ref. Figure 2). And after

a certain point, it becomes optimal to apply selectivity mode 2.

As per expectation and reason, when the predation is zero, an increasing level of predation-weight conversion (right-wards movement on the axis labeled ‘Conversion rate’) has no effect upon the net present value of neither selectivity modes. However, as the level of predation increases, the plot shows that increasing predation-weight conversion dampens the negative effect of predation upon the net present value and delays the shift in optimal selectivity. These results and insights are intuitive because any additional mortality has a negative impact on the potential of the prey stock, and with no predation-weight conversion, there will be no counteracting positive effect with the predator. However, with predation-weight conversion, an increasing level of predation means that the predator will consume more, and gain weight as a result, which means higher potential harvest from the predator stock.

Regarding optimal harvesting given each of the selectivity modes, the results show that increasing predation yields higher optimal fishing pressure on the predator stock – the harvest goes up and the spawning stock biomass is stabilized at a lower level. This is done to limit the increase in natural mortality of the prey stock, and thereby limit the reduction in the net present value of the prey stock. Meanwhile, the harvest from the prey stock is reduced to compensate somewhat for the predation effect on the size of the stock. Overall, these changes in the optimal harvesting strategy correspond to findings in biomass predator-prey models.

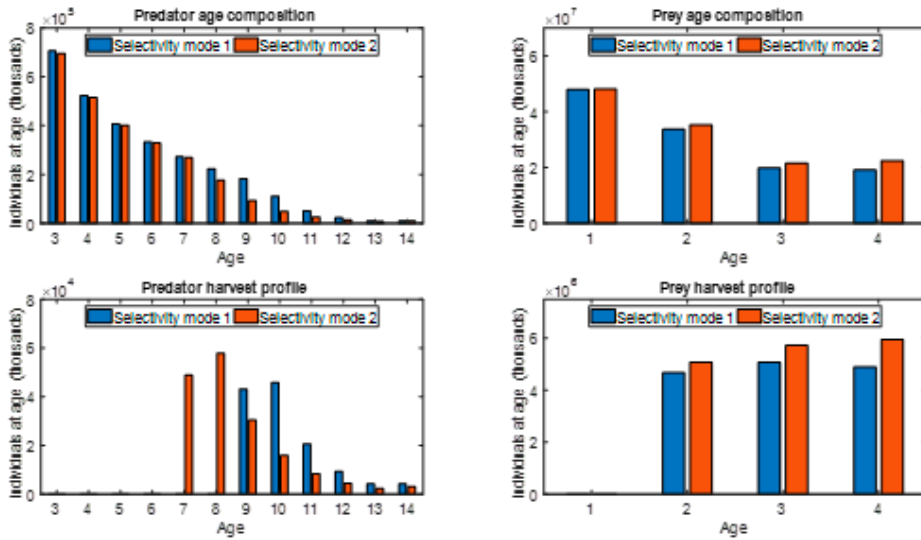


Figure 4: Optimal age compositions and harvest profiles in scenarios 1 and 2 for different selectivity modes with the level of predation set to 3 and the conversion rate set to 0

Figure 4 shows the optimal age compositions and harvest profiles in scenarios 1 and 2 with the level of predation set to 3 and the conversion rate set to 0. The figure clearly shows how the optimal age-composition and harvest profile given a selection pattern respond to changes in the selection pattern for high levels of predation. It is shown that shifting the selection pattern towards smaller predator individuals lead to a reduction in the overall size of the predator stock and a reduction in the relative number and harvest of large to small predator individuals, which also implies reduced harvest efficiency in terms of catch per unit effort. This result may be obvious to the reader. However, the figure also shows something more, which is less obvious. The changes in the overall size and age-composition of the predator stock yields an increase in the overall size of the prey stock and the relative number and harvest of large to small prey individuals. As such, the changes in the selectivity and harvesting policy does not only increase the gross harvest and catch per unit effort for prey, but it also improves the utilization of individual prey growth potential. In other words, the sole owner sacrifices utilization of individual predator growth potential not just to

limit the overall predation of the prey stock, but also to improve the utilization of individual prey growth potential. This is an interesting detail and insight which cannot be gained from biomass predator-prey models.

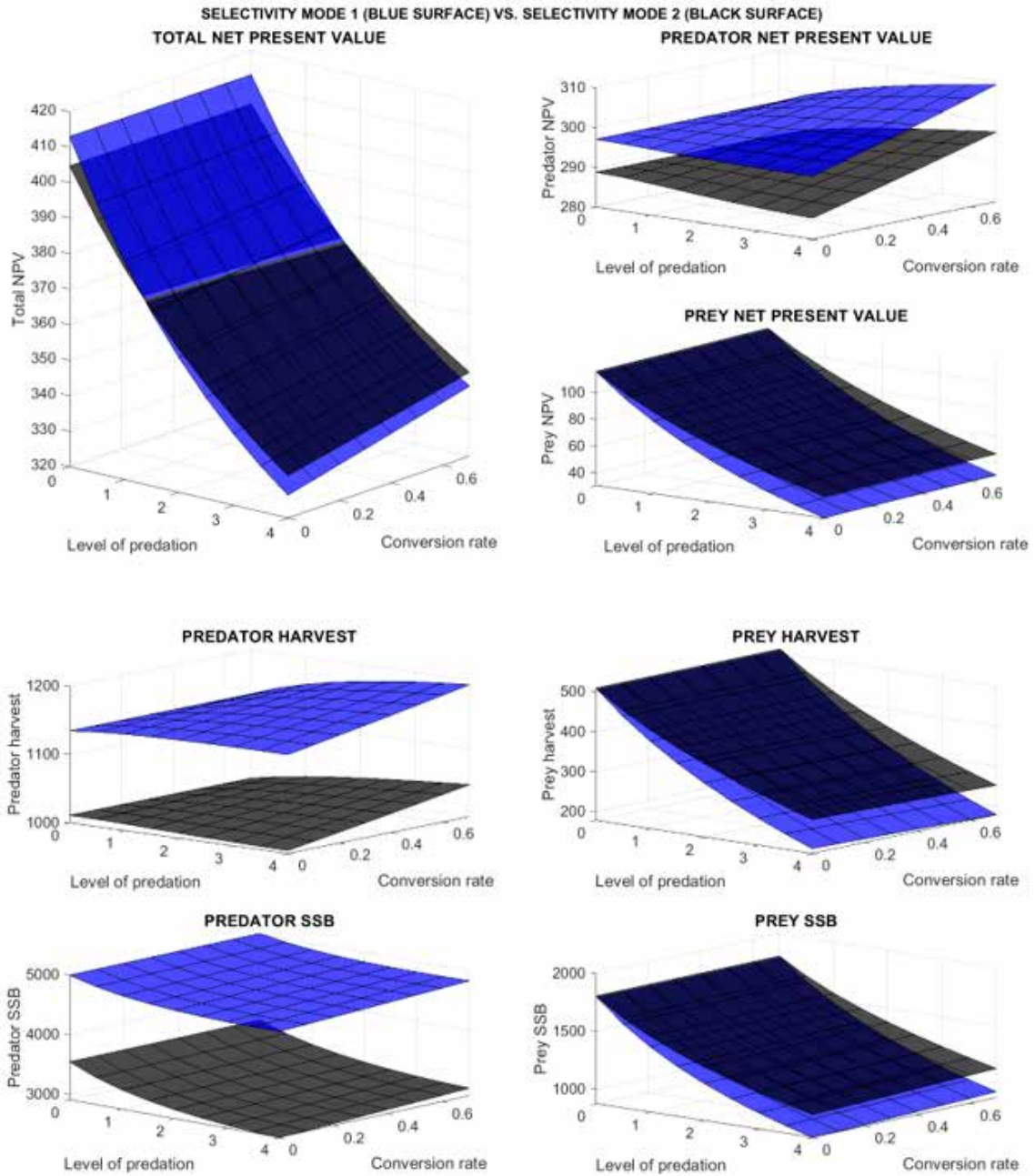


Figure 5: Key results from scenarios 3 and 4

Figure 5 shows the results from scenarios 3 and 4 in Table 3. That is, the scenarios with predation coefficients that increase disproportionately to base predator weights at age, and with non-uniform predation-weight conversion rates (ref. Table 3 and Figure 2). The results in Figure 5 go on to show that disproportional predation coefficients and non-uniform conversion rates leads to an earlier shift in preferred selectivity. Intuitively, this makes sense because of two phenomena. First, the cost of having many large predators in terms of reduced potential of the prey stock

increases when large predator individuals eat relatively more prey than small predator individuals. Second, the benefit of having access to large predator fish becomes relatively smaller when compared to having access to small predator fish because the relative differences in weights between the small and large predator fish shrinks for high prey stock levels. Both phenomena explain the earlier shift in preferred selection pattern. Regarding optimal harvesting, we witness strengthened effects of what is observed in the results for scenarios 1 and 2.

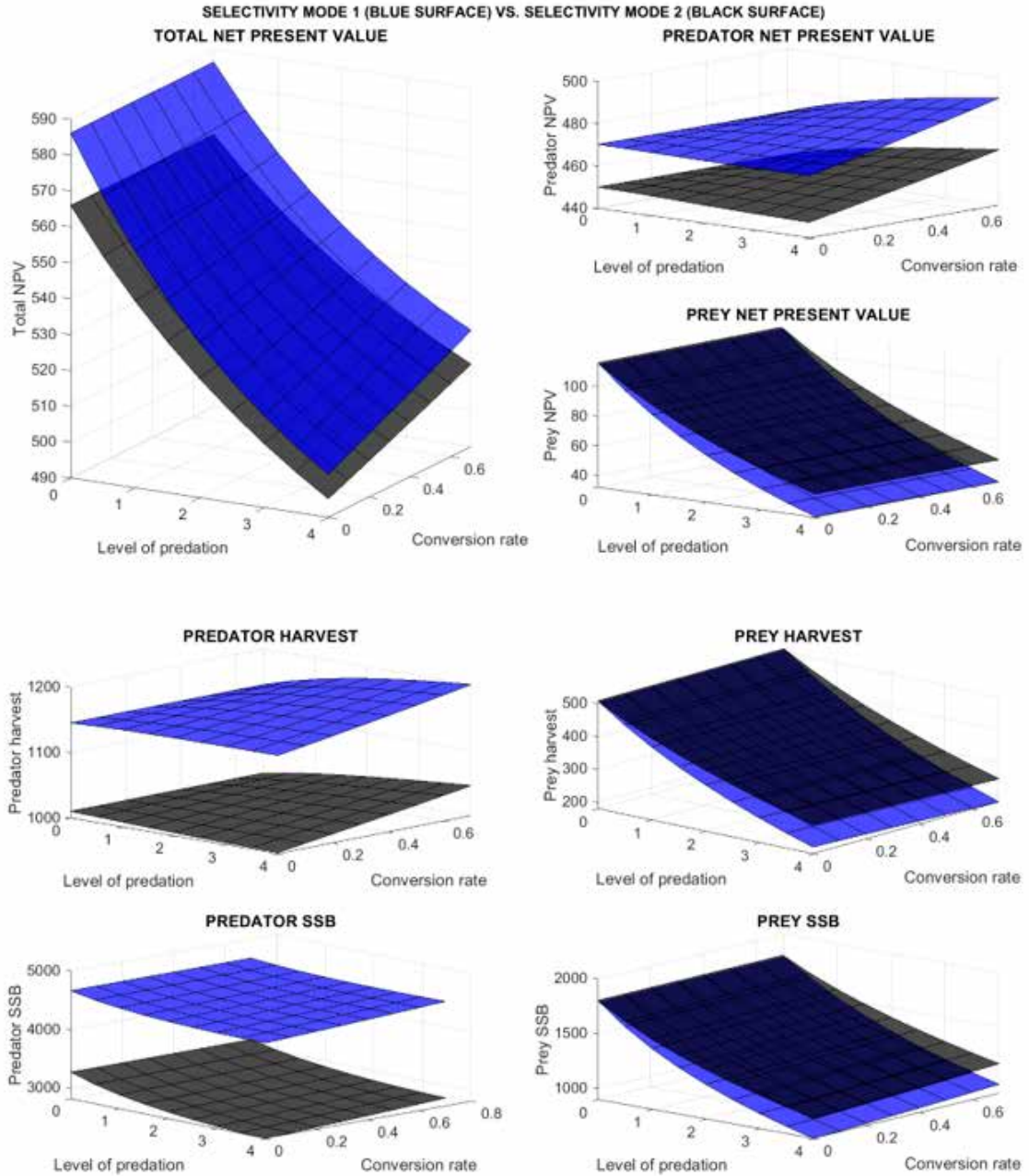


Figure 6: Key results from scenarios 5 and 6

Figure 6 shows the results from scenarios 5 and 6 in Table 3. That is, the scenarios with predation coefficients that increase disproportionately to base predator weights at age and non-uniform predation-weight conversion rates, and an increase in the relative price of predator to

prey (ref. Table 3 and Figure 2). The results show that an increase in the relative price of the predator counteract the shift in optimal selection pattern observed in scenarios 1-4. Intuitively, this is reasonable because high predator harvest and good utilization of the predator growth potential becomes relatively more valuable when the price of the predator becomes relatively higher compared to the price of prey.

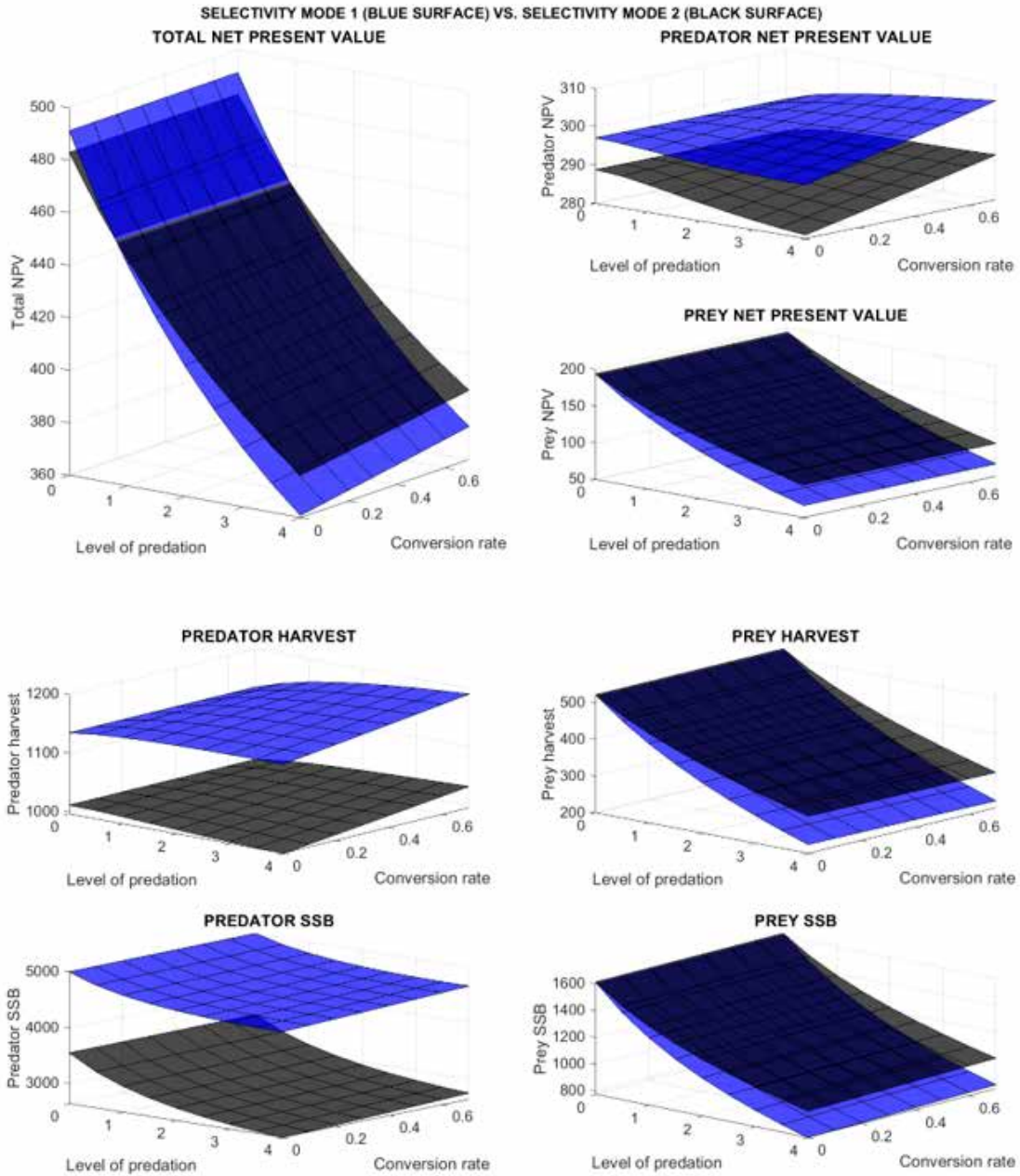


Figure 7: Key results from scenarios 7 and 8

Figure 7 shows the results from scenarios 7 and 8 in Table 3. That is, the scenarios with predation coefficients that increase disproportionately to base predator weights at age, and with non-uniform predation-weight conversion rates, and a decrease in the relative price of predator to prey (ref. Table 3 and Figure 2). As per expectation and reason, the results in Figure 7 shows the

opposite of the results from scenarios 5 and 6. This makes sense because high predator harvest and good utilization of the individual predator growth potential becomes relatively less valuable when the price becomes relatively lower.

Conclusion

This study applies dynamic optimization in an age-structured, multi-fleet, predator-prey model. While we reproduce insight from age-structured single-species bioeconomic models, we also show that preferred selectivity and optimal harvesting change with the level of predation and predation-weight conversion rates.

In single-species age-structured models, a classical and recurring finding is that it is optimal to spare young fish for future harvest. For zero predation, our results confirm this. However, for increasing levels of predation, the benefits of targeting large predators are counteracted by disadvantages in terms of higher prey mortality, worsened utilization of individual growth potential for the prey, and lower catch per unit effort for the prey. At some point, the disadvantages can outweigh the benefits of targeting only large predators, thereby making it optimal to target smaller predator individuals and increase the overall fishing pressure for the predator. Further, it is shown that increasing predation-weight conversion rates can counteract this, more so when assuming uniform predation-weight conversion rates than when assuming predation-weight conversion rates that decrease with age, which is more realistic. Biomass models cannot give such insights because they do not describe age-specific details, including e.g., age-specific catchability, predation, and weight at age.

The findings are interesting and important because they bring awareness to why managers should think twice before changing gear restrictions in direction of targeting bigger fish on basis of single-species analyses. Moreover, they display the usefulness and value of age-structured multi-species modeling, which has not received much attention in the research literature.

For future research, we may suggest investigating the effects of predation coefficients that are age-specific for both predator and prey. To narrow the focus of this study, we assumed predation coefficients that are age-specific for predator, but age-unspecific for prey—that is, a predator of age a has the same selectivity on prey of age 1 as prey of age 2, etc. In the real world, a predator of age 3 may for example have a higher selectivity for prey of age 1 than prey of age 4, while a predator of age 10 may have a higher selectivity for prey of age 4 than of age 1. It could be interesting to study the implications of this for optimal selectivity and harvesting.

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Appendix

Table 5: Predator natural mortality rates

Age	3	4	5	6	7	8	9	10	11	12	13	14
$M_{pred,a}$	0.3	0.25	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2	0.2

Table 6: Prey base natural mortality rates

Age	1	2	3	4
$M_{prey,i}$	0.2	0.2	0.2	0.2

Table 7: Predator exogenous growth factors

Age	3	4	5	6	7	8	9	10	11	12	13	14
$w_{pred,a}$	0.2	0.4	0.666	0.863	1.116	1.439	1.824	2.286	1.81	2.017	1.649	1.43

Table 8: Prey weights

Age	1	2	3	4
$W_{prey,i}$	0.004	0.01	0.02	0.03

Table 9: Predator and prey recruitment parameters

Parameter	Numerical specification
α_{pred}	725 000
α_{prey}	128 000
β_{pred}	50 000 000
β_{prey}	50 000

Table 10: Predator maturity

Age	3	4	5	6	7	8	9	10	11	12	13	14
$v_{pred,a}$	0	0.003	0.049	0.27	0.58	0.81	0.94	0.98	0.99	1	1	1

Table 11: Prey maturity

Age	1	2	3	4
$v_{prey,i}$	0	0.5	1	1

Table 12: Predation mode 1 with scaling factor SC_p set to 1

Age	3	4	5	6	7	8	9	10	11	12	13	14
$p_{pred,a,1}$	0	0	1.00E-08	1.68E-08	2.56E-08	3.70E-08	5.14E-08	6.95E-08	8.38E-08	9.97E-08	1.13E-07	1.24E-07
$p_{pred,a,2}$	0	0	1.00E-08	1.68E-08	2.56E-08	3.70E-08	5.14E-08	6.95E-08	8.38E-08	9.97E-08	1.13E-07	1.24E-07
$p_{pred,a,3}$	0	0	1.00E-08	1.68E-08	2.56E-08	3.70E-08	5.14E-08	6.95E-08	8.38E-08	9.97E-08	1.13E-07	1.24E-07
$p_{pred,a,4}$	0	0	1.00E-08	1.68E-08	2.56E-08	3.70E-08	5.14E-08	6.95E-08	8.38E-08	9.97E-08	1.13E-07	1.24E-07

Table 13: Predation mode 2 with scaling factor SC_p set to 1

Age	3	4	5	6	7	8	9	10	11	12	13	14
$p_{pred,a,1}$	0	0	1.00E-08	1.85E-08	3.08E-08	4.81E-08	7.20E-08	1.04E-07	1.34E-07	1.70E-07	2.03E-07	2.36E-07
$p_{pred,a,2}$	0	0	1.00E-08	1.85E-08	3.08E-08	4.81E-08	7.20E-08	1.04E-07	1.34E-07	1.70E-07	2.03E-07	2.36E-07
$p_{pred,a,3}$	0	0	1.00E-08	1.85E-08	3.08E-08	4.81E-08	7.20E-08	1.04E-07	1.34E-07	1.70E-07	2.03E-07	2.36E-07
$p_{pred,a,4}$	0	0	1.00E-08	1.85E-08	3.08E-08	4.81E-08	7.20E-08	1.04E-07	1.34E-07	1.70E-07	2.03E-07	2.36E-07

Table 14: Conversion modes with scaling factor SC_w set to 0.5

Age	3	4	5	6	7	8	9	10	11	12	13	14
Mode 1 Υ_a	0	0	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5	0.5
Mode 2 Υ_a	0	0	0.5	0.45	0.4	0.35	0.3	0.25	0.25	0.25	0.25	0.25

Table 15: Predator fleet catchability modes

Age	3	4	5	6	7	8	9	10	11	12	13	14
Mode 1 $q_{pred,a}$	0	0	0	0	0	0	6.00E-07	1.20E-06	1.20E-06	1.20E-06	1.20E-06	1.20E-06
Mode 2 $q_{pred,a}$	0	0	0	0	6.00E-07	1.20E-06	1.20E-06	1.20E-06	1.20E-06	1.20E-06	1.20E-06	1.20E-06

Table 16: Prey fleet catchability

Age	1	2	3	4
$q_{prey,i}$	0.00E+00	5.00E-07	1.00E-06	1.00E-06

Table 17: Economic parameters

Economic Parameters	Numerical specification
T	100
r	0.05
P_{pred}	Scenarios 1-4 and 7-8: 15 Scenarios 5-6: 22.5
P_{prey}	Scenarios 1-6: 15 Scenarios 7-8: 22.5
C_{pred}	5000
C_{prey}	5000

Table 18: Predator initial values

Age	3	4	5	6	7	8	9	10	11	12	13	14
$N_{pred, a,t=0}$	705521	522663	407050	333265	272854	223394	182899	106845	44534	18562	7737	6754
$W_{pred, a,t=0}$	0.2	0.6	1.26	2.14	3.276	4.74	6.59	8.91	10.77	12.82	14.51	15.97

Table 19: Prey initial values

Age	1	2	3	4
$N_{prey, a,t=0}$	48443982	30465415	18558716	22190726

This study presents a bioeconomic, age-structured, multi-fleet, predator-prey model. By solving the model for a range of scenarios and parameter values, we show that preferred selectivity and optimal harvesting change with the levels of predation and predation-weight conversion rates. While the model reproduces insight from age-structured single-species and biomass predator-prey models, it also shows that positive scaling of age-specific predation coefficients can shift the preferred selection pattern towards smaller predator individuals and increase the overall fishing pressure for the predator. This involves sacrificing utilization of predator growth potential to achieve better utilization of prey growth potential, both at an individual level and at the stock level. In addition, it involves sacrificing predator harvest efficiency to achieve better prey harvest efficiency. The model also shows that positive scaling of predation-weight conversion rates can counteract the abovementioned. To the best of our knowledge, this represents novel findings. The findings are important because they bring awareness to why managers should think twice before changing gear restrictions in direction of targeting bigger fish on basis of single-species analyses, in which selectivity studies are common. Moreover, they display the usefulness and value of age-structured multi-species modeling, which has received limited attention in the bioeconomic literature so far, as opposed to age-structured single-species modeling and biomass multi-species modeling.

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