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A size-based ecosystem model

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A Size-Based Ecosystem Model

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Abstract

Ecosystem Management requires models that can link the ecosystem level to the operation level. This link can be created by an ecosystem production model. Because the function of the individual fish in the marine ecosystem, seen in trophic context, is closely related to its size, the model groups fish according to size. The model summarises individual predation events into ecosystem level properties, and thereby uses the law of conservation of mass as a framework. This paper provides the background, the conceptual model, basic assumptions, integration of fishing activities, mathematical completion, and a numeric implementation. Using two experiments, the model's ability to act as tool for economic production analysis and regulation design testing is demonstrated. The presented model is the simplest possible and is built on the principles of (i) size, as the attribute that determines the predator–prey interaction, (ii) mass balance in the predator–prey allocation, and (iii) mortality and somatic growth as a consequence of the predator–prey allocation. By incorporating additional assumptions, the model can be extended to other dimensions of the ecosystem, for example, space or species. The formulation and description of the present model can serve as a reference for future work.

Keywords: Ecosystem-model, size-based-model, trophic-model, numeric, fishery, economic.

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1 Introduction

In response to the over-exploitation of the marine ecosystems and the collateral consequences of fishing—habitat destruction, incidental mortality of non target species, evolutionary shifts in population demographics, and changes in the function and structure of ecosystems (Pikitch et al., 2004)—there are increasing calls for a management of the marine ecosystem with a broader perspective. There are many terms that describe this same idea (Arkema et al., 2006). This paper uses the term “Ecosystem Management,” for this management of the ecosystem in a broad perspective, and interprets Ecosystem Management as a management theory that merges the ideas of an organisation hierarchy in nature and strategic planning based on a planning hierarchy—with ecosystem as the strategic planning level.¹

Many papers on ecosystem management emphasise the need for ecological models (e.g. Christensen et al., 1996; Garcia et al., 2003). In addition, the ability to create a quantifiable link from the strategic level—the ecosystem—to the operational level—fish at an aggregated level not larger than a shoal—will, from a management planning view, be a prerequisite for a successful Ecosystem Management. This link can be created by an ecosystem production model where operation can be summarized to the scale of the ecosystem.¹

With the analysis of Gordon (1954) and Schaefer (1954), the use of population stock models as the basic assumption, when analysing the production of fishing grounds, was introduced. Since then, the bulk of bioeconomic literature (Clark, 1985, 1990; Clark and Munro, 1975, and many others) has assumed some kind of population model where the basic assumption is that production is a function of the stock. Stock models treat the interaction of the stock with other parts of the ecosystem as exogenous. That is, the population is regarded as an autonomous system with only the fishing as an external influence.

Many economists have recognised one-species models as inadequate and thus have analysed two species (Clark, 1985, 1990) or three species stock models (May et al., 1979). Even though these approaches give valuable insight, they still consider other parts of the ecosystem as exogenous. This, however, has not been ignored. For example, Clark (1985) writes:

“The two-species differential-equation [stock models] . . . are little more than caricature of the real complexity of marine foodwebs. At a somewhat

¹This particular view of Ecosystem Management, and arguments in the following that refer to this footnote, is the result of a more comprehensive analysis and discussion found in Ravn-Jonsen (2009) which will be supplied by the author on request.

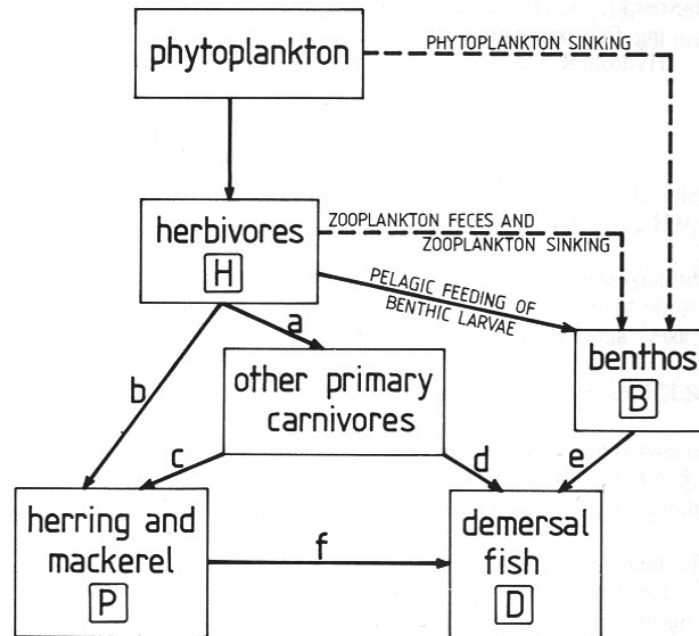


Figure 1: Diagrammatic representation of the principal energy flow to the fish species. From Jones (1982).

more realistic level, [a reference to the figure of Jones (1982), figure 1] is a representation of the principal energy flows among fish species in the North Sea. But this model is also obviously a drastic simplification” (Clark, 1985, p. 202)

The approach of Jones (1982) is totally different from the population stock models normally used in bioeconomic analysis. This model attempts to model production as a consequence of the flow of energy and matter in the ecosystem. Polovina (1984) followed the same approach in his “Ecopath” model, later further developed into an integrated software package “Ecopath with Ecosim” (Christensen and Walters, 2004).

Production models for economic analysis will normally be expected to have at least two properties: i) The flow and use of resources must obey the physical law of mass conservation, and ii) the model has to identify a restriction on input or output to create scarcity within in the system of interest.¹ Even though Ecopath type models, which internalise energy and mass flows, are ecosystem production models, they are

limited in viewing the ecosystem as an interaction of species. Models of this type cannot be expected to give the long term predictability needed for strategic planning, whereas an ecosystem production model structured around functional components can be expected to give a relatively well defined attractor for the system.¹ Additionally, models like Jones (1982) and Ecopath are simulation models and very complex. Even though these models may be good at evaluating how environment and fishing impact the ecosystem, as Clark (2006) notes regarding complex simulation models, the reasons underlying the model's prediction may be obscured.

Recently, ecosystem models with properties other than species have developed into a state suited for economic analysis. This model type builds on a long tradition for research in the distribution of biomass in the marine ecosystem with respect to body size, first presented by Sheldon et al. (1972) and Sheldon et al. (1973). The origin of this research was a search for a holistic description of biota with properties at the ecosystem level. The distribution of biomass with respect to the size of the organisms seemed, across ecosystems, to show predictable properties for small particles in the pelagic waters. Sheldon et al. (1977) included larger fish in a theory that relates fish production with primary production in the sea. This theory interprets the observed distribution of organisms with respect to size as a consequence of the trophic system. That is, primary production is performed by small particles in the sea. Secondary producers are found in a wide range of sizes, and in the sea, predation is characterised by the predator being larger than what it consumes. In this way, energy captured by small primary producers pass through a food chain of successively larger consumers, thereby creating a specific distribution of numbers or biomass with respect to organism size. Benoît and Rochet (2004) formulated the theory into a time dependent continuous model where the dynamic of the system is driven by predation and subsequent somatic growth of the predator. The Andersen and Beyer (2006) formulation of this model excels in providing a formulation that allows for an analytic solution for equilibrium without a fishing. The model presented in this paper is basically analogous to Benoît and Rochet (2004), with some minor additions inspired by Andersen and Beyer (2006) which allow for analytical solutions for equilibrium without fishing.

The intention of the present paper is first to direct resource economic attention to a specific type of model where the dynamic in the system is driven by predation and subsequent somatic growth. The Benoît and Rochet (2004) model is therefore formulated as an ecosystem production model that allows for economic analysis of the exploitation of the marine ecosystem by a fishing. That is, it is an example of the production model required for Ecosystem Management to link from the ecosystem to the operational level. Second, because the model is meant to be an ecosystem management tool, it must be transparent in how the results in the economic analysis are

consequences of the assumptions. Additionally, results must be able to be duplicated. Therefore, in order to make the results transparent, reproducible, and extendable to other aspects important to the management of fishing, the model will be thoroughly described. This article therefore provides the underlying assumptions, a description of the implementation, a discussion of choices in the model, and possibilities for extension.

Section 2 gives a thorough description of the model and numerical implementation and parameterisation. Section 3 provides two simple experiments to establish the maximum rent point and open access point for the system. Section 4 discusses different choices made in the implementation of the model and the possibilities for extension to other dimensions. Some technical details are laid out in the appendix. These details are important for a fully comprehension of the implementation of the model, but not to understand its general structure.

2 The model

In this section, the model and numeric implementation and parameterisation are specified. The elements of the model will first be introduced in a conceptual manner, without explicit discussion of assumptions and functions. In following paragraphs, assumptions will be specified at different levels—first at a conceptual level and then at the specific functional level. Behind the model is a theory of distribution with respect to the size of the organism which follows specific rules. These rules are used to parameterise at a primary level in paragraph 2.6. In paragraph 2.7, numeric implementation is described, followed by a parameterisation of the system.

2.1 The concept

The purpose of the present model is to model a marine ecosystem based on a trophic system, with special focus on secondary production in the system. In other words, higher trophic levels are emphasised, while the input of primary producers is taken as external. The atomic production unit of this marine ecosystem is the individual fish,² and production is the somatic growth of the fish. In order to produce, the fish has to consume other fish. The fish is then also a product, a product that can be caught by humans or be internally distributed between production units. Thus, the atomic product of the marine ecosystem is the individual fish, and this product may

²The model does not make distinctions according to phylogeny. Accordingly, “fish” refers to merely an organism.

be internally allocated by a predation interaction, or may be caught by humans as an outlet from the ecosystem.

In a production model for economic analysis, mass conservation will normally be modelled into two distinct features: i) mass conservation in the allocation between production units, and ii) production as a consequence of allocated resources.¹ Mass conservation in allocation means that a resource used by a production unit must be supplied either externally or internally. That is, a consumed fish must correspond to an eaten prey if it is not supplied from external sources. Production as a consequence of allocated resources means that, in the marine ecosystem, the predator will grow only as a result of the consumed prey. Modelling every single organism in an ecosystem is impossible, so fish must be stratified appropriately. When fish are stratified, internal allocation between production units can be described as an input–output matrix with strata as both rows and columns. An ecosystem production model can then be constructed by letting the change of a group i with mass of s_i be modelled as:

$$\frac{\partial s_i}{\partial t} = F_i(w_i, z_{1,i}, z_{2,i}, \dots, s_i) - \sum_u z_{i,u} - y_i \quad (1)$$

where w_i represents a resource that is restricted to w_\bullet at the system level, and the elements $z_{u,i}$ are elements of an input–output matrix \mathbf{z} representing internal allocation as a consequence of predation. $z_{u,i}$ thus represents the quantity individuals in unit i consume from a unit u per time unit. The input–output matrix itself will be a function of \mathbf{s} : $\mathbf{z} = \mathbf{z}(\mathbf{s})$. The element y_i represents human extraction from the resource, and the production function F_i must include the maintenance, respiration and reproduction cost of the units in the group.

As mentioned previously, the fish in the model (1) are expected to be stratified *appropriately*. Stratified *appropriately* means that fish are stratified in a manner so the predator–prey interaction matrix $\mathbf{z}(\mathbf{s})$ is predictable. This predictability can be expected if the fish are stratified according to their function in the trophic system.¹ In the marine ecosystem, the function of the individual fish, seen in a trophic context, is closely related to its size. For example, two fish of the same size, but of different species, have much more in common with respect to food preference and predator risk, than, for example, two fish of the same species but of different sizes (Jennings et al., 2001; Scharf et al., 2000). Furthermore, predators in the marine ecosystem are generally considerably larger than their prey, and therefore body size is a rough indicator of trophic level (Borgmann, 1987). In other words, the distribution of individuals with respect to size can be seen as mapping the trophic system.

As a result, organisms in the sea in the model are stratified according to body mass m , referred to as size. The strata, or bins, are made infinitely small, transmuting strata

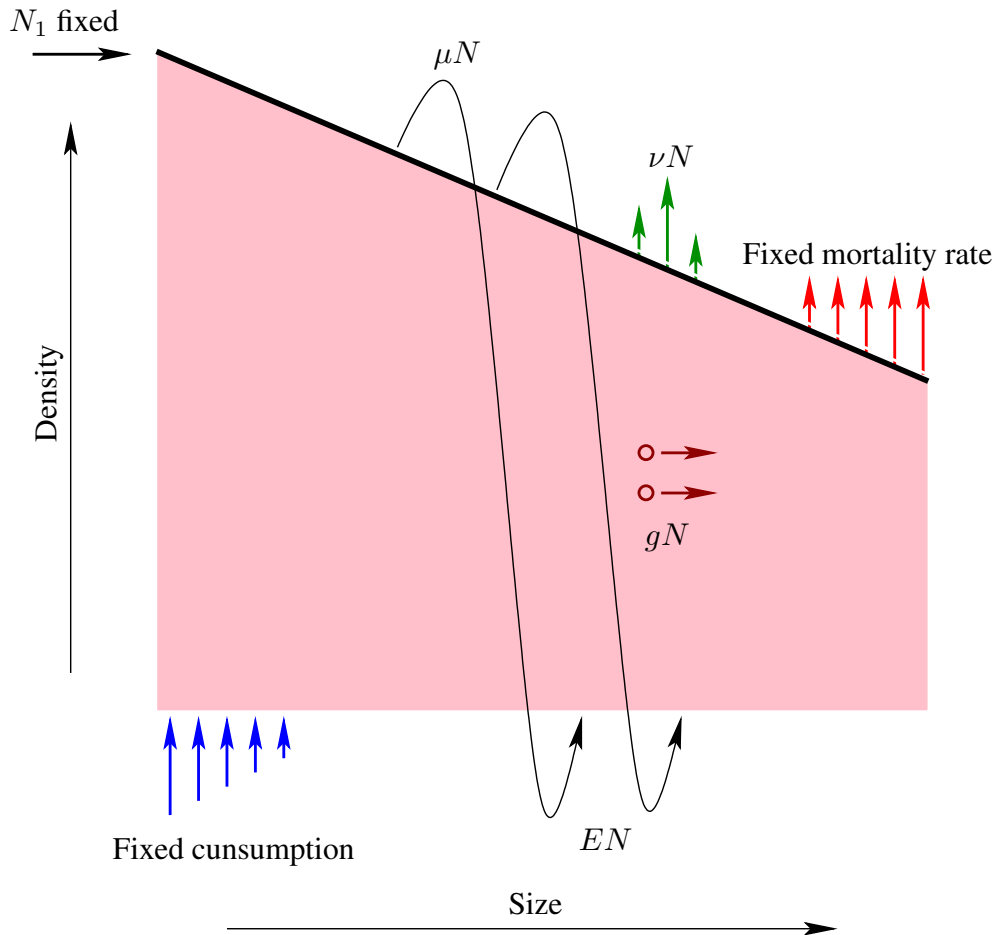


Figure 2: The elements of the model. See the text for explanation.

into a continuum of m . The models' state variable is concerned with the number of fish in the sea at a given size. The state variable $N(t, m)$ gives the density of fish of size m at time t and is referred to as the spectrum. Strictly speaking, density is defined both with respect to volume and mass. The density with respect to volume merely signifies that the model is representative of one cubic meter of water, and units are therefore in per cubic meter of sea. Density with respect to weight signifies that, in order to know the number of fish in an interval of size, for example, between m_1 and m_2 , the density must be integrated: $\int_{m_1}^{m_2} N dm$.

In figure 2, the processes in the model are illustrated. The diagram illustrates

the population spectrum with size as the abscissa and density as ordinate. The black line thus illustrates $N(m)$ and the pink illustrates that N is a density. To know the distribution of the fish, N must be integrated and hence, the area under the curve must be calculated. The N is drawn as a line. If the two axes are both logarithmic, a pristine ecosystem without fishing is expected to form a straight line with a slope of approximately -2 (Andersen and Beyer, 2006).

In the figure, two black curved arrows go from top to bottom, marked by μN at the top and EN at the bottom. These arrows represent the driver of the dynamic in ecosystem production: the predation interaction. This interaction creates a mortality of μN for the prey and leads to the consumption of EN for the predator. To be a production model there must be conservation of mass in every predation event. This is in the discrete model (1) secured by the input–output matrix z . As the strata becomes into a continuum of m , the predator–prey interaction matrix becomes, as a result, a two-dimensional interaction density. This approach preserves the principle of conservation of mass in the system—that is, for every consumed fish there is a corresponding demise.

Consumption leads to somatic growth g of the predator. Because a fish’s only attribute in this model is its size, a fish is a point in the m -dimension. When a fish grows, and therefore increases in size, its equivalent point moves up the m -dimension with speed g . The total effect of all fish with somatic growth is a flux—a number of particles passing a given point—of gN . This is in the figure 2 illustrated by the dark red points and arrows marked gN . In the model, growth is a consequence of consumed prey $g = g(E)$. Somatic growth is always smaller than consumed food, and the difference represents defecation, respiration, and reproduction.

In the top of the figure, green arrows marked νN represent mortality due to fishing, the same principle of conservation of mass applies to this interaction. What is caught has to equal what leaves the ecosystem.

From the predator–prey interaction and fishing interaction, growth and mortality are derived, and this leads to the dynamic of the spectrum. As growth leads to a flux gN of particles in the spectrum, the dynamic can be described with a flow equation controlling the state variable:

$$\frac{\partial N}{\partial t} = -\frac{\partial gN}{\partial m} - \mu N - \nu N \quad (2)$$

The partial differential equation (2), known as the Kendrick–von Foerster equation, is the main engine in the model. To turn the equation into a model, assumptions are required regarding the predator–prey interaction, growth function, and how fishing extracts fish from the system. These assumptions follow in the later paragraphs.

This description and the equation system developed below describe a spectrum with no ends. To turn this into a numerical model, the spectrum must be limited and the process related to the spectrum beyond and below the bounds must be supplied as an external impact. The model contains three external impacts:

1. Organisms in the lower end of the spectrum will have main prey outside the spectrum. This is addressed by applying fixed extra consumption to the lower end of the spectrum, represented in figure 2 by the blue arrows.
2. Organisms in the upper end of the spectrum will have main predators outside the spectrum. This is addressed by applying a fixed extra mortality rate to the upper end of the spectrum, represented in figure 2 by the red arrows.
3. The first point N_1 in the spectrum must be supplied at every iteration cycle as a boundary condition. It is in the numeric implementation supplied by a fixed value corresponding to a level without fishing.

In the following paragraphs, this conceptual model will be developed first into a mathematical description, and will be followed by numerical implementation and parameterisation. The development of the model is performed in steps from general conceptual functions towards specific functions.

2.2 The conservation of mass

A central element in the model (1), important for the model to be a production model, is the physical law of conservation of mass, represented by the input–output matrix z . This matrix tracks all predation events, and thereby allows for summations of predation events to produce system level properties. The conservation of mass in the single predation event is reflected as a mass balance on the system level—that is, the mass of all consumed prey equals the mass of all predation victims. This mass balance principle is a very strong concept for modelling, as the principle of mass conservation is an identity and therefore can be summarised to the system level without any accumulation of errors.

In the model, organisms in the sea are characterised by one attribute: mass $m \in \mathbb{R}_+$. The main function of the trophic system, when secondary production is the focus, is the predator–prey interaction represented by z in model (1). Because strata have been transformed into a continuum of m , the predator–prey interaction matrix becomes, as a result, a two-dimensional interaction density. The distribution of the predator–prey interaction will thus be described by the two-dimensional interaction density

$\Phi(m_p, m_r)$, given the density of the interaction between prey with mass m_p and predator with mass m_r . The density of mortality of prey with mass m_p , in figure 2 indicated by μN , can then be found as $\int_0^\infty \Phi(m_p, m_r) dm_r$. The density of consumed mass by predators with mass m_r , in figure 2 indicated by EN , will be $\int_0^\infty m_p \Phi(m_p, m_r) dm_p$. If the mass of predation victims and the consumption of predators are integrated over prey and predators, respectively, the two-dimensional interaction density produces the mass balance of the system as

$$\int_0^\infty m_p \int_0^\infty \Phi(m_p, m_r) dm_r dm_p \equiv \int_0^\infty \int_0^\infty m_p \Phi(m_p, m_r) dm_p dm_r \quad (3)$$

On the left-hand side, the biomass of all consumed prey is indicated and on the right-hand side, the biomass of all predators' consumption is indicated. This mass balance identity (3), where the mortality and consumption are calculated on their respective sides, serves as a foundation for the model. It has two concepts: the individuals described by their respective mass as a continuum, and the two-dimensional predator–prey interaction density describing the allocation caused by predation.

2.3 Assumptions

In the mass balance identity (3) of the predation interaction, there are no assumptions besides the law of conservation of mass. To expand this mass balance identity into a model, assumptions are required for i) how fish are distributed in the sea, ii) how the predator–prey interaction can be described, iii) how consumed mass will be converted into somatic growth of the individual, and iv) how mortality not covered by the predator–prey interaction can be described. These assumptions will be submitted as conceptual functions before specific functions employed in present model are presented in paragraph 2.4.

1. **The distribution in the sea.** This model assumes that individuals have been distributed randomly and independently in the sea as by a Poisson process. The density of individuals in the sea N , in figure 2 illustrated by the black line, is thus a function of only time t and mass of the individuals m

$$N = N(m, t) \quad (4)$$

but independent of location in the sea. The dimension of N is individuals per volume per mass, so strictly speaking N is a density both with respect to space and mass, where the former is a consequence of random distribution assumed equally throughout the sea.

2. **The predation.** The interaction between predator and prey is governed by i) a predator preference function $\phi(m_p, m_r) \in [0, 1]$ (with a dimension of individuals⁻²) indicating predators with mass m_r preference for prey with mass m_p , and ii) the predators search volume $v(m_r)$ (dimension volume per time), and iii) a functional response f . A functional response is the relationship between the available prey and the consumption of the predator (Holling, 1959). In the formulation of the present model, the functional response $f \in]0, 1]$ with $f = 1$ for no available food and decreasing with increasing availability of prey, approaches zero for an infinite amount of prey.³

A predator with a search volume of v will, as trawls the sea, encounter other fish in its search volume. The density of fish with mass m_p within the search volume of a fish with mass m_r will be $N(m_p)v(m_r)$. If the fish has a preference for the fish it encounters given by ϕ , there is a density of potential interaction $\bar{\Phi}$:

$$\bar{\Phi}(m_p, m_r) = v(m_r)\phi(m_p, m_r)N(m_p)N(m_r) \quad (5)$$

(dimension is per volume per weight per time). The predator is, however, limited in its consumption by of functional response $f(\bar{\Phi}, m_r)$. The realised interaction density is then:

$$\Phi(m_p, m_r) = \bar{\Phi}(m_p, m_r)f(\bar{\Phi}, m_r) \quad (6)$$

The density of mortality for prey with mass m_p is determined by:

$$\mu(m_p)N(m_p) = \int_0^\infty \Phi(m_p, m_r) dm_r \quad (7)$$

where μ is a hazard function or the instant mortality rate with dimension per time per individual

The density of consumption with respect to predators with mass m_r is then determined by:

$$E(m_r)N(m_r) = \int_0^\infty m_p\Phi(m_p, m_r) dm_p \quad (8)$$

where E is the expected consumption for a predator with mass m_r with dimension weight per time.

³Functional response is, in economic terms, an expression of the declining marginal production-capacity of the predator with respect to prey.

3. **Somatic growth.** Ingested food used by the fish ultimately results in defecation, respiration, reproduction, and growth. The expected growth of the individual is assumed to be described by a function of expected consumption:

$$\text{Expected} \left(\frac{dm}{dt} \right) = g(E) \quad (9)$$

When a fish increases its weight, it will move up in this system's mass dimension with speed $\frac{dm}{dt}$. The flow of individual fish up through the mass dimension will, at a specific point on the mass dimension, be expressed as a flux, or the number of individuals passing the point per time. So, somatic growth prompts, as a result of (9), a flux of gN , which is illustrated in figure 2 by dark red arrows marked gN .

4. **Other mortality.** The only mortality besides predation considered in the present model is the mortality caused by fishing. Even though it in assumption 1 is assumed that the distribution of fish is independent, fish in reality are clustered and fishermen target a specific size. This is modelled by assuming that fishing vessels trawl the sea with a fishing selection function of $\theta(m, m_f)$, indicating the gear and fisher "preference" for fish of mass m when vessels have target m_f . Fishing vessels distribute effort, so the density of effort of all vessels in combination can be described by $\Upsilon = \Upsilon(m_f, t)$. Fishing can then be described as a density of fishing interaction Θ :

$$\Theta(m, m_f) = \theta(m, m_f)N(m)\Upsilon(m_f) \quad (10)$$

In the population, the impact is a fishing mortality hazard ν determined by:

$$\nu(m)N(m) = \int_0^\infty \Theta(m, m_f) dm_f \quad (11)$$

and the resulting harvest density H with respect to target size m_f :

$$H(m_f) = \int_0^\infty m \Theta(m, m_f) dm \quad (12)$$

By integrating (11) over fish size m and (12) over vessel target m_f the mass balance identity in the fishing interaction are produced:

$$\int_0^\infty m \int_0^\infty \Theta(m, m_f) dm_f dm \equiv \int_0^\infty \int_0^\infty m \Theta(m, m_f) dm dm_f \quad (13)$$

with the total mass of victims of fishing on the left-hand side and the total mass of the harvest on the right-hand side.

Recall that a consequence of the approach describing the population as a density on a continuous mass dimension is that the individual fish is a point in the mass dimension. When the individual fish exhibits somatic growth, it will move up the mass dimension. The somatic growth of all the individual fish will therefore be equivalent to a flow of particles in the mass dimension. Therefore, the McKendrick-von Foerster equation (2) can be employed to model the dynamic of the system in numeric implementation.

2.4 Functions for modelling

To construct a mathematical model out of the concepts and assumptions of paragraphs 2.2 and 2.3, this section supplies the specific functions applied in the present model. These functions are inspired by Andersen and Beyer (2006), and chosen because they allow for analytic solutions to a system without fishing. Table 1 gives an overview of all symbols used. The mathematical model consists of the following parts:

- The preference function, which determines the preference of predators for prey, corresponds to a log normal probability density:

$$\phi(m_r, m_p) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\left(\frac{\log\left(\frac{m_r}{m_p\beta}\right)}{\sigma}\right)^2\right) \quad (14)$$

where β is the characteristic predator prey mass ratio and σ is a measure of the breadth in the search pattern.⁴

- For the search volume function is used:

$$v(m_r) = \gamma m_r^q \quad (15)$$

where γ , the search volume prefactor, and q , the search volume exponent, are parameters.⁵

⁴The parameter σ corresponds to the breadth parameter σ' in the erratum to Andersen and Beyer (2006) as $\sigma = \sqrt{2\sigma'}$

⁵The prefactor γ must to correspond to the prefactor γ' in Andersen and Beyer (2006) be $\sigma\sqrt{2\pi}$ times bigger i.e., $\gamma = \sigma\sqrt{2\pi}\gamma'$

Table 1: Symbols used in the model

Symbol	Description	Unit	Type
m	Mass of fish	g	Variable
t	Time	s	Variable
N	Density of fish	$\text{m}^{-3}\text{g}^{-1}$	Dependent
ϕ	Preference	–	Function
Φ	Interaction density	$\text{m}^{-3}\text{g}^{-2}\text{s}^{-1}$	Function
v	Search volume	$\text{m}^{-3}\text{s}^{-1}$	Function
f	Functional response	–	Function
μ	Mortality hazard	s^{-1}	Function
E	Consumption	g s^{-1}	Function
g	Growth	g s^{-1}	Function
θ	Fishing selection	–	Function
Θ	Fishing interaction density	$\text{m}^{-3}\text{g}^{-2}\text{s}^{-1}$	Function
ν	Fishing mortality hazard	s^{-1}	Function
ς	Breadth of fishing selection	–	Control
Υ	Effort density	$\text{m}^{-3}\text{g}^{-1}$	Control
H	Harvest density	$\text{m}^{-3}\text{s}^{-1}$	Output
R	Revenue density	$\text{\$ m}^{-3}\text{s}^{-1}\text{g}^{-1}$	Output
C	Cost density	$\text{\$ m}^{-3}\text{s}^{-1}\text{g}^{-1}$	Output
P	Price	$\text{\$ g}^{-1}$	External
c	Cost per. effort	$\text{\$ s}^{-1}$	External
σ	Food preference breadth	–	Parameter
β	Characteristic predator prey ratio	–	Parameter
γ	Search volume prefactor	$\text{m}^3\text{s}^{-1}\text{g}^{-q}$	Parameter
q	Search volume exponent	–	Parameter
h	Maximum food intake prefactor	$\text{g}^{n-1}\text{s}^{-1}$	Parameter
n	Maximum food intake exponent	–	Parameter
ϵ	Food conversion factor	–	Parameter
κ	Spectrum density prefactor	$\text{g}^{\lambda-1}\text{m}^{-3}$	Parameter
λ	Slope of equilibrium spectrum	–	Parameter

- For the functional response a Holing type II functional response is used:

$$f(\bar{\Phi}, N, m_r) = \left(1 + \frac{\int_0^\infty m_p \bar{\Phi}(m_p, m_r) dm_p}{hm_r^n N(m_r)} \right)^{-1} \quad (16)$$

where h and n are parameters. As

$$\left(1 + \frac{\bar{\Phi}}{hm_r^n N} \right)^{-1} \xrightarrow{\frac{\bar{\Phi}}{N} \rightarrow \infty} hm_r^n$$

hm_r^n can be interpreted as the individual's maximum food intake under infinite food supply. h is then the maximum food intake prefactor and n is the maximum food intake exponent.

Note that the integral in equation (16) equals the total consumption if there were no functional response. This will be proportional with $N(m_r)$, which can be cancelled out of the fraction. The fraction is therefore the expected consumption of the individual if there were no functional response divided by maximum food intake. f is then decreasing and a strictly concave function of the density of any prey size and has a value between zero and one.

- For the growth function a simple conversion of food into growth by a conversion factor ϵ is used:

$$g = \epsilon E \quad (17)$$

In the presence of an assumption of a power law for the biomass size spectrum, the conversion parameter ϵ , as it follows from appendix 2.6, is determined from the other parameters.

- The fishing selection function, which determines the “preference” for fish of size m when the target of the vessel is m_f , corresponds to a log normal probability density:

$$\theta(m, m_f) = \frac{1}{\varsigma\sqrt{2\pi}} \exp \left(-\frac{1}{2} \left(\frac{\log \left(\frac{m}{m_f} \right)}{\varsigma} \right)^2 \right) \quad (18)$$

where ς is a measure of the breadth of the fishing pattern of the vessel. Both ς and the effort density Υ are control parameters.

2.5 The economic model

Fishing vessels are exploiting the resource with a target of m_f , a breadth of ς and a density of effort Υ . The total effort V (proportional to the number of fishing vessels per day) in the interval Ω can be calculated as:

$$V = \int_{\Omega} \Upsilon(m_f) dm_f \quad (19)$$

The fishing fleet will have a density of revenue and cost of:

$$R(m_f, \Upsilon) = \int_0^{\infty} P m \Theta(m, m_f) dm \quad (20)$$

$$C(m_f, \Upsilon) = c\Upsilon \quad (21)$$

where $P = P(m)$ is the value per weight of landed fish, and c is the cost of applying a unit of effort. The total revenue and cost in monetary value per volume per time is, respectively,

$$TR(\Upsilon) = \int_0^{\infty} R(m_f, \Upsilon) dm_f \quad (22)$$

$$TC(\Upsilon) = c \int_0^{\infty} \Upsilon(m_f) dm_f \quad (23)$$

2.6 The equilibrium spectrum

Behind the formulation of this model, based on many years of observation following Sheldon et al. (1972) and Sheldon et al. (1973), is an expectation that the spectrum, in the absence of fishing, has a steady state solution where the spectrum can be described by a power law. In other words, an equilibrium population density exists:

$$\overset{\star}{N} = \kappa m^{-\lambda} \quad (24)$$

where κ is a prefactor describing the magnitude of the spectrum and the exponent λ is the “slope” of the spectrum. This steady state solution without fishing will be referred to as the equilibrium spectrum. Andersen and Beyer (2006) found that the exponent λ , with formulation of functions as in paragraph 2.4 and with the additional assumption of all individuals in an equilibrium spectrum having the same functional response $\overset{\star}{f}$, can be described by the physiological parameters of the individual fish by:

$$\lambda = 2 + q - n \quad (25)$$

As can be seen in appendix A, where the equilibrium spectrum is analysed, the parameters in the model are interlinked. If n and q are given, the model additionally has seven other parameters: σ , β , ϵ , γ , h , κ and \tilde{f} . If five of these are given, the rest follow. In addition, as can be seen in appendix A, some constants can be calculated both analytically and numerically, and thereby validates the numerical implementation.

2.7 Numerical implementation

In this section, the numeric implementation of the equation system, as set up in previous paragraphs, is described. The purpose is to make a simulation model where the model system can be used as an experimental ecosystem where fishing is the treatment or control. The output will be the harvest and its revenue and the resulting state of the ecosystem represented by the density spectrum.

Representing results from analysis of the biomass or number spectrum in double logarithmic diagrams is common because this gives an easily visualised interpretation. For example the equilibrium population \tilde{N} , if it follows equation (24), will show up as a straight line. The view of mass and number spectra are generally the most meaningful if, at least, the scale of mass is equidistant in the logarithm to the mass. Setting a grid equidistant in the logarithm to the mass, if measured in the mass dimension, means that the grid distance Δm will change throughout the grid, making numeric calculus operations awkward. Therefore, in agreement with the approach of Benoît and Rochet (2004), the whole equation system given above is transformed into functions of x where $m = \exp(x)$. Thus, the grid distance Δx will be fixed and numerical calculus operations are straightforward. At the same time, the dimension x will impute a trophic view onto the system. Because the predator–prey ratio b is constant through the system, the x dimension can approximately be linear transformed into trophic level τ by

$$\tau(x) \approx a + \frac{x}{\log(b)}$$

where b is the predator–prey ratio and a is a constant:

$$a = 1 - \frac{\log(m_1)}{\log(b)}$$

where m_1 is the typical mass of primary producers.

The transformation from mapping against mass m into mapping against x where $m = \exp(x)$ will, at the same time, transform the target of vessels from m_f to ξ on the same scale as x , where $m_f = \exp(\xi)$. The dimension of ξ and x is, of course, the

same, but it is kept separate because fishing is not performed all over the spectrum. The grid of ξ does therefore not need to encompass the entire grid of x . By keeping x and ξ separated, computation can therefore be eased. Table 2 gives an overview of the transformed equations.

The fish community is represented by J data points (x_j, N_j) , $j = 1, 2, \dots, J$ in the log-mass \times population-density space. The points in the log-mass dimension are fixed and equally spaced with a distance of Δx . The fishing fleet is represented by L data points (ξ_l, Υ_l) , $l = 1, 2, \dots, L$ in the log-target-mass \times effort-density space. Points in the ξ dimension are fixed and equally spaced with a distance of $\Delta \xi$.

The main engine of the numeric implementation is the transformed flow equation:

$$\frac{\partial N}{\partial t} = -\frac{\partial gN}{\partial x} e^{-x} - \mu N - \nu N \quad (26)$$

This partial differential equation is transformed into a discrete approximation:

$$\frac{\Delta N_j}{\Delta t} = -\frac{\Delta (g_j N_j)}{\Delta x} e^{-x_j} - \mu_j N_j - \nu_j N_j \quad (27)$$

and an iteration routine calculates the value of N in the population density dimension with time steps of Δt .

To secure stability in the system, an upwind scheme (Press et al., 2007) is used. In an upwind implementation $g_j N_j - g_{j-1} N_{j-1}$ is used as $\Delta (g_j N_j)$. However, the system can be further stabilised by the additional use of an implicit formulation.⁶ In an upwind implicit formulation $g_{j,t} N_{j,t+\Delta t} - g_{j-1,t} N_{j-1,t+\Delta t}$ is applied as $\Delta (g_j N_j)$ (implicit only in N). The flow equation in the upwind implicit formulation appears similar to:

$$\begin{aligned} \frac{N_{j,t+\Delta t} - N_{j,t}}{\Delta t} = & -\frac{g_{j,t} N_{j,t+\Delta t} - g_{j-1,t} N_{j-1,t+\Delta t}}{\Delta x_j} e^{-x_j} \\ & - \mu_{j,t} N_{j,t+\Delta t} - \nu_{j,t} N_{j,t+\Delta t} \end{aligned} \quad (28)$$

This equation is rearranged so that terms of N are collected:

$$\begin{aligned} N_{j,t} = & N_{j-1,t+\Delta t} \underbrace{\left(-\frac{g_{j-1,t} \Delta t}{\Delta x} \right)}_{A_j} \\ & + N_{j,t+\Delta t} \underbrace{\left(1 + \frac{g_{j,t} \Delta t}{\Delta x_j} + \mu_{j,t} \Delta t + \nu_{j,t} \Delta t \right)}_{B_j} \end{aligned} \quad (29)$$

⁶K. H. Andersen, personal communication

Table 2: Equations with x as variable

Mass	$m(x) = e^x$
Equilibrium density	$\overset{\star}{N}(x) = \kappa e^{-\lambda x}$
Search volume	$v(x) = \gamma e^{qx}$
Predator preference	$\phi(x_p, x_r) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\left(\frac{x_r - x_p - \log\beta}{\sigma}\right)^2\right)$
Potential interaction	$\bar{\Phi}(x_p, x_r) = v(x_r)\phi(x_p, x_r)N(x_p)N(x_r)$
Functional response	$f(\bar{\Phi}, N, x_r) = \left(1 + \frac{\int_{-\infty}^{\infty} \bar{\Phi}(x_p, x_r) (e^{x_p})^2 dx_p}{hNe^{nx}}\right)^{-1}$
Realised interaction	$\Phi(x_p, x_r) = \bar{\Phi}(x_p, x_r)f(\bar{\Phi}, x_r)$
Expected mortality	$\mu(x_p)N(x_p) = \int_{-\infty}^{\infty} \Phi(x_p, x_r)e^{x_r} dx_r$
Expected consumption	$E(x_r)N(x_r) = \int_{-\infty}^{\infty} \Phi(x_p, x_r) (e^{x_p})^2 dx_p$
Fishing selection	$\theta(x, \xi) = \frac{1}{\varsigma\sqrt{2\pi}} \exp\left(-\frac{1}{2}\left(\frac{x - \xi}{\varsigma}\right)^2\right)$
Fishery interaction	$\Theta(x, \xi) = \theta(x, \xi)N(x)\Upsilon(\xi)$
Fishing mortality	$N(x)\nu(x) = \int_{-\infty}^{\infty} \Theta(x, \xi)e^{\xi} d\xi$
Harvest density	$H(\xi) = \int_{-\infty}^{\infty} \Theta(x, \xi) (e^x)^2 dx$
Revenue density	$R(\xi, \Upsilon) = \int_{-\infty}^{\infty} p\Theta(x, \xi) (e^x)^2 dx$
Cost density	$C(\xi, \Upsilon) = c\Upsilon$
Total revenue	$TR(\Upsilon) = \int_{-\infty}^{\infty} R(\xi, \Upsilon)e^{\xi} d\xi$
Total cost	$TC(\Upsilon) = c \int_{-\infty}^{\infty} \Upsilon(\xi)e^{\xi} d\xi$
The flow equation	$\frac{\partial N}{\partial t} = -\frac{\partial gN}{\partial x}e^{-x} - \mu N - \nu N$

Then, by first calculating vectors \mathbf{A} and \mathbf{B} and supplying $N_{1,t+\Delta t}$, the rest of $\mathbf{N}_{t+\Delta t}$ can be calculated as:

$$N_{j,t+\Delta t} = \frac{N_{j,t} - N_{j-1,t+\Delta t}A_j}{B_j} \quad (30)$$

where vectors \mathbf{A} and \mathbf{B} are

$$A_j = -\frac{g_{j-1,t}\Delta t}{\Delta x} \quad (31)$$

$$B_j = 1 + \left(\frac{g_{j,t}}{\Delta x_j} + \mu_{j,t} + \nu_{j,t} \right) \Delta t \quad (32)$$

Details related to the values of $N_{1,t+\Delta t}$ and A_1 are given in appendix B.

At every iteration step, the interaction densities Φ and Θ are calculated for all grid points expanded to two dimensions (prey \times predator and fish \times fishing, respectively) by the functions given in table 2. The vectors of gN , μN and νN are calculated by approximating integrals using summation over the grid point. Corrections for moving from infinite to finite intervals are treated below.

2.8 Boundary and initial values

The model needs to be supplied with a set of initial values for N for $t = 0$. Any \mathbf{N} will work, but if nothing else is stated, the model begins from the equilibrium spectrum:

$$\mathbf{N}_{t=0} = \mathbf{N}^* \quad (33)$$

In the model description, there is no consideration of how and where the spectrum starts and ends. The model only gives the trophic system for secondary producers with both prey and predators. The model will then simulate an interval of an infinite spectrum. In appendix B.2, details related to incorporating the part of the spectrum that is outside the model as an external influence are described. It consists, as mentioned in paragraph 2.1, of three parts.

1. Organisms in the lower end of the spectrum will have main prey outside the spectrum. This is addressed by applying fixed extra consumption to the lower end of the spectrum, represented in figure 2 by the blue arrows. When the input to the model system is fixed, different levels of fishing will not affect the input. Therefore, the economic inference relates solely to the dynamic caused by the predator-prey interaction and not from changes in external input.

2. Organisms in the upper end of the spectrum will have main predators outside the spectrum. This is addressed by applying a fixed extra mortality rate to the upper end of the spectrum, represented in figure 2 by the red arrows. Applying a fixed rate of mortality, not just a fixed level of mortality, ensures that when the population density drops, so does the external mortality.
3. The first point N_1 in the spectrum must be supplied at every iteration cycle as a boundary condition, and is supplied as the equilibrium level without fishing.

Additionally, in the appendix B.1 correction of errors related to the implicit upwind scheme is considered.

2.9 Setting the parameters

The model contains several parameters related to the theoretical model and numeric implementation. Some parameters in the theoretical model are related to observable properties in nature and can, therefore be empirically parameterised. Included in this group are the parameters of the equilibrium spectrum, i.e., magnitude κ and slope λ . The present model builds on a theory where the macroscopic observation, the spectrum, is explained by a behavioural and physiological theory of the individual fish. There is little hope for empirical parameterisation of specific parameters in the behavioural model. However, the consequences of the behaviour in the form of the total interaction density Φ is, in principle, observable. If the equilibrium spectrum is assumed to be observed with the interaction density, there is still some margin left where the parameters must be selected based on the preferred behaviour of the model system, at least until a better approach is available. In appendix C, this is performed, along with the parameters related to numeric implementation. An overview of the values assigned to the parameters in the implementation of the model is given in table 3 and 4.

Regarding the parameters of the numerical implementation, the ideal would be that the numerical implementation do not add anything to the behaviour of the model system. This is not possible. However, what can be achieved is, through proper parameterisation of the numeric model, minimising the numeric implementation's influence on the system. There will, however, always be a trade-off between computation time and reduction in the numeric implementation's influence. Thus, the goal is to achieve a proper balance.

Table 3: Parameters in the biological model

Symbol	Description		Unit	
σ	Food preference breadth	1.8	–	a)
β	Characteristic predator prey ratio	100	–	b)
q	Search volume exponent	0.8	–	b)
f^*_{γ}	Characteristic search volume prefactor	2000	$\text{m}^3\text{year}^{-1}\text{g}^{-q}$	c)
f^*	Equilibrium functional response	0.5	–	a)
n	Maximum food intake exponent	0.75	–	b)
κ	Spectrum density prefactor	0.005	$\text{g}^{1+q-n}\text{m}^{-3}$	c)
γ	Search volume prefactor	4000	$\text{m}^3\text{year}^{-1}\text{g}^{-q}$	d)
h	Maximum food intake prefactor	25.3	$\text{g}^{n-1}\text{year}^{-1}$	d)
ϵ	Food conversion factor	0.213	–	d)
λ	Slope of equilibrium spectrum	2.05	–	d)

a) Tested in appendix C

b) After Andersen and Beyer (2006)

c) Set to resemble the North Sea (K. H. Andersen, personal communication)

d) Derived as explained in appendix

Table 4: Properties of the grid

Symbol	Description			
Δt	Time step	1/6	year	a)
J	Number of grid points, biological	141	–	a)
x_1	Smallest grid point, biological	0	$+\log(\text{g})$	
x_J	Largest grid point, biological	14	$+\log(\text{g})$	
L	Number of grid points, fishery	variably	–	
ξ_1	Smallest grid point, fishery	variably	$+\log(\text{g})$	
ξ_L	Largest grid point, fishery	variably	$+\log(\text{g})$	

a) Tested in appendix C

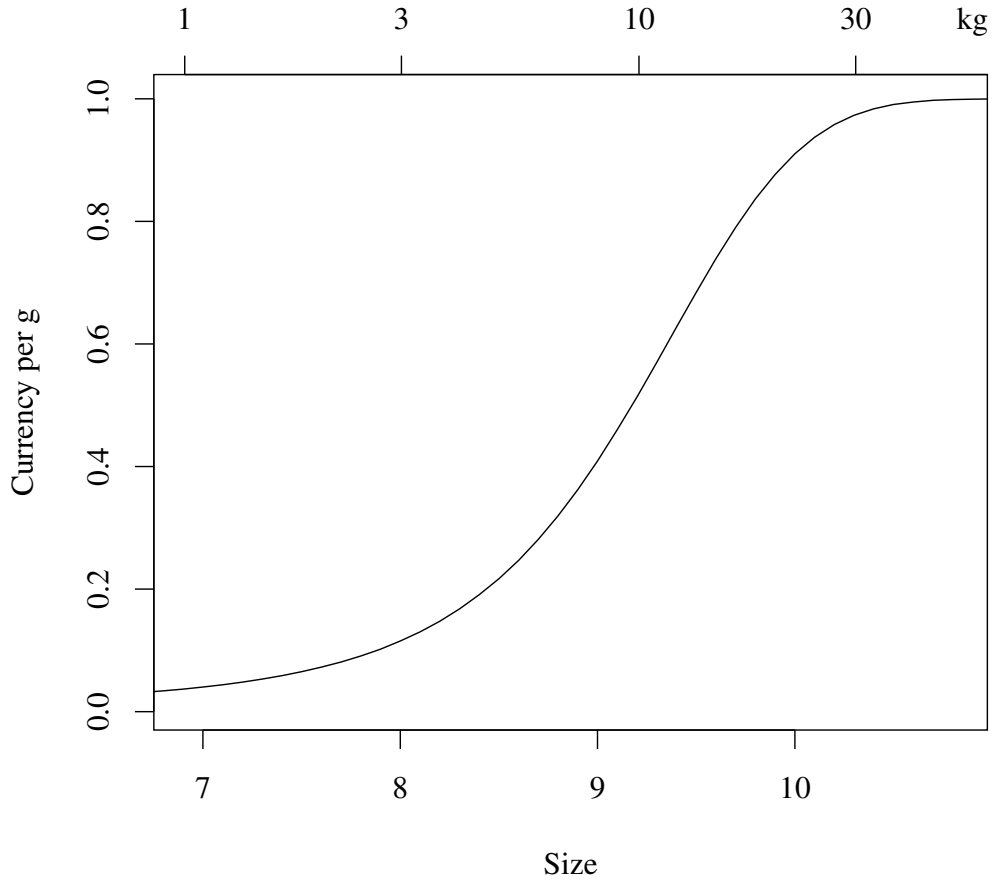


Figure 3: The price function used in the experiment

3 Experiments

3.1 Methods

To illustrate and evaluate the model, two experiments are performed: A) An experiment to find the sustainable production and sustainable rent level, and B) an experiment to find the open access solution using adaptive fishing agents.

In both experiments, a sigmoid price function is used:

$$P(m) = (1.0375 \exp(-3.0895268 \exp(-0.0001603 m)) - 0.0375) \text{ \$ g}^{-1}$$

illustrated in figure 3 and a fixed cost of

$$c = 0.0004 \text{ \$ m}^{-3}$$

where the \$ is used as a symbol for an arbitrary currency. The breadth parameter ς is disregarded in the fishing selection function as a control and kept fixed at $\varsigma = 1$. See appendix C.5 for details related to ς .

Experiment A

In the experiment, fishing is limited to target one size. Different treatments are given in the form of different effort levels and target sizes for fishing. The model system is run for each treatment until convergence to a steady state where the output in the form of population density, harvest amount, revenue, and cost is recorded as one observation. In total, there are 1,320 applied treatments. For details, see below.

Convergence criteria The numerical model is run until a coefficient of variation CV of any point in the \mathbf{N} is smaller than 10^{-5} for the last twenty-five years

$$CV_j < 10^{-5} \forall j; CV_j = CV(\mathbf{X}_j) | \mathbf{X}_j = \{N_{j,t}, N_{j,t-1}, \dots, N_{j,t-24}\}$$

This is interpreted as convergence to a steady state solution. After convergence, the system is run for an additional twenty-five years and the means of population density, harvest and revenue are recorded together with other relevant observation. If this convergence is not reached within 1,000 years, the iteration routine is stopped and the observation is marked as “no convergence”.

Fishing parameters The fishing effort is concentrated to a single point, $L = 1$, and the $\exp(\xi)\Delta\xi$ is, for convenience set to one, leaving the density of effort in the only point Υ_1 equal to the total effort V (proportional to the number of vessels).

$$V = \Upsilon_1 e^\xi \Delta\xi = \Upsilon_1$$

The $\xi \times V$ space is examined by testing all combinations of

$$\xi \in \{8.0, 8.1, \dots, 11.9, 12.0\}, \quad V \in \{0.001, 0.01, 0.1, 0.2, 0.3, \dots, 2.9, 3.0\}$$

given a total of 1,320 observations.

Experiment B

The experiment starts from a steady state without fishing. Fishing is added with the same grid distance as the population grid $\Delta\xi = \Delta x$. Fishing is initiated with effort density Υ set to 10^{-5} for all points. After each iteration step, the profit density is evaluated. If the profit is positive at a specific size, effort is increased at that point, and if it is negative, the effort is decreased. The adaptation routine works on the ratio between the density of revenue R and the density of cost C , and an adjustment parameter ϑ . The next period's effort is calculated as:

$$\Upsilon_{j,t+\Delta t} = \begin{cases} \Upsilon_{j,t} \left(1 + \frac{10\vartheta R_{j,t}}{C_{j,t}} \right) & \text{if } \frac{R_{j,t}}{C_{j,t}} < 1 \\ \Upsilon_{j,t} \left(1 + \frac{\vartheta R_{j,t}}{C_{j,t}} \right) & \text{if } \frac{R_{j,t}}{C_{j,t}} \geq 1 \end{cases}$$

The adjustment is then ten times more powerful for losses compared to profits. This is an experience-based adjustment. Without this more powerful reaction on losses, the system often exhibits intense oscillation and pulls fishing. The same behaviour can be a result of an excessively large value of ϑ . In the experiment $\vartheta = 0.1$ and the system is run until the system reaches convergence criteria for a steady state. The parameterisation of this function is totally *ad hoc*, with the purpose of finding the open access steady state point. With another parameterisation of the adaptation function, a steady state may not be reached.

3.2 Results

Experiment A

All treatments of Experiment A have reached criteria for convergence. Each observation is composed of an input in the form of a target ξ and an effort V . In steady state, this leads to an output in the form of a harvest with the properties of total harvest volume H_\bullet and a mean size of harvest \bar{x} . In figure 4, the physical output is shown as a surface in the control space, $\xi \times V$ space. Note that the landed mean size is smaller than the target size, and that the mean size decreases with an increase in effort if the target size is fixed. In figure 5, the control parameters are shown as surfaces in sustainable yield space, $\bar{x} \times H_\bullet$ space. The figure illustrates that the set of possible sustainable yields is curtailed to the lower left part. If a sustainable yield is close to the upper boundary, a marginal increase in sustainable harvest volume will require a relatively high increase in effort, and at the same time, the target size must be increased if mean size of harvest must be maintained.

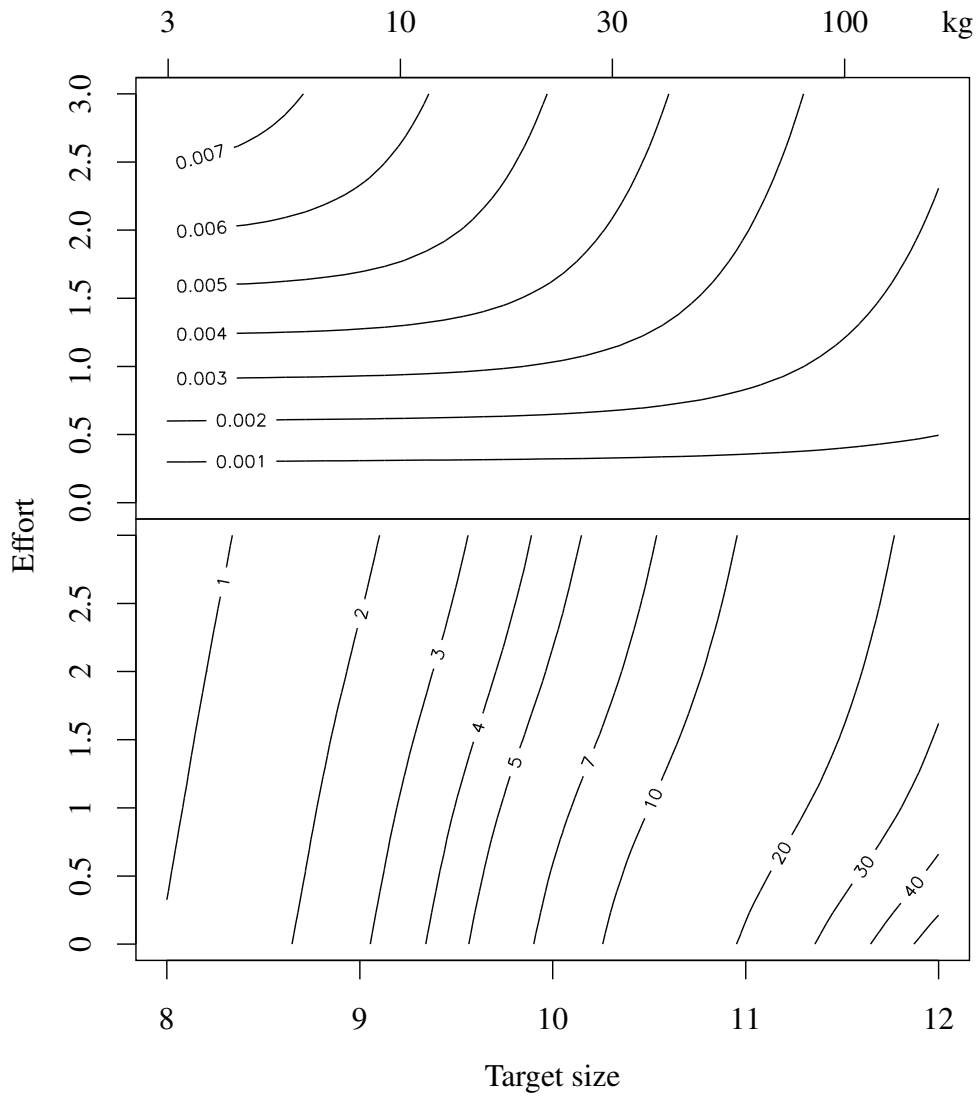


Figure 4: Sustainable physical output from Experiment A presented as surface in the control space, target size \times effort space. In the upper diagram harvest volume in $\text{g m}^{-3}\text{year}^{-1}$ is shown and in the lower diagram, the mean size of harvest in kg is shown .

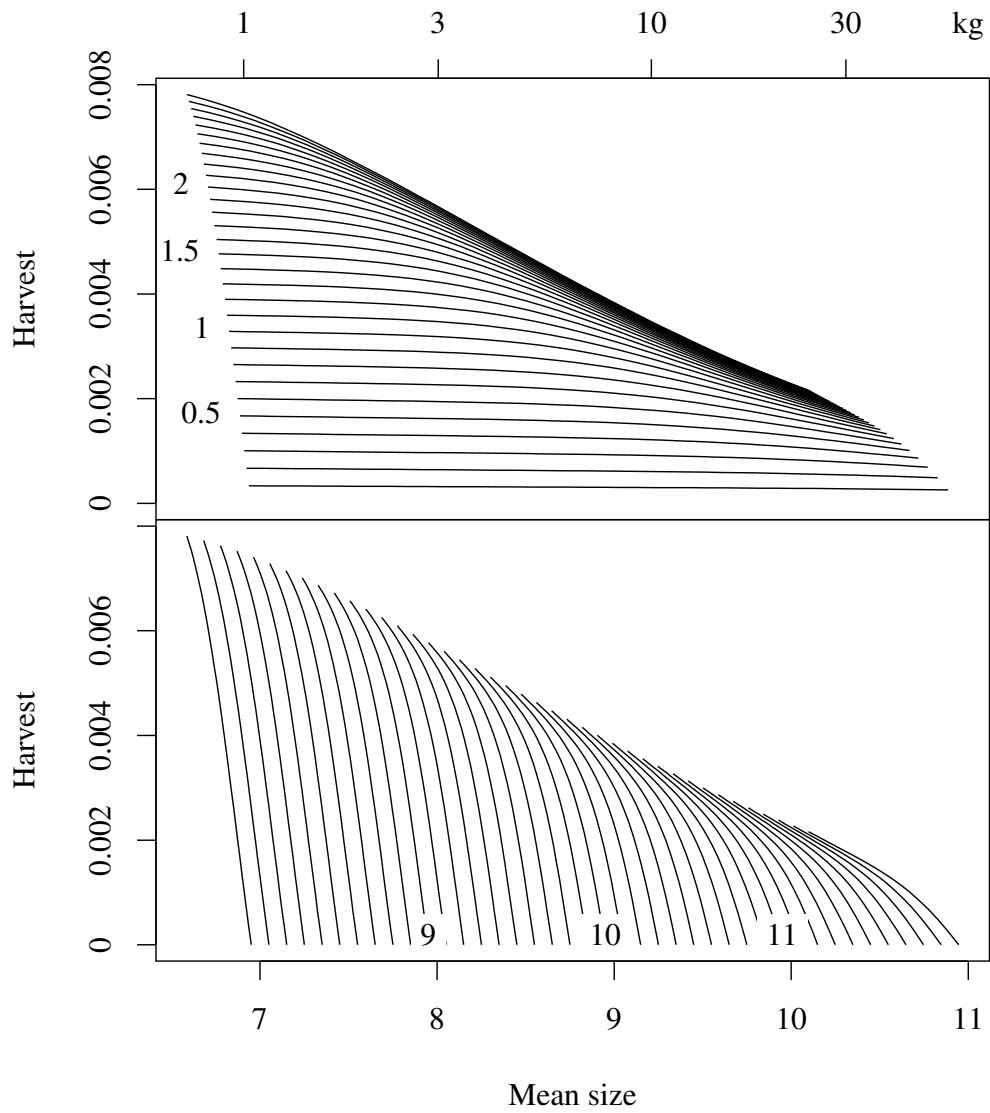


Figure 5: Control variables relationship with physical output in Experiment A. In the upper diagram the target size is shown, and in the lower diagram effort is shown as surface in the sustainable yield space, mean size \times harvest volume space.

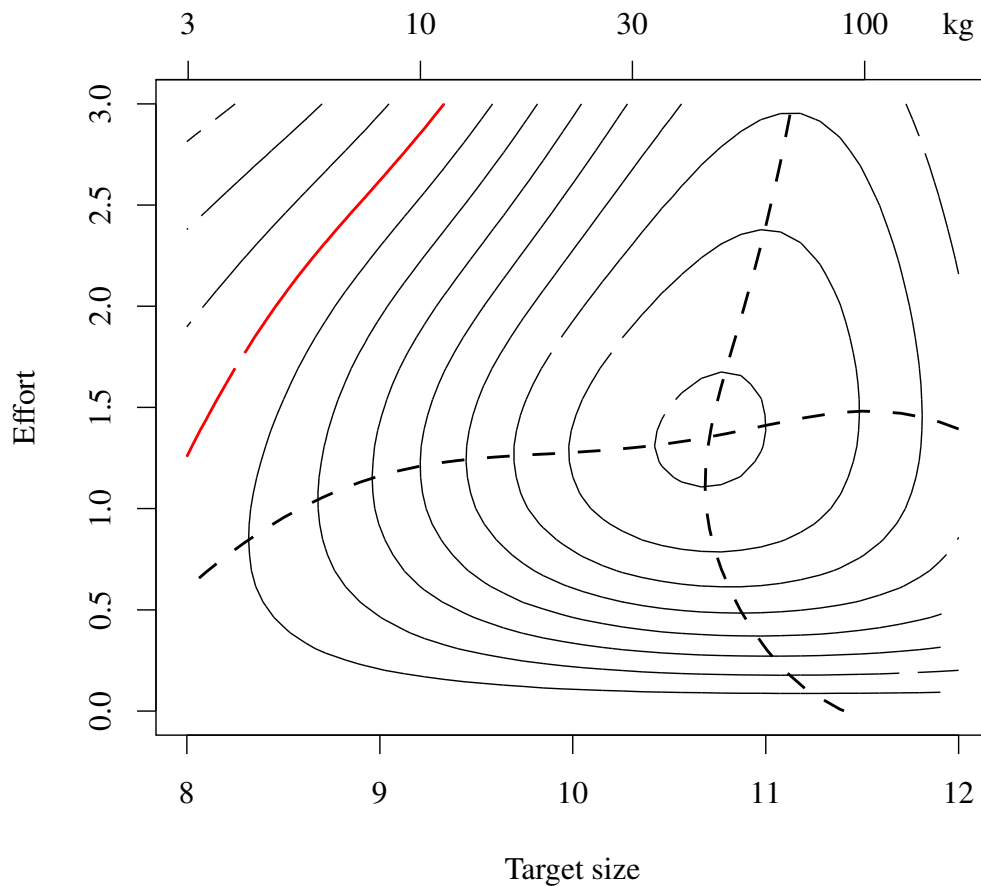


Figure 6: The diagram shows rent contours in the control space; target size \times effort space. The red line is the zero rent contour, while the stationary point is the maximum rent point. The vertical dashed-line indicated the points of maximum rent given a fixed effort, while the horizontal dashed-line indicates points of maximum rent given fixed target size.

When harvest and effort are transformed into monetary units, the output is summarised in total cost TC and total revenue TR , resulting in a rent π . Figure 6 shows the sustainable yield rent surface in the control space. The rent surface is concave with a well-defined maximum rent point.

Experiment B

In Experiment B, the population reaches convergence after 4,399 years. The effort density, controlled by adaptive fishermen, does not reach criteria for convergence, but continuous small adjustments with a coefficient of variation around 0.28. In figure 7, effort density and population density are presented in black, and for a comparison, these are shown for the maximum rent scenario in Experiment A. The population density is plotted relative to the equilibrium spectrum. As seen in the upper diagram, the population structure changes as a consequence of fishing. Some parts of the spectrum decrease while others increase. Because this is the consequence of a change in the availability of prey and predation hazards, this is known as a trophic cascade. The population density decreases at the target size, while it increases below the target. This, combined with the slope in the equilibrium spectrum, results in the landed mean size being smaller than target size. Table 5 contains a comparison of the central output variables from the maximum rent and the open access scenario.

4 Discussion

The concept

The presented model builds on the physical law of conservation of mass. Conservation of mass in the single predation event is reflected as a mass balance on the system level. In other words, the mass of all consumed prey equals the mass of all predators' consumption. Because the principle of mass conservation is an identity, and therefore can be summarised to the system level without any accumulation of errors, the mass balance principle is a very strong concept for modelling. In a discrete model, the mass balance is ensured by an input–output matrix. In a model with a continuous size dimension, like the present model, the input–output matrix becomes a two-dimensional density of input and output: a predator–prey interaction density.

When predation is described with the two-dimensional interaction density where the two dimensions are mass of predator and mass of prey, the conservation of mass in the individual predation event has the consequence of mass balance on the system level as shown in equation (3). Organising predation in this way then ensures the

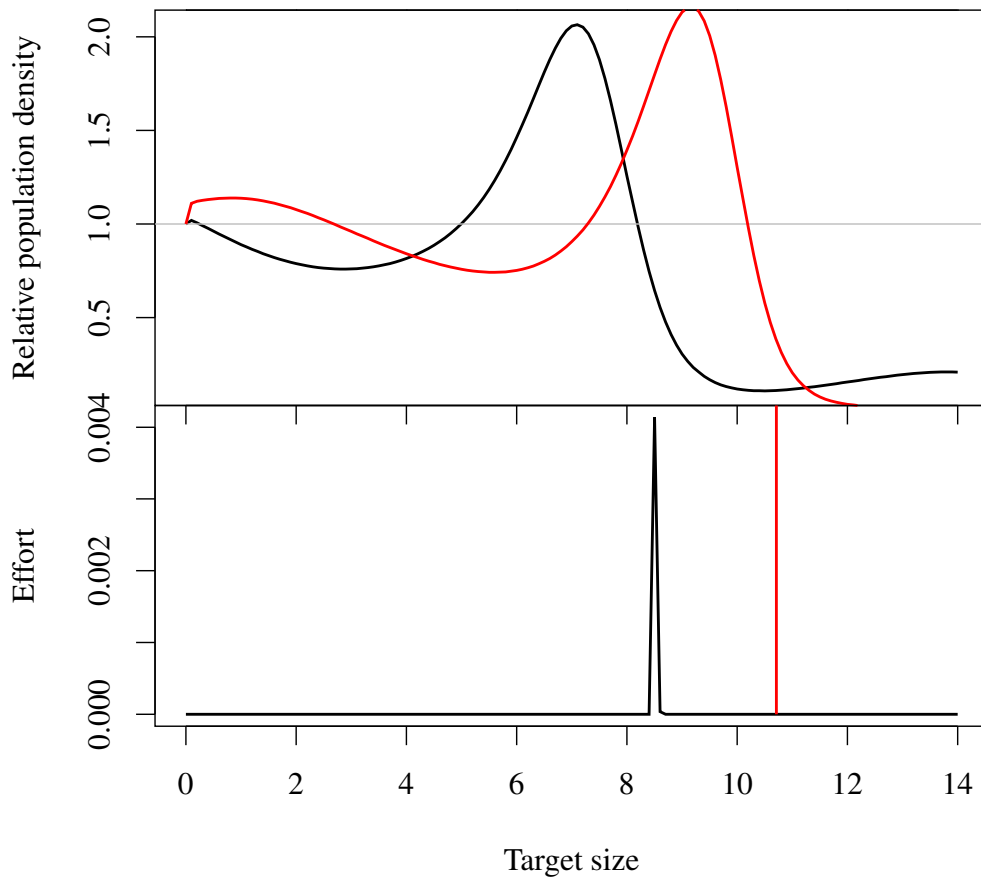


Figure 7: The Convergence scenario of Experiment B, open access, compared with maximum rent in Experiment A. In the upper diagram, the population density relative to the equilibrium spectrum is shown and in the lower diagram, the density of effort. Experiment B is plotted with black and Experiment A with red.

Table 5: Compare of the output from open access and maximum rent for a single owner. Target size for the open access case is given as the mean of the effort density Υ . Target size and mean size of harvest are both given on the logarithm scale of the model and converted into kg. The \$ is a symbol for an arbitrary currency.

Variable		Open Access	Max Rent	Unit
Target size	ξ	8.50	10.71	+ log(g)
		4.92	44.73	kg
Total effort	V	2.05	1.35	year ⁻¹
Mean size	\bar{x}	7.19	9.29	+ log(g)
		1.32	10.85	kg
Harvest	H_{\bullet}	5.990	2.912	10 ⁻³ g m ⁻³ year ⁻¹
Total cost	TC	8.213	5.419	10 ⁻⁴ \$ m ⁻³ year ⁻¹
Total Revenue	TR	8.213	21.809	10 ⁻⁴ \$ m ⁻³ year ⁻¹
Rent	π	0.000	16.390	10 ⁻⁴ \$ m ⁻³ year ⁻¹

conservation of mass and allows for a continuum in the mass-dimension. By building the model on this principle, the energy and nutrition flow of the trophic system are internalised and drive the dynamic of the model. The model is then a trophic-dynamic model, and size, according to which individuals are grouped, can be seen as a proxy for the trophic level. The concept, where predation is described as a two-dimensional interaction density, can then work as a framework for ecosystem production models for economic analyses.

The assumptions that extend the framework set by the two-dimensional interaction density was presented in two steps: the conceptual assumptions and the specific applied functions. The conceptual assumptions are the simplest possible and they can easily be extended. Below, the four conceptual assumptions are discussed, along with the functions used in the present model. A discussion of details in implementation and results of the experiments follows.

Distribution

In this model, the simplest approach is taken with respect to distribution of fish. The individuals are assumed to be distributed randomly in the sea. This allows for a simple description of the distribution of fish: a density in mass and time. However, this is a simplification because fish, in reality, have a clustered distribution in the sea.

Adding dimensions to the distribution of individuals that will be both meaningfully with respect to economic and ecologic interpretation is easy. From an economic view, space has been recognised as important in the management of fishing for a long time (Gordon, 1954; Warming, 1911), and marine protected areas are high on the agenda as ecosystem management tools. While space may be the most obvious dimension to add to the model, dimension in the functional space of the fish can also be added. The model of Andersen and Beyer (2006) operates with life story as an extra functional dimension. This adds an extra dimension to the distributions of individuals; in this case, the asymptotic maximum size in a von Bertalanffy growth equation is added. As species can be mapped onto life history (but not the reverse), including life history can bring the model closer in a dimension other than size that is important in human appreciation and valuation of fish: the species. While extending the model to more dimensions in space will lead to more dimensions in the interacting distribution, including more functional dimensions, if the predation functionality is still only a function of size, does not necessarily lead to more dimensions in the interacting distribution.

The predation

The conceptual idea that predation is a consequence of the aggregated hunt of individual predators is a cornerstone in the theory of Benoît and Rochet (2004) for explaining the empirical observation of the distribution of individuals with respect to size in the sea. The use of power functions have a close link to studies of body-size functional relationships (Huxley, 1932; Peters, 1983), and the use of the Gaussian function as a preference function facilitates the analytic solution of the equilibrium without fishing activity (Andersen and Beyer, 2006).

With respect to economic results, a change of the preference function will probably not change much. However, a change of a combination of the functional response and the preference function towards a more agent-based approach might result in changes in the resulting population density, and thereby the cost of fishing and rent. The employed functional response is a Holling type II. The reasoning behind the Holling type II functional response is the division of the predator's time into search time and handling time. If, to be more realistic, handling time is a function of the size of the prey, the preference function could be set to optimise the predator's consumption (with some noise added). If, then, the density of prey increases, the proper functional response will not be to eat more or less with the same preference, but the response will be to change the preference in order to optimise consumption under the new density. Incorporating this kind of response might change the resulting trophic cascade and

thereby the economic interpretation.

Growth

The expected growth of the individual is assumed to be able to be described using a function of expected consumption. The assumption, as written in (9), may seem trivial, but there are two reasons why it is written explicitly as an assumption. First, the reason is mathematical. When stochastic entries are transformed, the existence of a simple transformation of the expected values is not given, but it depends on the distribution of the entries and the transformation. There is then a potential for systematic errors when scaling from the individual level to the system level. The second reason, more importantly, is that this assumption is as central as the law of conservation of mass. For a production model, the conversion of mass in the allocation between production units is central, along with the concept of production as a consequence of allocated resources. The consequence of a predator eating a prey is the somatic growth of the predator, therefore this assumption of somatic growth as a function of consumption is a central concept of the model.

The present growth function, with simple conversion efficiency, can be extended to account for both respiration and reproduction allocation of consumed food. If the model is extended with a functional dimension, this must be reflected in the growth function given a density of growth with respect to that dimension. The model of Andersen and Beyer (2006) incorporates this with the von Bertalanffy growth function.

Fishing

The representation of fishing and harvesting by the two-dimensional fishing interaction density, because it ensures mass balance, is as fundamental for the conceptual model as the predator–prey interaction density. The fishing selection preference function, which indicates the preference of gear and the fisherman in combination, is a Gaussian function in this paper. As discussed in appendix C.5, there is ample room for improvement in the understanding of the trade-off between narrowing the selection and the corresponding cost of a reduced harvest. Nevertheless, in the formulation, there is a clear link to the real world, as effort has the unit of volume per time. However, this measure is only based on the assumption of randomly distributed fish. If the fish are clustered and the fisherman has knowledge of where these clusters are, the amount of water trawled will be less for the same fishing interaction. Therefore, currently, without empirical data, the model of how the fisherman interacts with the

ecosystem must be viewed as an *as if* approach where control parameters are not observable in the real world.

Parameters

Parameters in the biological model are set according to the theory of a equilibrium density spectrum in an ecosystem with no fishing have properties of $\dot{N} = \kappa m^{-\lambda}$. The parameters of this equation is observable in nature. Other parameters in the biological model are more speculative, but the result in the form of the density of interaction is also an observable property. Appendix C discusses which parameters are set according to the behaviour of the model system. In future developments of the model, getting as many of the parameters established based on empirical observations will be challenging.

Numerical implementation

There are details in the numerical implementation that affect the output of the model. The most important detail is how consumption enters the system. In the present model, a fixed amount of mass per time is supplied. An alternative is to allow the model to be supplied via a fixed background spectrum that extends the spectrum below the model. In that case, the individuals in the lower end of the model spectrum will feed partially on the background spectrum. The input to the model system will then be dependent on the density. For comparison of results from different treatments, comprehending what drives the difference is important. Because the focus for this model is the trophic interaction and the economical trade-off between targeting small or large fish, an input dependent on the form of the trophic cascade in the system would be inappropriate. Therefore, the fixed input is employed in the present model.

In the first grid point, the population density must be supplied at each step of the iteration routine. In the model, this is done by setting the population density for the first point equal to the equilibrium value, $N_{1,t} = \dot{N}_1$. Because the change in density at the second grid point is determined by the gradient of flux gN , because the flux is proportional to total input EN , and because this is supplied externally and fixed in each step, the actual value of $N_{1,t}$ does not influences the flux. Therefore, the density at the second grid point is also not influenced. The only influence the density at the first point has in the system is through its loss as prey in the predator–prey interaction. Here, the value of $N_{1,t}$ will have an impact, but the impact is small and a fixed N_1 can be viewed as part of the fixed input.

Including recruitment would be a natural extension of the model; that is, to let the input of individuals in the lower end, $N_{1,t}$, be a function of density in the upper end. This is, however, not an option with the present modelling of external input. As discussed above, the $N_{1,t}$ influence on the system is almost negligible. Additionally, the concept of species, as a prerequisite for dealing with recruitment, is not easily incorporated in the model. One approach for dealing with species in an ecosystem will be to link a species model to size-based model; let the size-based model determine the predation and somatic growth in the species model; and let the species model determine the genetic composition of the population in the size-based model.

Correcting for systemic overestimation

In the numeric implementation of the model, there is, due to the upwind scheme, a systemic overestimation of ΔN . This is corrected in the present implementation by an extra mortality rate. This correction is only accurate when the system is in the equilibrium state without fishing. There seems, however, according to appendix C.1, not to be any notable errors caused by the correction when there is a trophic cascade in the system. There is, to my knowledge, no other report of a problem related to systematic overestimation when this kind of model is implemented numerically. It would seem to be good practice to report the details of how this problem is handled in future work with this type of model.

Price and costs

In the present work, price and cost are without any empirical basis. It might seem to be a problem to ascribe price to a given size. There are many different species, each with a different price. This is, however, not a problem. All that needs to be known is the expected distribution of species at a given size, an assortment. If the average price of the species with respect to weight is multiplied with the assortment, the result is the expected price with respect to size. In the model, the cost is closely linked to the fishing selection function. Empirical data on gear selection and fisherman's knowledge of fish clustering, combined with detailed knowledge on prices on factor input in fishing can produce an empirically based cost function.

Fisherman's adaptation

The fisherman's adaption in Experiment B describes quiet, simple behaviour. The behavioural model must be considered as *ad hoc* because the parameters are chosen with the aim of finding a steady state solution. There is no empirical data supporting

these specific parameters. However, having this tool and refining it is important. For example, if a restriction on maximum total harvest is placed on fishing, whether the expected improvement in rent will occur in the system can actually be tested. In that case, the adaptation function has to be extended to a market where the rights for harvest are allocated to those with highest shadow prices on an extra unit. Other restrictions may require other types of adaptation.

The experiments

The simple experiments performed in this paper illustrate two of several possible uses of the model: 1) To investigate production of the ecosystem as a production unit given a specific control, as in Experiment A, and 2) to predict the input control and the output harvest from the ecosystem given a specific set of adaptive agents, as in Experiment B. As illustrated in table 5, the rent in Experiment B under open access is inferior to the rent in Experiment A under single owner control. Even though the model is not parameterised to a specific ecosystem and market, and the values in the table therefore must be seen as illustrative only, the inefficiency of the use of a common pool resource where multiple agents make decisions on control input is illustrated once again. As summarised in table 5, the present model shows that agents under open access, in addition to supplying excessive effort, target fish of an inferior size. The resulting output in the open access scenario compared with the maximum rent scenario has a bigger harvest volume, but the size of landed fish are smaller and yield a lower price. A contribution of the present model is thus the ability, in an economic analysis, to incorporate the dimension of size in a production model, which is a dimension that is important in the functionality of the ecosystem and in the demand function of landed fish.

Experiments like Experiment A can investigate the production economics of the ecosystem. The economic analysis will, nevertheless, not be complete before the analysis is performed in a capital theoretic setting where inter-temporal balancing can be addressed. This is left for future work. Experiment B can easily be extended to include agents adapting to a specific type of regulation regime. This will move control of the system to the institution of regulation. It will then be possible to test the potential of regulations in mitigating the inefficiency created by multiple agents use of the resource as a common pool.

In this article, all results are presented from systems close to steady states. Steady state situations are probably not found in nature, so here, dynamic systems under constant change must be expected. The aim of the model is, however, to create an ecosystem model suitable for long-term, strategic planning in the context of ecosys-

tem management of marine ecosystems. Thus, the analysis of a steady state system is vital because it enables long-term prediction of consequences of specific management actions and can serve for setting strategic goals for the ecosystem. Steady state analysis can also be seen as the first step in research. When behaviour in steady states is understood, a dynamic system can be investigated as a next step.

Conclusion

The presented model is a production model for a marine ecosystem where the dynamic is caused by modelling the predation and subsequent somatic growth. The model is formulated as an ecosystem production model that allows for economic analysis of the exploitation of the marine ecosystem by fishing activity. The model is then an example of the production model required for ecosystem management to create a link from the ecosystem to the operational level. The model is the simplest production model possible, built on the principles of (i) size, which is the attribute that determines the predator–prey interaction, (ii) mass balance in the predator–prey allocation, and (iii) mortality and somatic growth as consequences of the predator–prey allocation. Other aspects important for the ecosystem management can, as discussed above, be added, or other functions can be applied to the conceptual model. The formulation and description of the present model can therefore serve as a reference for future work.

Acknowledgements

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A The equilibrium spectrum

Behind the formulation of this model is an expectation that the spectrum, in the absence of fishing, has a steady state solution where the spectrum can be described by a power law. That is, there exists an equilibrium population density:

$$\overset{\star}{N} = \kappa m^{-\lambda} \quad (34)$$

The exponent λ is under the assumption that all individuals have the same equilibrium functional response $\overset{\star}{f}$:

$$\lambda = 2 + q - n \quad (35)$$

With the formulation of functions in paragraph 2.4, the integrals in the model can in equilibrium be calculated analytically.⁷ There will, in equilibrium, be an equilibrium potential interaction distribution $\overset{\star}{\Phi}$, and there will thus be an equilibrium of consumed food $\overset{\star}{E}$ with properties of:

$$\begin{aligned} \overset{\star}{E}\overset{\star}{N} &= \int_0^{\infty} m_p \overset{\star}{f} \overset{\star}{\Phi}(m_p, m_r) dm_p \\ &= \overset{\star}{f} \alpha_1 m^{2n-q-2} \end{aligned} \quad (36)$$

where

$$\alpha_1 = \kappa^2 \gamma \beta^{q-n} \exp\left(\frac{\sigma^2 (q-n)^2}{2}\right) \quad (37)$$

⁷Andersen and Beyer (2006) show in their appendix how the integrals are solved.

The equilibrium functional response is then:⁸

$$\begin{aligned} f^* &= \left(1 + \frac{\alpha_1 m^{2n-q-2}}{h m^n \dot{N}^*} \right)^{-1} \\ &= \left(1 + \frac{\alpha_1}{\kappa h} \right)^{-1} \end{aligned} \quad (38)$$

Additionally, there will be an equilibrium mortality rate μ^* with properties of:

$$\begin{aligned} \mu^* \dot{N}^* &= \int_0^\infty f^* \Phi^*(m_p, m_r) dm_r \\ &= f^* \alpha_2 m^{2n-q-3} \end{aligned} \quad (39)$$

where

$$\alpha_2 = \kappa^2 \gamma \beta^{n-1} \exp\left(\frac{\sigma^2 (1-n)^2}{2}\right) \quad (40)$$

In the steady state scenario, and in the absence of fishing, the flow equation (2) becomes:

$$\frac{\partial \dot{N}^*}{\partial m} = -\mu^* \dot{N}^* \quad (41)$$

The conversion efficiency ϵ can therefore be determined by:

$$\begin{aligned} -\mu^* \dot{N}^* &= \frac{\partial \dot{N}^* \epsilon \dot{E}}{\partial m} \quad \Longleftrightarrow \\ -f^* \alpha_2 m^{2n-q-3} &= \frac{\partial}{\partial m} \left(\epsilon f^* \alpha_1 m^{2n-q-2} \right) \quad \Longleftrightarrow \\ -\alpha_2 m^{2n-q-3} &= (2n - q - 2) \epsilon \alpha_1 m^{2n-q-3} \quad \Longleftrightarrow \\ \epsilon &= \frac{\alpha_2}{(2 + q - 2n) \alpha_1} \\ &= (2 + q - 2n)^{-1} \beta^{2n-q-1} \exp\left(\frac{\sigma^2 (1-q)(1+q-2n)}{2}\right) \end{aligned} \quad (42)$$

⁸This does not prove that the f^* is independent of m because this is the assumption for equation (35)

In the calibration of the model, if n and q are given, there will be a link between β , σ and ϵ : If two are given, the third is determined by (43). If these four parameters are given and the fifth is calculated, there is a link between κ , γ , h and $\overset{\star}{f}$ given by (38). If three are given, the fourth can be calculated. Furthermore, the constants α_1 , $\overset{\star}{f}$, α_2 and ϵ can be calculated from the analytic results in equations (37), (38), (40) and (43), and can be compared with a numerical calculation using the equations (36), (16), (39) and (42), thereby confirming the validity of numerical integration and differentiation. The numerical implementation uses the numerical method (equations (36), (16), (39) and (42)) to calculate the constants, and thereby is flexible to a change in specific functions that do not allow for analytical solutions to the equilibrium spectrum.

B The numerical implementation

The first point in the numeric implementation (x_1, N_1) cannot be calculated from equation (30) as N_0 is not known, and likewise, equation (31) the A_1 cannot be calculated as g_0 is unknown. The first point therefore must be supplied at each iteration step. This is done by setting the first point equal to the equilibrium value in each time step

$$N_{1,t+\Delta t} = \overset{\star}{N}_1 \quad (44)$$

The rest of N can then be calculated by (30). As the first elements of A are not needed in the calculation, it is just assigned the value of zero

$$A_1 = 0 \quad (45)$$

B.1 Systematic overestimation

The purpose of the numeric implementation of the model is to produce a model capable of giving proper estimates of production in the system. There is, however, a systemic overestimation when moving from the continuous formulation (26) to the discrete upwind version of (27). In an equilibrium without fishing, the biomass flux is in the continuous version

$$\overset{\star}{g}\overset{\star}{N} = \epsilon\alpha_1\overset{\star}{f}e^{x(2n-q-2)}$$

where α_1 and $\overset{\star}{f}$ are constant in the system as defined in appendix A. The first part of the right-hand side of (26) is then

$$\frac{\partial \overset{\star}{g}\overset{\star}{N}}{\partial x} e^{-x} = (2n - q - 2) \epsilon\alpha_1\overset{\star}{f} e^{x(2n-q-3)}$$

This is in the upwind numeric method estimated by

$$\frac{\Delta g_j^* N_j^*}{\Delta x} e^{-x_j} = \frac{\epsilon \alpha_1 f^* \left(e^{x_j(2n-q-2)} - e^{(x_j-\Delta x)(2n-q-2)} \right)}{\Delta x} e^{-x_j}$$

this prompts a systemic overestimation of $\frac{\partial g N}{\partial x} e^{-x}$ of the magnitude of

$$\epsilon \alpha_1 f^* e^{x_j(2n-q-3)} \left(2n - q - 2 + \frac{e^{-\Delta x(2n-q-2)} - 1}{\Delta x} \right)$$

This overestimation can be rectified by an extra mortality rate of

$$\check{\mu}_j = \kappa^{-1} \epsilon \alpha_1 f^* \left(2n - q - 2 + \frac{e^{-\Delta x(2n-q-2)} - 1}{\Delta x} \right) e^{(n-1)x_j} \quad (46)$$

This extra mortality rate, calculated by (46), is added with μ_j and ν_j in (32) and ensures the mass balance of the system. The numeric implementation is then able to reproduce the equilibrium spectrum. Notice, as

$$\lim_{\Delta x \rightarrow 0} \frac{e^{-\Delta x(2n-q-2)} - 1}{\Delta x} = -(2n - q - 2)$$

the $\check{\mu}$ in (46) will approach zero as Δx approaches zero, so the consequences of the correction can therefore be tested by changing Δx .

B.2 External predators and prey

Because only an interval of the spectrum is considered in the model, there are predators and prey beyond and below the population in the model. Because the lower end of the model spectrum has main prey outside the model and the upper part of the model spectrum has main predators outside the model, this is an external impact that must be incorporated.

From appendix A, it is known how large the feeding level and mortality must be in equilibrium:

$$E_j^* N_j^* = f^* \alpha_1 \exp((2n - q - 2) x_j) \quad (47)$$

$$\mu_j^* N_j^* = f^* \alpha_2 \exp((2n - q - 3) x_j) \quad (48)$$

where the constants α_1 , α_2 and $\overset{\star}{f}$ are set according to appendix A. With the constants calculated, the two vectors of theoretical feeding and mortality in the numeric model system are calculated as:

$$\overset{\star}{E}N_j = \overset{\star}{f}\alpha_1 \exp((2n - q - 2)x_j) \Delta t \quad (49)$$

$$\overset{\star}{\mu}N_j = \overset{\star}{f}\alpha_2 \exp((2n - q - 3)x_j) \Delta t \quad (50)$$

In the numeric model, the interaction density will be represented by a matrix of interaction densities. The realised interaction in the model system in equilibrium $\overset{\star}{\Phi}$ is calculated as:

$$\overset{\star}{\Phi}_{p,r} = \overset{\star}{f}v(x_r)\phi(x_p, x_r)\overset{\star}{N}(x_p)\overset{\star}{N}(x_r)\Delta t$$

the realised uptake and mortality are in the model without adjustments:

$$\widetilde{E}N_r = \sum_{p=1}^J \overset{\star}{\Phi}_{p,r} \exp(x_p)^2 \Delta x \quad (51)$$

$$\widetilde{\mu}N_p = \sum_{r=1}^J \overset{\star}{\Phi}_{p,r} \exp(x_r) \Delta x \quad (52)$$

There is now a difference between what the raw numerical model predicts—(51) and (52)—and what it must be if the spectrum were complete—(49) and (50). This difference is caused by external predators and prey and will be corrected by adding an extra consumption O_{EN} and mortality rate O_{μ} , illustrated by the blue and red arrows marked “fixed consumption” and “fixed mortality rate” in figure 2.

$$O_{ENj} = \overset{\star}{E}N_j - \widetilde{E}N_j$$

$$O_{\mu j} = \frac{\overset{\star}{\mu}N_j - \widetilde{\mu}N_j}{\overset{\star}{N}_j}$$

In this way, the model system is supplied by a fixed amount of external input in the form of 1) the flux of individuals caused by somatic growth, represented by N_1 , and 2) the supply of a fixed amount of consumed food represented by O_{EN} . At the other end of the spectrum, there is an output of 1) the flux of individuals growing out of the spectrum, and 2) mortality caused by O_{μ} .

To ensure that the system is only fed from below, all entire upper third of O_{EN} is set to zero. To limit the influence from outside to the upper and lower end of the modelled region, all values of O_{EN} and O_{μ} where the \widetilde{EN} and $\widetilde{\mu N}$ in the model system do not diverges from the theoretical EN^* and μN^* by less than 0.0001 relatively and absolutes are set to zero:

$$O_{ENj} = \begin{cases} 0 & \text{if } j \geq \frac{2J}{3} \\ 0 & \text{if } \left| \frac{\widetilde{EN}_j}{EN_j^*} - 1 \right| < 0.0001 \\ EN_j^* - \widetilde{EN}_j & \text{else} \end{cases}$$

$$O_{\mu j} = \begin{cases} 0 & \text{if } \left| \frac{\widetilde{\mu N}_j}{\mu N_j^*} - 1 \right| < 0.0001 \\ \frac{\mu N_j^* - \widetilde{\mu N}_j}{N_j^*} & \text{else} \end{cases}$$

The formulation of external input as consumption and output as a mortality hazard has the consequence of the external input being fixed while the output is dependent on the state of the system, i.e., on N .

In addition to the above input, when the functional response is calculated, there is a need to know to what the external input corresponds as potential external input

$$O_{\Phi j} = \frac{O_{ENj}}{f^*}$$

This is the amount of prey that is “invisible” to predators in the model system and corresponds to supplied food O_{EN} . The $O_{\Phi j}$ is added to the integral in the calculation of the functional response (16) in order to produce the right functional response, and hence the model to reproduce the equilibrium spectrum.

C Setting the parameters

While there seems general agreement on the slope λ of the spectrum, setting the magnitude of the spectrum κ is rather ad hoc. κ is set to resemble the North Sea,⁹ but empirical parameterisation is needed. In the dynamic model, the turnover rate in the interaction distribution is determined by the product of f and v . Therefore, the important parameters in the equilibrium spectrum are f^* and γ . When testing the effort of a

⁹K. H. Andersen, personal communication.

change in $\overset{\star}{f}$, the product $\overset{\star}{f}\gamma$ is kept constant, and thereby the realised predation is kept at what seems to be a proper level for the North Sea. β is the characteristic relative distance between the predator and the preferred prey and is set according to tradition.

All tests of parameters are performed in the same basic manner. An experiment is set up with the main parameters as given in table 3 and 4, except for the parameter being tested. From an equilibrium with no fishing, a sudden and vigorous fishing is initiated. This introduces an oscillation into the system. In figure 8, the oscillations are illustrated. In the diagrams, the relative population density for the years 176-200 after the introducing of fishing is shown. The diagrams show the relative population density, or, in other words, the population density relative to $\overset{\star}{N}$. In each diagram, the first year is plotted with a very light grey, and subsequent years are plotted with increasing intensity in grey ending with the last years in black. The red line indicates the mean density for the period. In the diagrams, the oscillation of the model system over some period clearly forms an attractor. Through tests and experiments, the coefficient of variance of the population density (CV) at each grid point is used as a measure for the width of the attractor. A steady state convergence is defined as all grid points, for the last twenty-five years, have CVs of less than 10^{-5} . The system is run either for some years or until convergence to a steady state. The output from different values of the parameters is compared, mainly graphically.

C.1 Setting the grid distance

The consequences of the different grid distance Δx , or the number of grid points L , are tested by varying $L \in \{36, 71, 141, 281, 561\}$. The model started with a population in a steady state with hard fishing and a maximum number of grid points. It thereafter runs for 200 years for each L .

The result is presented in figure 9. In the upper diagram, the mean of the relative population densities are compared, and in the middle diagram, the mean of the densities of harvest are compared, and in the lower diagram, the CVs are plotted on a logarithmic scale. All comparisons are done for the years 181–200. In the lower diagram, the CV for $L = 561$ is not present because the system is started from a steady state with this grid distance. Therefore, no oscillation is introduced in this case, and the CV for $L = 561$ is much lower than for the others.

As seen in the upper and middle diagrams, the smaller L becomes, the further from the $L = 561$ solution. However, the impact does not seem to be extreme before $L \leq 71$. In the lower diagram, there is a clear effect of damping of oscillations when L is reduced. This is probably a result of the upwind scheme where $\frac{\partial gN}{\partial x}$ is estimated to the left of the grid point, and therefore a point ahead of the grid point in the right-

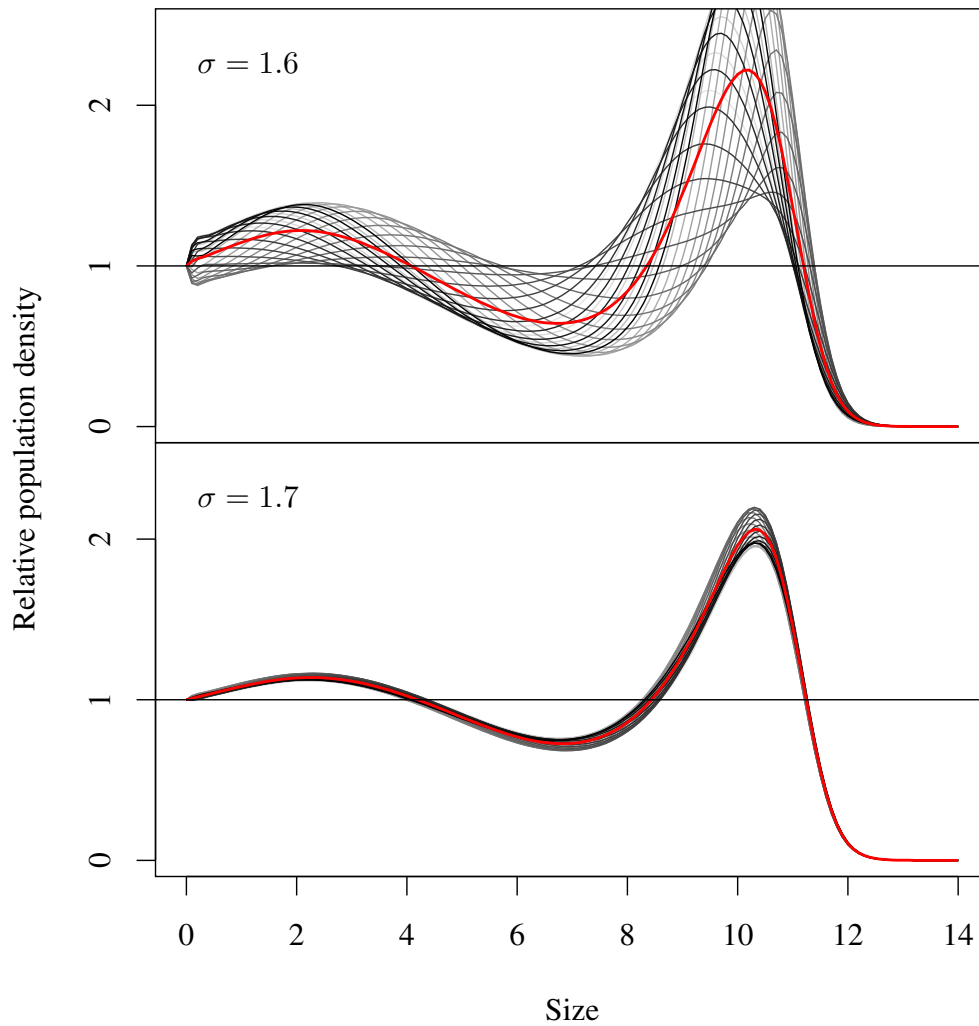


Figure 8: Testing parameter σ 's influence on the model system. The figure shows that the relative population density in year 176–200 for a model with $\sigma = 1.6$ in the upper diagram and for $\sigma = 1.7$ in the lower diagram. The first year of the time interval is plotted with a light grey, and subsequent years are plotted with increasing intensity in grey ending with the last years in black. The red line indicates the mean density for the period.

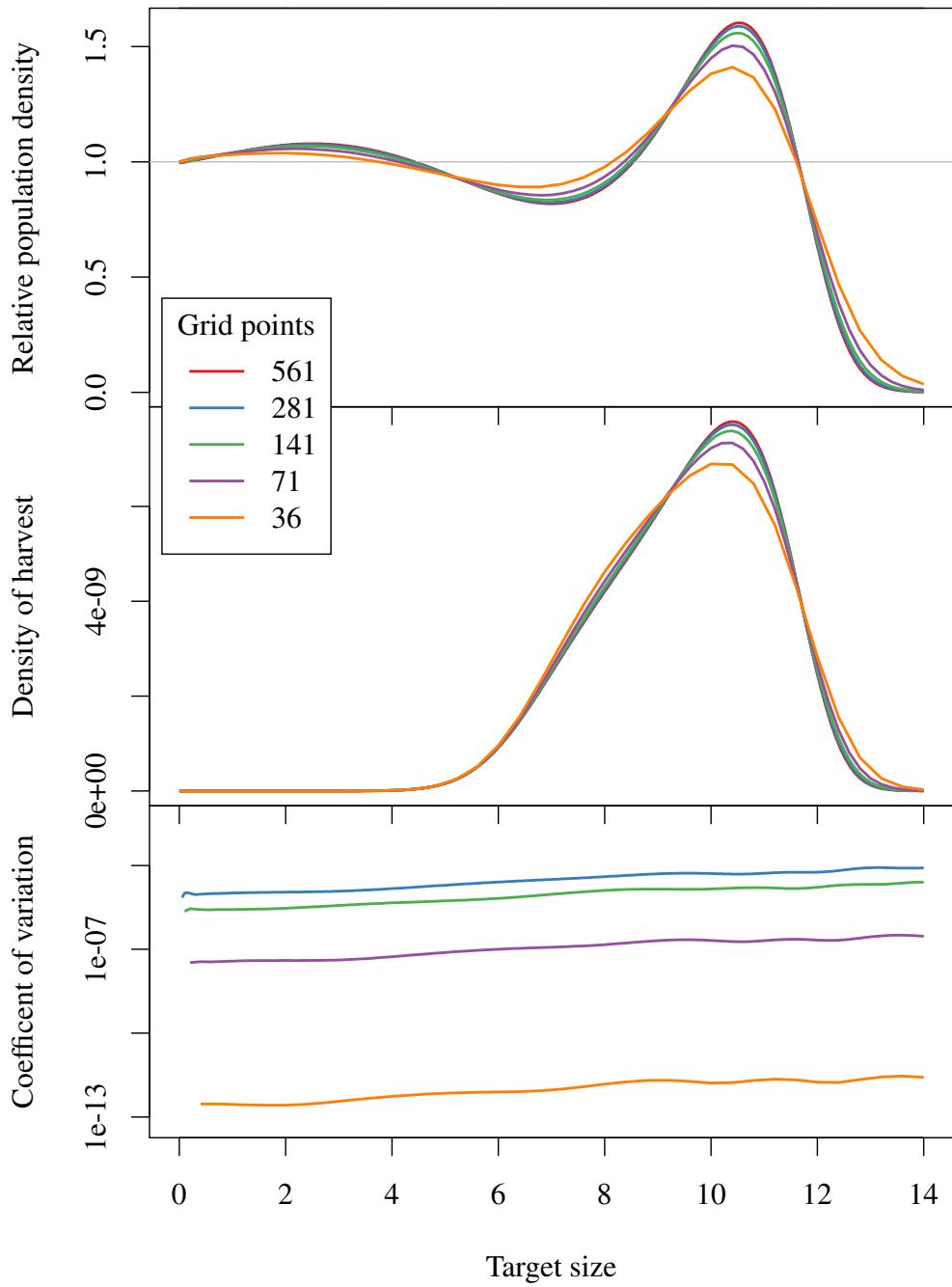


Figure 9: See page 54 for explanation.

moving oscillation. This test of different grid distance is also a test of the impact of the correction for the systematic overestimation of $\frac{\partial gN}{\partial x}$ as explained in appendix B.1. The difference in population density with different grid distances comes mainly from this correction and is only correct if the population is equal to \check{N} . There seems to be no notable impact on the model from the numeric implementation if the number of grid points is 141 besides some slight damping of the model system.

C.2 Setting the time step

The effect of a change on time steps is tested by running the standard experiment from \check{N} for 120 years after heavy fishing is introduced. The test is performed with $\Delta t \in \{1, \frac{1}{1}, \frac{1}{2}, \frac{1}{3}, \frac{1}{4}, \frac{1}{5}, \frac{1}{6}, \frac{1}{15}, \frac{1}{25}\}$. The result is presented in figure 10. In the upper diagram, the relative population densities are compared and in the lower diagram, the CVs are compared. As seen in the upper diagram, the relative population densities for year 120 are mostly equal with the differences not distinguishable in the diagram. There is, however, as shown in the lower diagram, a difference in the CVs of the population densities for years 101–120. Large time steps damp the system and make the CVs smaller. In order to have a system that, on the one hand, is not dampened by the numeric calculation scheme, but on the other hand, can reach a steady state within a reasonable amount of time, the time step in the model is set at six per year, $\Delta t = 1/6$.

C.3 Test of sigma

The consequences of changing the parameter σ is tested by running the system with values of $\sigma \in \{1.0, 1.1, \dots, 1.9, 2.0\}$ and other values as standard. The model system is started from \check{N} and heavy fishing is initiated, and the population density in years 176–200 and 376–400 is recorded. Furthermore, a test of when the model system meets the criteria of convergence is performed by allowing the system run until

Figure 9: The number of grid points influence on the model. The model starts with a population in a steady state with fishing and 561 grid points. The model is run for 200 years with 561, 282, 141, 71, and 36 grid points. In the upper figure, the most recent twenty year mean of relative population densities are shown. In the middle figure, the resulting densities of harvest are shown (the dimension is $\text{g m}^{-3} \text{ year}^{-1}$). In the lower diagram, the coefficients of variance for the population density over the last twenty years are shown on a logarithmic scale.

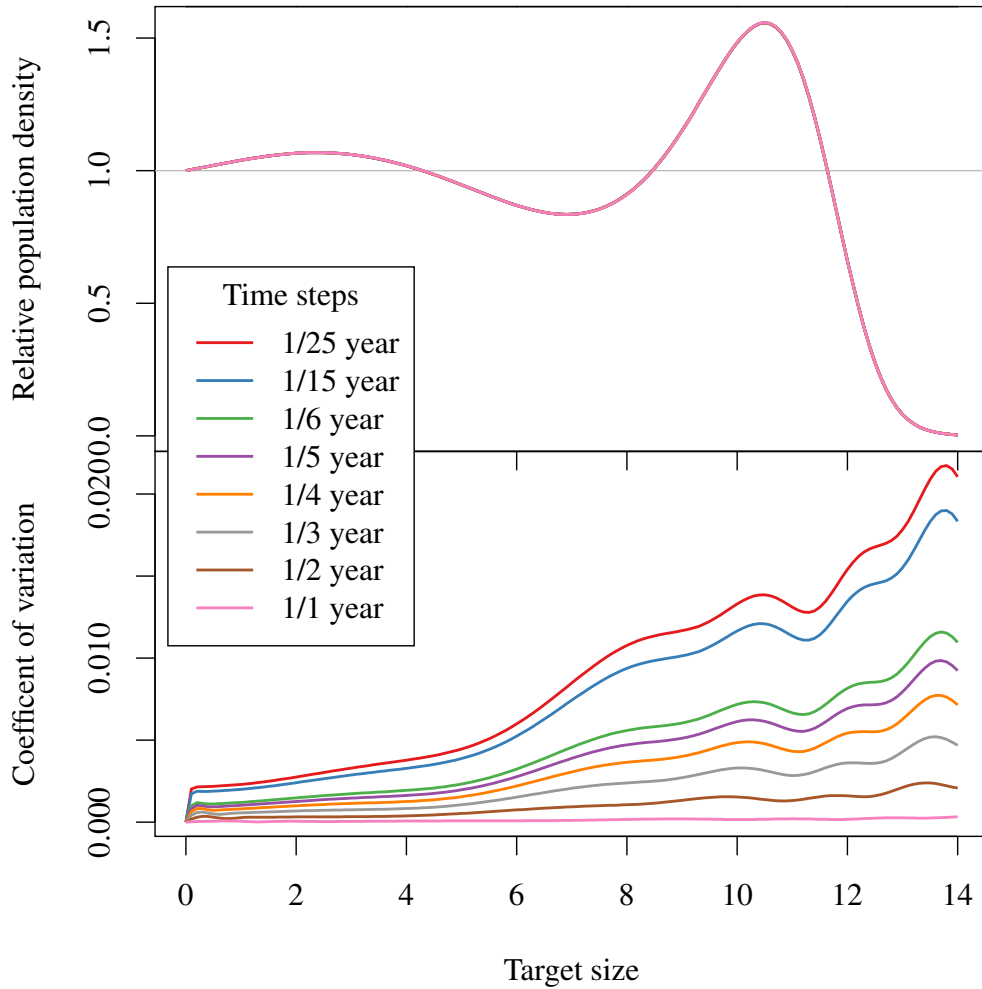


Figure 10: The time steps influence on the model system. The model is started from a steady state without fishing, and heavy fishing is applied and the model runs for 120 years with different time steps. In the upper diagram, the relative population densities for year 120 are shown. The diagram shows eight curves. However, they are almost equal and not distinguishable. In the lower diagram, the coefficient of variance of the population density for years 101–120 are shown.

Table 6: The dampening effort of different σ . The table gives the maximum coefficient of variance for the population densities in the period 176–200 and the period 376–400. In the column marked “year” the time elapsed for the model system to meet the convergence criteria of $CV < 10^{-5}$ is given. If the system does not reach the convergence criteria within 2,000 years a — is given.

σ	176–200	376–400	year
1.0	1.09	1.09	—
1.1	1.38	1.24	—
1.2	1.59	1.51	—
1.3	1.30	1.30	—
1.4	1.26	1.13	—
1.5	1.00	1.01	—
1.6	4.70e-01	4.72e-01	—
1.7	7.80e-02	7.05e-03	1083
1.8	5.93e-03	3.85e-05	511
1.9	3.87e-04	1.43e-07	328
2.0	2.63e-05	4.55e-10	245

$CV < 10^{-5}$ or 2,000 years has elapsed. In figure 8, an example of the output is presented in the form of two diagrams. In table 6, the maximum CV for the two periods is presented for all tests. From the table, the impact of an increase in σ clearly dampens oscillation in the system, at least when $\sigma \geq 1.7$. In figure 11, the mean population densities after the convergence criteria have been met are plotted for the σ where the system converges within 2,000 years. The value of σ has some impact on the mean population density. The value of $\sigma = 1.8$ is chosen because this dampens the system so that it will come from a steady state without fishing to a new steady state with fishing within a reasonable amount of time.

C.4 Functional response

The impact of the parameterisation of the functional response is tested by running the system with $f^* \in \{0.1, 0.2, \dots, 0.8, 0.9\}$ while keeping the product $f^* \gamma$ constant. This way, the interaction density is unchanged. Additionally, the model is tested with a linear response, i.e., $f(\bar{\Phi}, N, m_r)$ is set to be an arbitrary constant. The model system is started from \bar{N} and a heavy fishing is introduced, and the population densities in years 201–220 are recorded. In figure 12, the mean of the relative population densities for

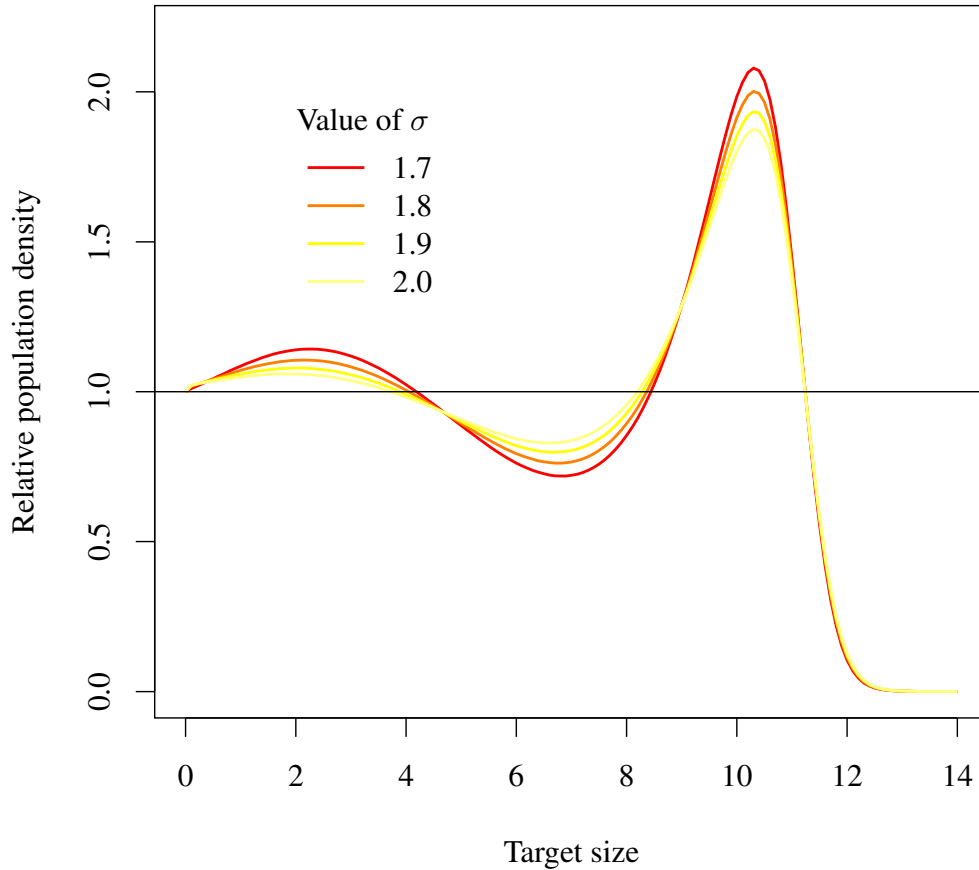


Figure 11: Test of σ impact on steady state solutions. The diagram shows the relative population density when the convergence criteria is met for different σ .

the years 201–220 are shown for all ten tests. Black plots the mean density for linear response, with yellow for $\tilde{f} = 0.9$, and the colour changes incrementally until $\tilde{f} = 0.1$ is red. A change in \tilde{f} seems to not generate a great impact on the densities. The consequences regarding dampening the system are ambiguous, and for some settings, the dampening of the system is reinforced with increasing \tilde{f} , and in other settings, the opposite occurs. For the experiments, a value in the middle $\tilde{f} = 0.5$ is chosen.

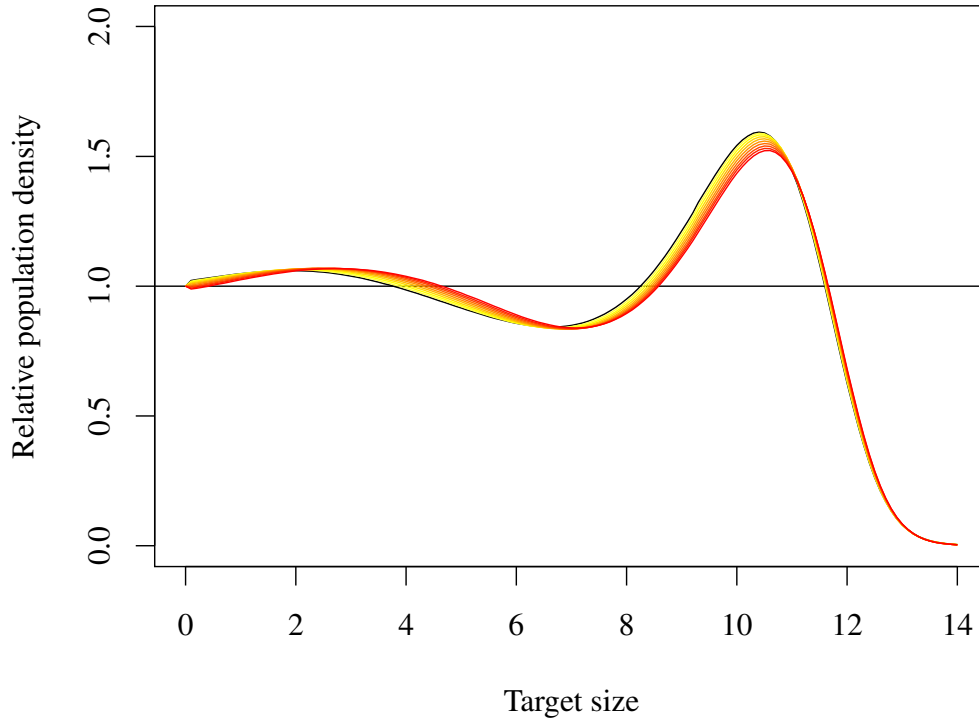


Figure 12: Test of the equilibrium response value. The diagram shows the mean of the relative population densities for the years 201–220 . Black plots the mean density for linear response, yellow $\hat{f} = 0.9$, and the colour changes incrementally until $\hat{f} = 0.1$ is red.

C.5 The fishing selection function

To investigate the influence of the breadth of the fishing selection function, the parameter ς , an experiments where the fishing effort is concentrated in a single point, as described for Experiment A (see paragraph 3.1), are set up. In each experiment, the system is run until the system converges to steady state. All parameters are set according to table 3, and the prices are the same as in Experiments A and B. The effort is kept constant at $V = 1.4$ while the $\xi \times \varsigma$ space is examined by testing all combinations of $\xi \in \{9.9, 10.0, \dots, 11.4, 11.5\}$ and $\varsigma \in \{0.5, 0.6, \dots, 1.9, 2.0\}$. The result of the experiment is shown in figure 13. The experiment shows that if the effort is constant, revenue can be increased by narrowing the selection function.

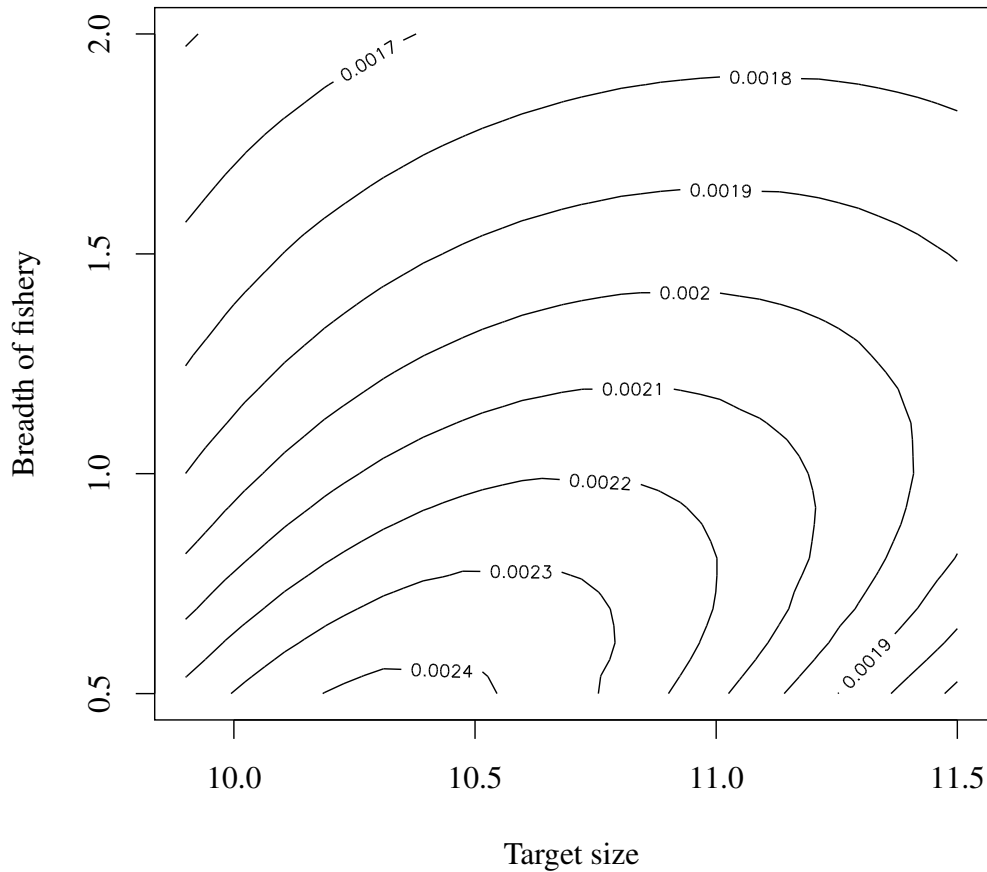


Figure 13: Revenue surface. The figure gives yearly revenue with fixed effort at $V = 1.4$, different target size ξ , and the breadth of fishing selection function ς .

In this model, the selection function is a combination of both the selectiveness of the gear and the fisherman choosing the spot in the sea where the target fish is. The trade-off between narrowing the selection function at the cost of a small harvest is reflected in the manner the area under the selection function changes when ς changes. In the formulation used in the present model, the normalised Gaussian function (18), the area is always 1. While this is a reasonable assumption for the part of the selection coming from fishermen choosing the location to fish, it is probably not correct with respect to an increase in the selectiveness of the gear. In the latter case, the area might have to decrease with increasing ς . The present formulation of the gear selection function is therefore not economically reasonable with respect to parameter ς when

the selection is narrowed too much. Because an optimisation routine will narrow the selection function to where it is economically unreasonable, the parameter ς is not considered to be a control variable, but, in the experiments, it is fixed at $\varsigma = 1$.

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