DEPARTMENT OF FOOD AND RESOURCE ECONOMICS
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# Implications for fisheries management by inclusion of marine ecosystem services

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Implications for fisheries management by inclusion of marine ecosystem services

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# Table of Content



## List of tables



### List of figures

**Acronyms**

| | |
|---|---|
| EBFM | Ecosystem Based Fishery Management |
| MEA | Millennium Ecosystem Assessment |
| MEY | Maximum Economic Yield |
| MSY | Maximum Sustainable Yield |
| NMV | Non-Market Values |
| ODE | Ordinary Differential Equation |

## Abstract

The application of ecosystem based management of the marine resources and focus on ecosystem services will influence the methodologies used for assessing the resources as well as the proposed regulation of the fisheries and other marine resources. The paper makes a review of ecosystem services and ecosystem based fishery management with the purpose of integrating these elements in a bioeconomic model. As a part of the model development, a logistic predator-prey model is examined thoroughly. On this basis, a numerical model is created. The model can include several species at different tropic layers, hence simulation a small food web. The key purpose of the numerical analysis is to develop a practical tool that can assess the management policies when a broader range of ecosystem services, species interactions and externalities are taken into account. The model can include several species at different trophic layers and, hence, simulate a small food web, while at the same time assess the economic effects of fishing on this food web. In general, the analyses indicate that species modelled with interaction may sustain less fishing pressure than if they are modelled without species interaction. Besides interaction, the numerical model assesses how the economic result is affected by the inclusion of ecosystem services. This is done through the damage cost functions, which depends on effort and reduces the net value, and a set of non-market values, which are functions that depend on the stock of the species. The inclusion of these tends to favour reduction in effort levels, in some cases quite significantly. Management policies based on conventional MEY targets may in many cases rather well accommodate the broader range of ecosystem-based policy goals, due to the lower effort levels. The paper shows the shortcomings of conventional qualitative analytical approaches because of the complexities of marine ecosystems. Numerical models also show shortcomings, in particular because specific functional forms are used and data are short in many areas. However, it is shown that much insight can be gained from using such relatively simple models.

# 1. Introduction

The application of ecosystem-based management and focus on ecosystem services will influence the methodologies used for assessing the resources as well as the proposed regulation of the fisheries and other marine resources. Historically, bio-economic theory has mainly focused on single species models. Objectives have typically been oriented towards the maximization of the resource rent or net present value from a single species fishery exploited by a homogeneous fleet. In static analyses, focus is on the Maximum Economic Yield (MEY) whereas biologically oriented work mainly has Maximum Sustainable Yield (MSY) as a guiding principle. Assuming that the yield from a natural stock can be described by a logistic function and the costs of effort are linear, it is straightforward to determine single species MEY or MSY and, hence, produce simple management advice. However, this advice might be unsuitable if species interactions, broader ecosystem goals and fisheries impact on the ecosystem are taken into consideration. For example, research has indicated that the amount of effort related to MSY-targets can be too high in order to fulfil ecosystem goal, because the corresponding fishing pressure might be too high for some species and put them at risk of extinction (Legovic and Gecek 2010, Legovic et al. 2010). More complex models including for example two species have been known since Lotka-Volterra (1925, 1928), but such apparently small extensions complicate the analyses immensely (Clark 1990, 2010).

The growing interest in ecosystem analyses has been materialized in particular by the Millennium Ecosystem Assessment (MEA 2005). MEA divides the ecosystem services into four main categories; provisioning, regulating, cultural and supporting services. Ecosystem services, the contribution of ecosystems to human welfare, are more recently divided in three main categories whilst considering the supporting services as ecosystem processes rather than ecosystem services (CICES 2013, United Nations et al. 2013, Haines-Young and Potschin 2013). The demand for ecosystem services is based on the sum of people's willingness to pay for both services related to the marketable and non-marketable benefits (Pearce 2007, Fisher et al. 2008). A number of different valuation methods can be utilised to estimate the value of ecosystem services (Bateman et al. 2011, Bertram and Rehdanz 2013, Barbier 2007, Remoundou et al. 2009, Holland et al. 2010). However, the joint character of the production of ecosystem services can complicate the estimation (Freeman 2003).

The focus of ecosystem-based fishery management (EBFM) is to avoid degradation of ecosystems and to consider requirements of non-target species, protected species and habitats, to take trophic interactions into account and cover the effects of environmental influences (Pikitch et al. 2004, Fogarty 2014, Arkema et al. 2006). For example, conventional single-species approaches to the modelling of fish stocks are likely to conclude that marine mammals are detrimental to stocks, as they cannot take account of the range of indirect and more complex interactions (Morissette et al. 2012). Ecosystem-based management will require knowledge about the relationship between stocks of different species. These interconnections influence the ecosystem services and, subsequently, these services can be assessed economically. When looking at changes in fisheries policies after inclusion of more ecosystem services, the trade-offs are about the balancing of forgone revenues from fishing in the short term with the long term benefits from reduced fishing activity of a modified policy (Smith et al. 2010). If human activities alter the state of the ecosystem and the future flow of ecosystem services and if economic agents who receive the altered flows are not compensated, there is an ecosystem externality, which leads to inefficiencies (Tschirhart 2009, Crocker and Tschirhart 1992).

Bioeconomic models are useful for valuation of ecosystem services, because they can include the positive or negative effects on the economic yield of changing environmental factors (Smith and Crowder 2011). In addition, ecosystem services are often produced through a combination of different inputs, labour, capital and ecosystems. Kellner et al. (2011) present an example of model that includes: provisioning, such as catch of fish, regulating services consisting of habitat maintenance (e.g. Parrot fish contribute to coral regeneration by feeding on small macrophytes which compete with the corrals), and cultural services i.e. non-extractive recreational activities. Ecosystem models such as Ecopath with Ecosim (Christensen and Walters, 2004) and Atlantis (Fulton 2010) have been developed aiming at modelling the entire ecosystem. These ecological models, however, are not constructed for assessing all economic values produced by the ecosystem (Lassen et al 2013).

The impact of fishing on the marine ecosystems takes the form of direct damage and indirect effects via the food web. Some of the indirect effects can be modelled by including species interaction. With respect to the direct damage, it occurs through a number of effects; mortality of non-target fish species, seabirds and mammals, discards, damaging epifauna, smoothing and suspending of sediments, reducing seabed roughness, removing species that produce structure, damaging reefs, kelp and sea grass (Hilborn 2011, Auster and Langton 1999). These effects reduce diversity and non-market values and may damage productivity of stocks and thereby damage future fishing. Research regarding the physical effects of different gear types on different habitats has been carried out (Armstrong and Falk-Petersen 2008, Auster 1998). However, the extent to which the fishing sector causes externalities upon its own activities by reducing future catches through the habitat-fisheries interactions is not well known (Armstrong and Falk-Petersen 2008).

The indirect damage could be modelled as changes in intrinsic growth rate or carrying capacity. Ryan et al. (2014) examine fishing activities that affect the underlying biological productivity. These ecosystem externalities may be positive as well as negative. Fishing may damage habitat in ways that reduce productivity, however, in some cases it may also increase food availability, hence, increasing productivity of the target species. A simple model set up by Ryan et al. (2014) incorporates stock and crowding externalities as well as ecosystem externalities, and the effects on system dynamics, open-access equilibria, and optimal fishery regulation are outlined. The effect of ecosystem externalities on the harvest is modelled via the stock growth. An alternative way of including ecosystem externalities is to uses habitat as an additional state variable in a fishery where fishing effort causes habitat damage, which in turn affects fishery productivity negatively (Janmaat 2012).

The central research question in the present paper is to what extend conventional management policies based on the concepts of MEY and MSY are useful when a broader range of ecosystem services are taken into account and to provide guidance on what the potential adjustments could be. In order to analyse the effects of species interaction on ecosystem services, the work presented here first examines a simple predator-prey model subject to fishing. Given this basis, an additional species such as a top predator or a forage species as well as other ecosystem service elements are successively added, i.e. externalities and non-market values. The aim of the paper is to set up a model that through application of numerical methods can explore the effects of different types of species interaction and fleet compositions when externalities and non-market values are added, and hence provide appropriate and operational management advice given that ecosystem interactions and services are taken into account.

## 2. The model

The application of models that capture a wider range of ecosystem services in management of marine areas, other than those related only to commercial activities, is non-trivial. Ecosystem services that provide non-market values must be included, trade-offs must be made between different ecosystem services, and externalities from human activities must be taken into account. The following model optimises, economically, a multiple species and multiple fleet fisheries including both market and non-market values as in Kellner et al. (2011) and Johannesen and Skonhoft (2005). It includes negative externalities from the fishing activities in the form of a damage function. It maximizes the net present social value, S, of a flow of both market and non-market ecosystem services by choosing the fishing effort in each period. Details of the model are given in Appendix A.

$$Max\ S = \max_{ej(t)} \int_0^\infty e^{-\delta t} \left[\sum_{i=1}^{n} \sum_{j=1}^{m} \pi_{ij}(e_j(t), x_i(t)) - d_{ij}(e_j(t)) + v_i(x_i(t))\right] dt \qquad (1)$$

s.t. $dx_i/dt = g_i(\underline{x}_i) - h_{ij}(e_j, x_i)$

where $\pi_{ij}(e_j(t), x_i(t))$ is the profit (or resource rent) from fish species $i$ for fleet $j$, $d_{ij}(e_j(t))$ are externalities affecting species $i$ from the fishing activities of fleet $j$. $e_j(t)$ corresponds to the fishing effort of fleet $j$ in a mixed fishery and $x_i(t)$ is the stock of the $i$'th species. $v_i(x_i(t))$ is the net values of a stream of non-fishing ecosystem services obtained from species $i$. The net value may consist of gross value of ecosystem services and a cost related to maintaining a stock of the species. $g_i(\underline{x})$ is the growth function for species $i$, and $\underline{x}$ is a vector comprising all $n$ species included in the model, $(x_1, x_2, \ldots, x_n)$, such that species interaction is taken into account through the growth function. $h_{ij}(e_j, x_i)$ is the harvested biomass of species $i$ for fleet $j$. $t$ is time, and $\delta$ is the social discount rate whereas $n$ and $m$ represent the number of species and the number of fleets, respectively.

Provisioning services are covered by the profit function ($\pi$) with a related cost function. The regulating and cultural services are expressed in the value function ($v$). The benefits of these services are expected to increase with the stock of the species related to the services, but at a decreasing rate. The costs of these services are captured in the profit function $\pi$ as forgone profit and increased costs (e.g. marine mammals that consume a fraction of the potential harvest) or as direct damage on catch and gear, which can be modelled as a damage function dependent on the size of the stock of the particular species and deducted from the value function. The net value per species can be negative for some species, e.g. invasive species. Costs related to the regulating and cultural services can be taken into account in the value function *v*. The externalities created by human activities are included in the damage function (*d*). By-catch of marine mammals for example can be taken into account when estimating $v_i(x_i(t)$. In the present case, damage is modelled in a steady state without any time lag and regarded as temporary and not permanent. The externalities can also be positive, e.g. activity in fishing communities. Interaction between species is mediated through the stock function (*x*) and this interaction can have several expressions such as predator-prey and competition between species.

Analytical methods have limitations as compared to numerical methods when models become complex as the above. Even the two-species predator-prey model becomes very complex, and is not possible to derive full analytic dynamic solutions for more complex predator-prey systems (Kellner et al. 2011). Based on Clark (1990) it can be shown that a simple version of the model consisting of two interacting species and one fleet, one externality and one non-market value, cannot be determined analytically (Appendix A).

Therefore, numerical models must be applied in these more complex situations. However, numerical models require both specific functional forms and parameter inputs. In that respect, numerical models are subsets of general analytical models. One way to overcome the limitations of numerical models is to conduct sensitivity analyses with respect to both functional forms and data input. As the output of such exercises is extremely comprehensive, it is important to limit the sensitivity analyses to comprise only the most sensitive cases. In particular fishermen's behaviour, the growth functions of the fish stocks, the interaction between stock and the damage on or the benefit to the ecosystem are cases of interest. Frost et al. (2013) show how the application of numerical models can handle very complex and more realistic settings compared to simpler analytical models, including both a number of biological and technical conditions as well as fishermen's behavioural response to different policy measures, and hence provide a deeper insight into and better foundation for management recommendations.

The state equations of the model, $dx_i/dt = g_i(\underline{x},) - h_{ij}(e_j, x_i)$ may take many possible forms and need to be specified. The growth function $g_i(\underline{x})$ includes growth as well as mortalities due to predation and remaining natural mortality. For a thorough analysis of species interaction and ecosystem services linked to the species diversity, the species interaction needs to be more explicit and take into account species interconnections such as predator-prey relationships.

Models with different types of predator's functional responses must be considered for a realistic species interaction (Berryman 1992, Yodzis 1994). Ratio-dependent predation – in which the functional response of the predators depends on the ratio of prey to predators instead of the prey density – has been proposed as a more realistic feature (Arditi and Ginzburg 1989; Berryman et al. 1995a). It builds on the law of diminishing returns, which manifests itself as an increasing difficulty for a predator to meet its energy demands as its population density increases compared to the prey. On this background, Berryman et al. (1995b) extended the logistic predator-prey model to apply to any population in a food web of arbitrary complexity such that each species potentially can interact with any other species. The model defers from the conventional predator-prey models, because it does not conform strictly to the laws of mass conservation, which in conventional models mean that prey consumed is converted into predator growth at a certain rate. The starting point is per-capita growth rate from which is subtracted a number of terms that causes reduction of the intrinsic growth rate such as predation and competition for food and other resources. Hence, according to Berryman et al. (1995b), the general food web equation for the stock $x_i$ of species *i* can be given by:

$$\frac{1}{x_i}\frac{dx_i}{dt} = a_i - b_i x_i - \frac{x_i}{\sum_j c_{ij} x_j} - \frac{\sum_k d_{ik} x_k}{x_i} \quad (2)$$

Where $x_j$ are the stocks of species *j* that $x_i$ consumes, whereas $x_k$ are the stocks of species *k* that prey on $x_i$.

For simplicity in the following analysis, the multispecies model is reduced to a two species predator-prey model. In the numerical application, however, more species can be added. Assuming a simplified food chain with only one predator eating one prey, in the following denoted *x* for the prey and *y* for the predator and including the fishing mortality $F_i(h_{ij}(e_j, x_i))$ we get the following equations. In the following subscript *x* and *y* are used to refer to prey and predator, respectively.

$$\frac{1}{x}\frac{dx}{dt} = a_x - b_x \cdot x - \frac{d_x \cdot y}{x} - F_x \quad (3)$$

And

$$\frac{1}{y}\frac{dy}{dt} = a_y - b_y \cdot y - \frac{y}{c_y \cdot x} - F_y \quad (4)$$

Or in re-written form:

$$\frac{dx}{dt} = x(a_x - b_x \cdot x) - d_x \cdot y - F_x \cdot x \quad (5)$$

$$\frac{dy}{dt} = y(a_y - b_y \cdot y) - \frac{y^2}{c_y \cdot x} - F_y \cdot y \quad (6)$$

This predator-prey model is analysed in order to determine the existence of equilibriums and characterise the different types of potential equilibrium points (Appendix B). This is carried out because it is of particular interest under what conditions the two species are able to form stable equilibriums when fishing mortality is added.

Analytical solutions of bio-economic models as the ones discussed above are only possible in the simpler cases. To form the numerical version of the model, the Euler method is applied, in brief:

$\frac{dx}{dt}$ = $f(x) \approx \frac{\Delta x}{\Delta t}$, then the discrete version is:

$\frac{\Delta x}{\Delta t} = \frac{x_{k+1} - x_k}{\Delta t}$ this gives

$x_{k+1} = x_k + \Delta t \cdot f(x)$

Where $x$ corresponds to one of the species, $\Delta t$ is the time interval (here one year), $k$ is a specific time (year) so that $t_k = \Delta t \cdot k$. $f(x)$ is the state equation; growth minus harvest. In addition, the model needs an initial value, $x_0$.

The numerical model is constructed using equations (5) and (6). Two commercial species are included: a prey species and a predator. With respect to fishing, the model contains two different fleets of which one only catches the predator and the other catches a combination of prey and predator in a fixed proportion defined by the fishing gear. Fleet 1 represents a segment that uses passive gear types, such as net, hook or lines, whereas fleet 2 is assumed to use trawling equipment. Prices are different between species and fleet segments, but assumed to be fixed. Costs are modelled as a linear function of effort because the fishing industry is small relative to other sectors and, therefore, not able to impact input prices. The model is presented in details in Appendix C, and parameters as well as data used for estimation of model parameters are presented in section 3. A third species may be added optionally to the model either as a top predator at a higher trophic level that feeds on both of the other species or as a forage species at a lower trophic level that serves as feed for both the prey species and the predator. The inclusion of these species provides a more complex and perhaps a more realistic system and may facilitate the modelling of more ecosystem services, including the supporting services underpinning the predator-prey system. Interactions between the predator and prey species can be turned on and off in the model, making it possible to compare the case of no species interaction with the case where species interaction is assumed.

The model also have the facility to include the externalities or the damage function, $d_{ij}(e_j)$, one for each of the fleets and non-market values $v_i(x_i)$ corresponding to each of the 3 species. For simplicity, it is assumed in the present context that damage is only dependent of fleets $j$. Furthermore, it is assumed that the damage function has the functional form $d_{ij}(e_j) = k \cdot e_j(t)^l$, where $k$ and $l$ are constants, $k > 0$, $l \geq 1$, and it is assumed that it can be linear or convex. Positive externalities (e.g. activities in coastal towns) may occur from effort in some settings, but are not considered here. Low damage cost scenarios will probably not affect the potential decisions to a significant degree, unless it is accumulated over time, if it is of permanent character or regeneration of the ecosystem is slow. In the following focus is on moderate to high damage. Damage may occur as mortality of non-target fish species, seabirds and mammals, as well as damage on benthic ecosystems and reefs. Both the exponent $l$ and scale coefficient $k$ can be adjusted. In the present context, the two fleets cause similar damage at low effort levels, but the damage function for fleet 2 has a larger exponent than the function for fleet 1, such that the damage inflicted by fleet 2 becomes significantly larger than for fleet 1 at higher effort levels. With respect to the non-market values $v_i(x_i)$, it is assumed that it is increasing for increasing stocks but with a decreasing marginal value, $v_i'(x_i) > 0$ and $v_i''(x_i) < 0$ (e.g. Clark et al. 2010, Pearce 2007). When the stock decreases towards a minimum viable population, the marginal value is expected to increase strongly (Pearce 2007). The non-market values are modelled in the general form s· $x_i(t)^r$, where *s* and *r* are constants, $s > 0$, $0 \geq \mathrm{r} \geq 1$. Both the exponent *s* and scale coefficient *r* can be adjusted.

Behavioural aspects of the model can be managed by an investment/disinvestment or entry/exit function, $I$, that depends on profit. Investment is, for simplicity, assumed to be linear in profit ($\pi$). Thus, positive profits give positive investment, i.e. increase in effort, while negative profit means negative investment, i.e. decrease in effort.. The investment rate and disinvestment rate per unit of profit *v* ($v = I/\pi$) determine the rate of entry and exit, and the entry-exit rate is here chosen to have the same value and set at a moderate level that allows development of a dynamic fleet.

The numerical analysis is conducted by running a series of simulations as well as optimizations using the Premium solver facility in Excel. The results are shown as graphs with detailed comments. The simulations are conducted by setting a specific effort level and letting the model find equilibrium where the dependent variables: biomasses, harvest, etc. become stable, and then recording these results. This is done for a series of effort levels in order to display the relationships between effort and the dependent variables in equilibrium as a function of the interaction of species and marine services. In addition, simulations are conducted based on the assumption that fishing effort is a function of profit so that positive profits give positive investment, i.e. increase in effort while negative profit means negative investment, i.e. decrease in effort. Complementary to these simulations, a number of optimisations are carried out to analyse specific issues. In the optimisations, the solver is set to find the effort levels (investments) that provide the highest net present value for a given time period.

Three different types of model specifications are used: A two-species model without species interaction, a two-species model with interaction and a three-species model. The three-species model includes an additional species, which have been modelled both as a top predator and as a forage species. The two-species model without interaction is included, as it provides a parallel to the conventional single species framework. The two-species model with interaction is used as the baseline model, because it is this model that has been analysed analytically and that thus forms basis for the parameter estimates. Effort is normalized such that the combined effort for the two fleets in the baseline model is set at 100 for the effort level where both species are fished down to 0. Similarly, the baseline model is used to determine an index of 100 for harvest and revenue respectively, such that the maximum harvest (prey and predator combined) and maximum revenue in equilibrium represent 100. Cost, profit, damage, non-market values and net value are subsequently expressed in relation to this index. Also, maximum stock in equilibrium (corresponding to no fishing) for the prey in the two-species interaction model is set to index 100 against which other stocks are normalized for display in the graphs. Although MSY and MEY normally are single-species concepts, in the following they are also used when referring to the combined MSY and MEY in the two-species model.

## 3. Data

The analytical solution of the two species predator-prey model can determine the existence of equilibriums and characterise the different types of potential equilibrium points. For numerical solutions, parameters must be estimated. Parameters and values used for the numerical model are shown in table 1. The growth and interaction parameters for the two principal species, i.e. the prey and the predator, are determined empirically using fishing and biomass estimates for cod and herring from the Baltic Sea. The same parameters were determined for the North Sea for comparison. Although cod prefers sprat to herring (Heikinheimo 2011), the herring is chosen as a prey species here, because it represents a very common species, which are known to interact with cod, and because long time series exists for herring and cod (ICES 2012, ICES 2013). The parameter estimation is carried out using minimized square differences between the annual observed (stock plus the landings, and for cod plus the discards) and estimated biomasses (using the predator-prey model from 3.2) for the two species.

The growth parameters *a* and *b* in the estimations are higher for cod than herring reflecting a faster growth rate and a lower carrying capacity for herring (K = a/b with no interaction). In the model, the parameter estimates for the period 1989-2011 from the Eastern Baltic Sea are used even though longer time series are available, because stocks levels were much higher in the years before the mentioned period, and thus do not represent the current situation. The eastern Baltic area is used as the case study because this area is well described and there are well-known interactions between the common species here, including top predators such as seals. However, after this estimation, parameters were in some cases adjusted in order to ensure realistic results using the two species model. For the 3rd species, named *z* in the following, the parameters for the top predator (e.g. grey seal in the Baltic Sea) and for the forage species (forage species could be small fish species or invertebrate species that provide food for both prey and predator), are chosen such that their biomasses and interaction are realistic compared to the two main species. The carrying capacity of the forage species is set at the same level as the prey *x*, but with a much higher growth rate. For the top predator, the grey seal population in the Baltic Sea is used as an example. It has been estimated that the historic maximum population is presumed to be up to 100,000 individuals (Harding and Härkönen 1999). Using an average size of 200 kg, the listed parameter is obtained.

Prices are set such that they are similar to the prices of cod and herring for the period (STECF 2013). Prices are differentiated for the predator species between the two fleets based on the assumption that fleet 1 is specialised in catching this species and can therefor get a higher price. Cost per unit of effort in the table represents that a high cost situation is set such that profit can be a maximum of 20 % of the revenue. An alternative setting with up to 60 %-65 % profit is used for a low cost situation (here costs are $0.35*u_1$ and $0.35*u_2$). $v_1$ and $v_2$ are the investment rate/disinvestment rates per unit of profit for fleet 1 and 2. $\delta$ is the discount rate.

***Table 1. Parameter values used in the numerical model.***

| | | | |
|---|---|---|---|
| x carrying capacity | 2780000 tonnes | $a_{z\text{-}fs}$ (forage sp.) | 2 |
| y carrying capacity | 583000 tonnes | $b_{z\text{-}fs}$ (forage sp.) | 0.0000007196 |

| | | | |
|---|---|---|---|
| $z_{tp}$ carrying capacity | 20000 tonnes | $d_{zx}$ (forage sp.) | 0.3 |
| $z_{fs}$ carrying capacity | 2780000 tonnes | $d_{zy}$ (forage sp.) | 0.2 |
| $a_x$ (prey) | 0.3474 | $q_{x1}$ | 0 |
| $b_x$ (prey) | 0.000000125 | $q_{x2}$ | 0.0008 |
| $c_{xz}$ (prey) | 30 | $q_{y1}$ | 0.001 |
| $d_{xy}$ (prey) | 0.15 | $q_{y2}$ | 0.0007 |
| $d_{xz}$ (prey) | 0.9 | $p_{x1}$ | 0.3 (EUR/kg) |
| $a_y$ (predator) | 0.68975 | $p_{x2}$ | 0.25 (EUR/kg) |
| $b_y$ (predator) | 0.000001183 | $p_{y1}$ | 1.1 (EUR/kg) |
| $c_{yx}$ (predator) | 15 | $p_{y2}$ | 0.95 (EUR/kg) |
| $c_{yz}$ (predator) | 30 | $u_1$ | 350 (1000 EUR/vessel) |
| $d_{yz}$ (predator) | 0.45 | $u_2$ | 450 (1000 EUR/vessel) |
| $a_{z\text{-}tp}$ (top predator) | 0.15 | $v_1$ | 0.00015 |
| $b_{z\text{-}tp}$ (top predator) | 0,0000075 | $v_2$ | 0.00015 |
| $c_{zx}$ (top predator) | 1 | $\delta$ | 3.5% |
| $c_{zy}$ (top predator) | 1 | | |

Sources: Own estimates

Subscript *x, y, z* are used to refer to the 3 different species. In addition, $z_{tp}$ corresponds to the top predator and $z_{fs}$ to the forage species. $c_{yx}$ is the interaction effect on the predator stock by the prey stock, and $d_{xy}$ is the predation on the prey by the predator, etc.

# 4. Results

## 4.1 Results from qualitative analysis in a Predator-Prey model

The predator prey model analysed in the present context is outlined in equations (3)-(6) above in its most simple form, i.e. without including top predators or forage fish species. In this form the model includes one predator and one prey, which are both being harvested by fishermen. It has been shown (see Appendix B) [1] that, depending on the equilibrium values of the prey *x* and predator *y*, the system can enter both stable equilibria (i.e. stable node, stable focus and a centre) and unstable equilibria (i.e. unstable focus, unstable node and saddle point). Figure 1A-B show an example on how the different equilibrium points are distributed in the state space for the equilibrium points for *x* and *y*. The figure is drawn in such a way that for the given parameter values there is the possibility for a centre, stable focus and node, saddle point and unstable focus. E.g. if the equilibrium point is ~(*x*,*y*)=(3,5) it is a stable node, while if the equilibrium point is ~(*x*,*y*)= (1,6) it is a saddle point. It must be noted that also unstable nodes or unstable focus may exist, if both prey and predator stocks are low. Thus when/if the numerical evaluations outlined below reaches equilibrium, guidelines can be given about which type of

[1] Recall that equilibrium point can have the following character: Stable node, unstable node, saddle point (unstable), stable focus, unstable focus and center (stable).

equilibrium this may be. However, it must be remembered that the equilibrium system will change when more species are added to the system. Again, given the complexity of equilibrium points already seen for the simple two-species system, this underlines how complex a full ecosystem model will be, and why it is most often not possible to give analytic solutions, neither dynamic or static to such systems, which is why numerical ecosystem models, as the one analysed below, are useful. Appendix B gives a thorough description of the qualitative analysis.

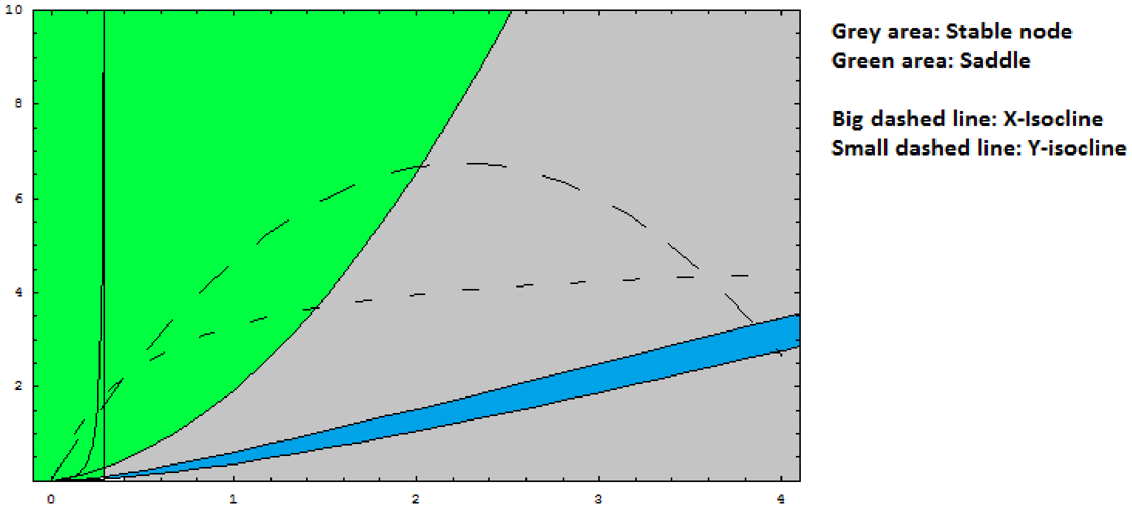


***Figure 1. Distribution of different equilibrium points.***

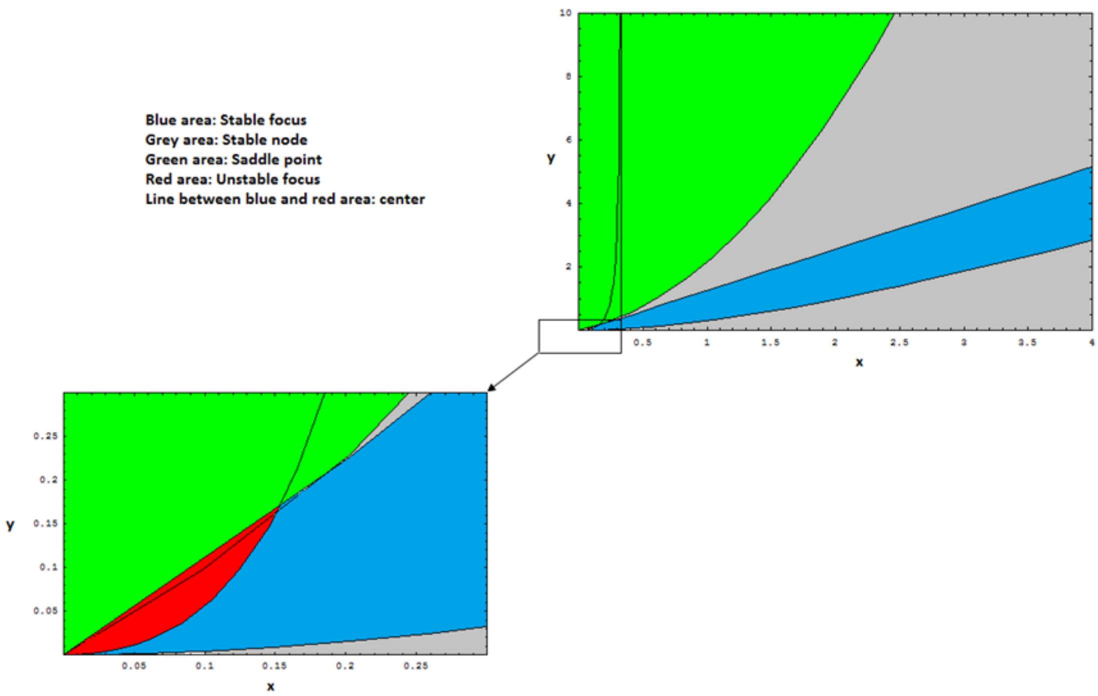


***Figure 2. Distribution of different equilibrium points. Continued.***

### 4.2 Results from numerical analysis

In this section, the result of the numerical analysis that estimates the effect of fishing activity when a broader ecosystem approach, that includes species interaction and ecosystem services which are not of commercial character, is applied. The cases analysed here represent just a few of the potential situations that could be relevant to look at. Eight examples are analysed either through simulation (fig. 3-5, 8-10) or through optimization (fig. 6-7). The model has been established for optimization. However, simulations can also reveal important features of the interactions. Simulations are conducted in two ways; with investment behaviour as the driving force (fig. 3-4, 9) or with the effort level as an exogenous variable, that determines the output (fig. 5, 8, 10). In the latter case, effort is increased in a stepwise fashion, and for each step, the effort level is held constant and equilibrium is allowed to form. It is as such assumed that the effort level can be maintained until equilibrium. The indicators recorded at equilibrium (steady state), corresponding to a sustainable yield, are biomasses, harvest, revenues, costs, profits, damage, non-market values (NMV) and net values. Hence, the results of the simulations here depict a static fisheries model.

In the simulations, where effort is regarded as exogenous, a fixed ratio of efforts for the two fleets has been used. This is a simplification, which facilitates the assessment of the result. It may be noted that the proportions chosen are just a few among all the possible fixed effort proportions. The ratio between the effort of the two fleets has been set in such a way that MSY of the prey and MSY of the predator are reached at the same effort level. With the applied parameters, the ratio between the two efforts is very close to 1:1. In addition, optimisations are carried out where the economic exogenous decision variable is investment behaviour, which determines entry and exit to the fishing fleets and hence fishing effort. The assumption is that fishing effort is a function of profit such that fishing vessels enter or leave the fishery depending on whether the profit is positive or negative. The optimisations are based directly on the model (1). They are carried out with a time horizon at 40 years and the simulations for a longer period, if necessary.

Figure 3 show the development in stock for the prey and predator in the two-species model with interaction, when investment/disinvestment behaviour is assumed in the model. Hence, here fleets can operate independently and are not bound by a fixed effort relationship.

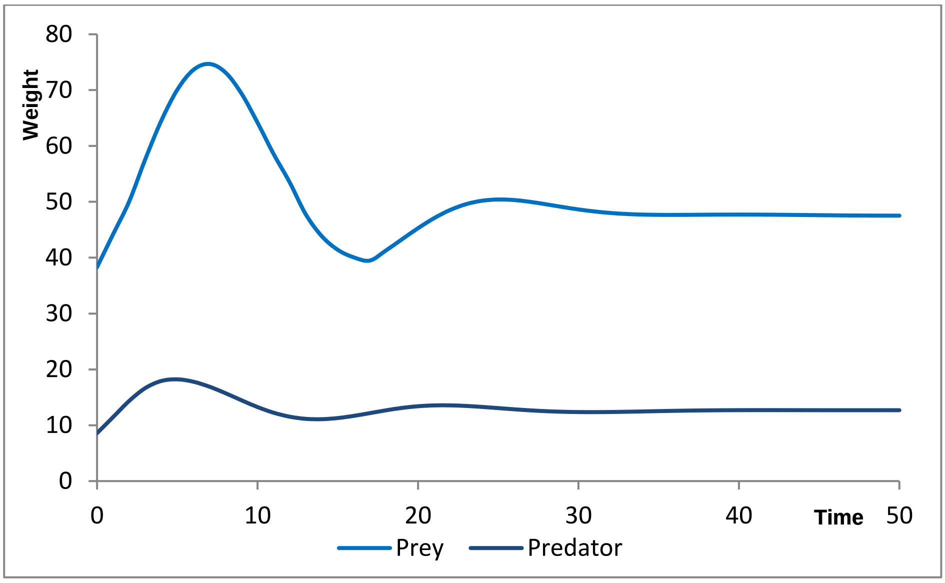


***Figure 3. Development of stocks, two-species model, investment behaviour.***

The above case shows a smooth long-term development of stock. The harvest costs that are used in the profit function for this case are based on the parameters that represent a high cost situation in table 1. However, if the three-species model and low costs are applied, as it is shown in figure 4 (where only the two commercial species are shown), the harvest does not stabilise and the species are fished down, beginning with the prey, then the predator and finally the top predator. This illustrates the risks involved if effort is guided by profit as the criteria for investment decisions. This may also occur for the two-species model if the initial stocks or initial effort is high, but not for the two-species model with no species interaction. The stock extinction happens because a too large fleet capacity is built up and cannot be reduced in time to avoid fishing down the stocks, which are more sensitive to pressure when species interaction is included. And with the set of parameters from table 1, the three-species model is even more sensitive to profit-driven expansions of effort. However, tests show that the extinction of the stocks can be avoided if entry of vessels (investment) is sufficiently slower than exit (disinvestment).

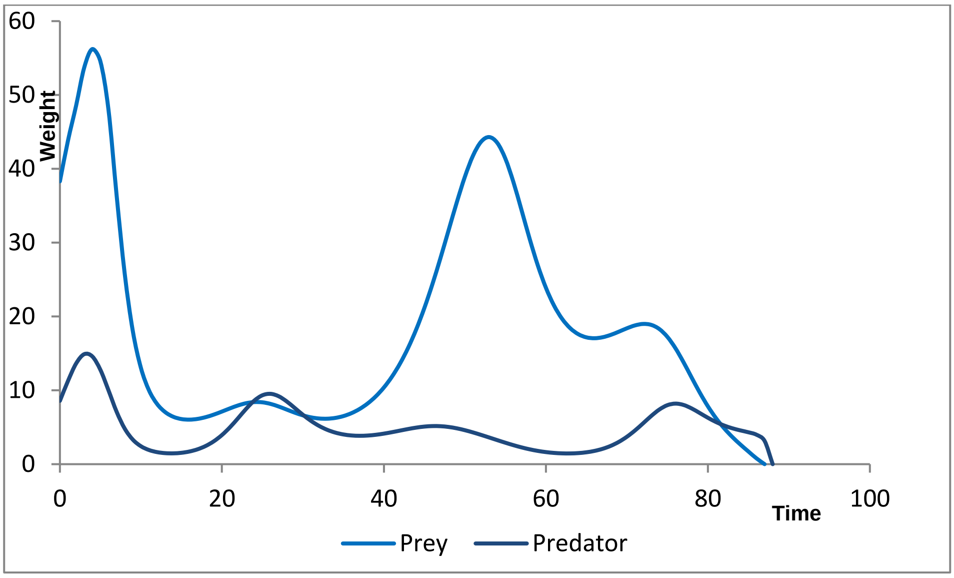


***Figure 4. Development of stock, three-species model, investment behaviour and low cost.***

Figure 5 displays the result of a high damage cost on the optimal policy for the 3 different model specifications treated in the above sections: two-species model without interaction, two-species model with interaction and the three-species model. For all models, there is a large difference between the optimal effort level and the level indicated by a MSY-based policy (model without interaction in fig. 5). The difference is particularly large if the MSY-policy is based on single-species framework (similar to the two-species model without interaction) and the reality involves heavy damage and interaction between the three species. It is also apparent that myopic behaviour that maximises profit without taken the externality into account will result in too high an effort level, and will bring the net value down close to zero. The case is characterised by low operational costs. In the event of high operational costs, the difference between the optimal effort level and the level indicated by a MSY-policy will be even more pronounced.

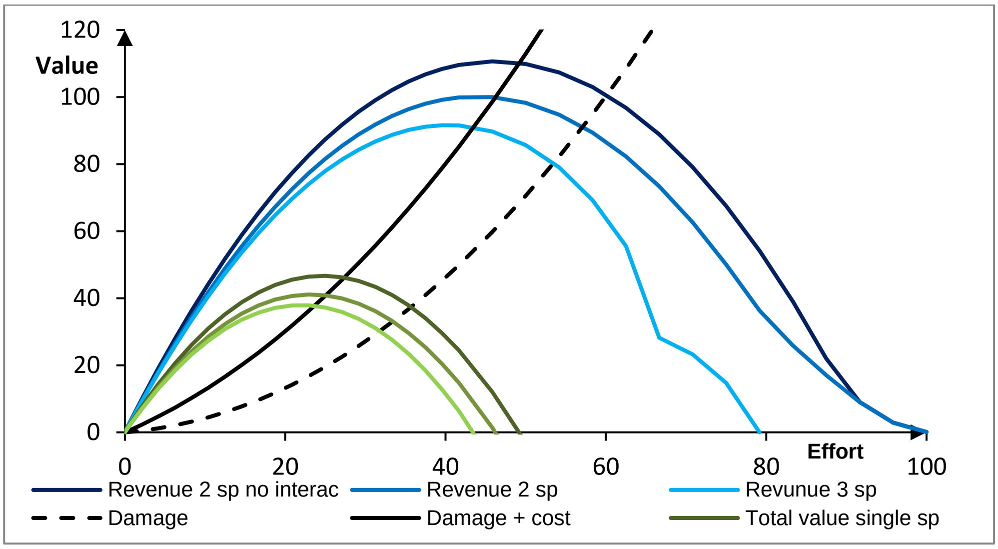


***Figure 5. Revenue and net value at equilibrium, low cost-high damage.***

Figure 6 shows the development of revenue and profit of a simple optimisation. The optimisation includes the restriction that biomasses cannot be fished down in the last year. Hence, the biomasses of year 41 will equal the initial biomasses. The result is very oscillating revenue and profit. In the optimisation an oscillating effort shows superiority to a constant effort. In actual fisheries, this pattern is not seen as fishing quotas are set on an annual basis and there are significant opportunity cost for both capital and labour.

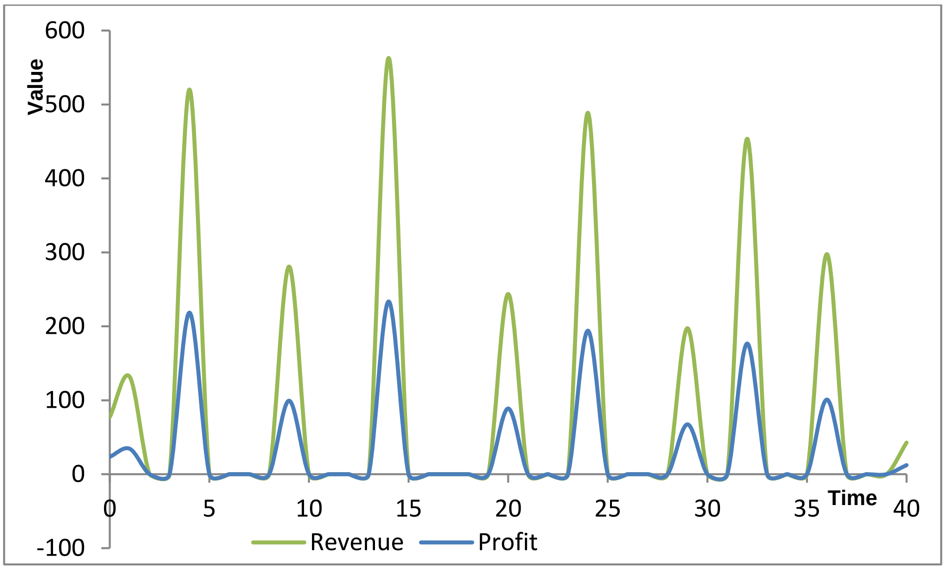


***Figure 6. Optimisation: Revenue and profit, two-species model and high cost.***

If optimisation of profit is carried out without taking the damage cost into consideration effort levels can become very high as the case in figure 6, and so will the corresponding damage. The total discounted net values (profits minus damage costs) are in this case negligible. If on the other hand the damage costs were internalised by restrictions on effort or a tax on the damage, then optimisation would turn out as in figure 7. Here the objective of the optimisation is changes from profit to the net value. Under these assumptions, the discounted value of profit is reduced to a little more than 80 % than profit without restrictions, but the discounted net value increase by orders of magnitude. It appears from the optimisations that because the damage functions are different for the two fleets, there is a reallocation of effort between fleets when damage is taken into account. The result is a higher net value, but there will also be a considerable reallocation of fishing effort from fleet 2 to fleet 1. The result is an increased harvest and a lower stock of the predator and a lower harvest and higher stock for the prey species. This result points to a need for regulation that targets the individual efforts of the two fleets if they cause different degrees of damage, e.g. a tax directed on the fleet that inflict damage on the marine environment.

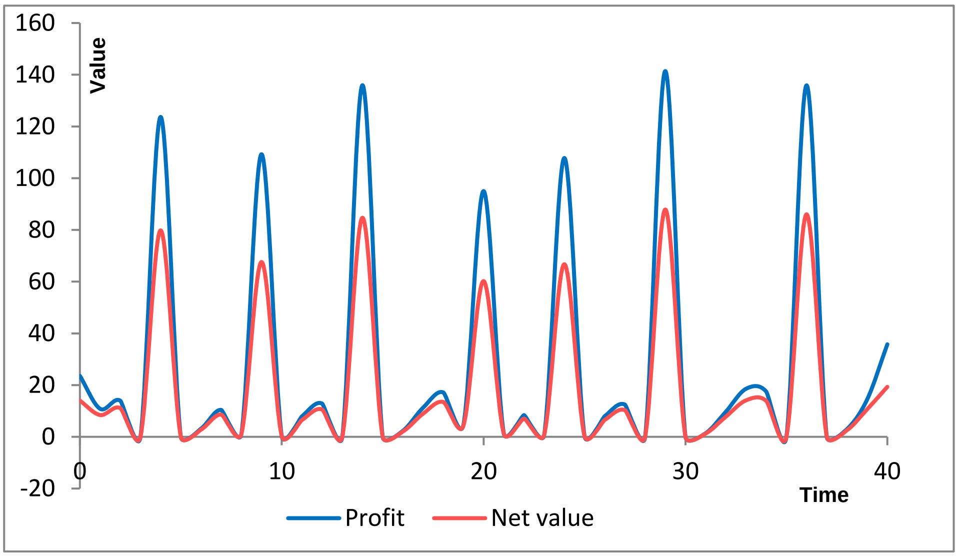


***Figure 7. Optimisation: Profit and net value, two-species model and damage.***

Damage may affect the ecosystem and the food web in many ways. One important issue is whether the fishing activities damage the underlying food web and hence reduces the productivity of commercial fish stocks. In other words, it reduces an important supporting service and thereby it may damage future fishing. In order to handle this complex issue, the three-species model is set up such that the forage species represents the underlying food chain that supports the prey and the predator species. In figure 8, it is assumed that damage is inflicted on the forage species stock, which is modelled as an inversely proportional function of the size of the damage cost. It is calibrated such that the stock of the forage species is reduced to 50 % of its maximum stock at an effort level, which gives the combined MSY for the predator and prey. The damage function has a convex form (see section 2). The damage caused to the forage species stock has a significant effect on the revenue and profit compared to the situation without damage, a case that is shown in the figure as well. Both species collapse at effort levels just above the level corresponding to MSY. Although the damage is significant, MEY-based policy is still an appropriate guidance for advice on fishing level. A policy based on MSY seems, however, risky as the stock may collapse near MSY.

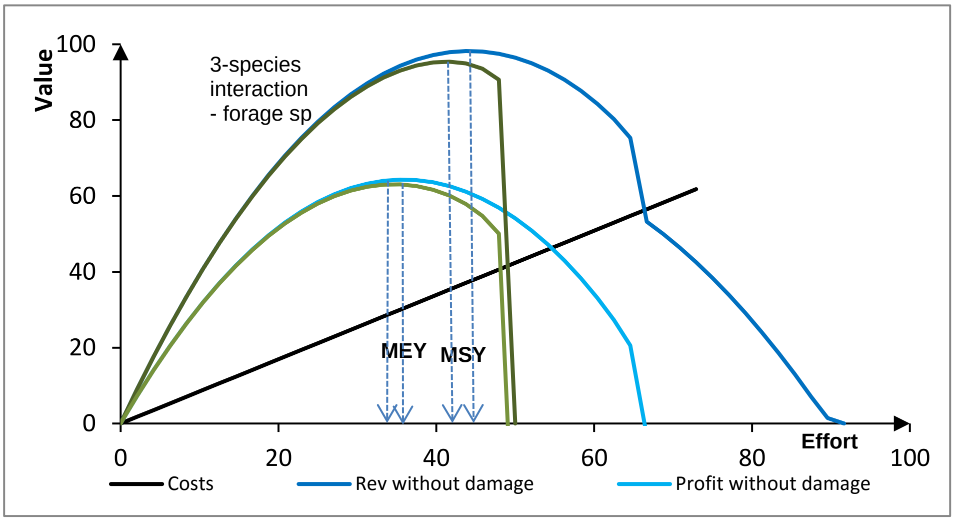


*Figure 8. Revenue and profit at equilibrium, damage to forage species.*

In figure 9, the development of revenue, profit and damage cost over a 50 years period is shown for the two-species model, when investment/disinvestment behaviour is assumed in the model. Profit goes to 0, because the investment behaviour causes fishermen to dissipate the profit, and the situation ends in a bionomic equilibrium. Damage costs reach the same level as revenue. It illustrates that a management system, which is determined by investment behaviour only, can lead to the dissipation of any potential profit and to a negative net result if damage costs are included, as shown in the figure.

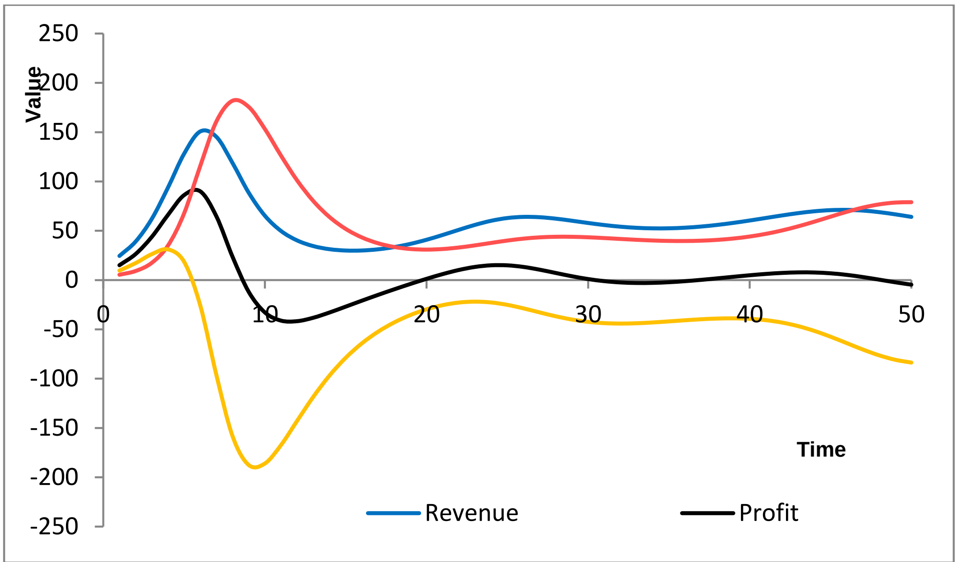


*Figure 9. Development of revenue, profit and damage, medium damage-low cost.*

Figure 10 illustrates a case where non-market values (NMV) has a large influence on the total value. However, this situation will only occur if the NMV is sharply declining with a decreasing stock brought about by increasing effort (here reaching 0 close to MSY), meaning that the species in question are highly sensitive to increases in effort. In addition, a high value of NMV is needed. In the case shown in figure 10 a MSY-based policy will result in loss of most of the NMV and almost half of the total value. An MEY-based policy will - in this case - still safeguard almost half of the NMV and most of the total value.

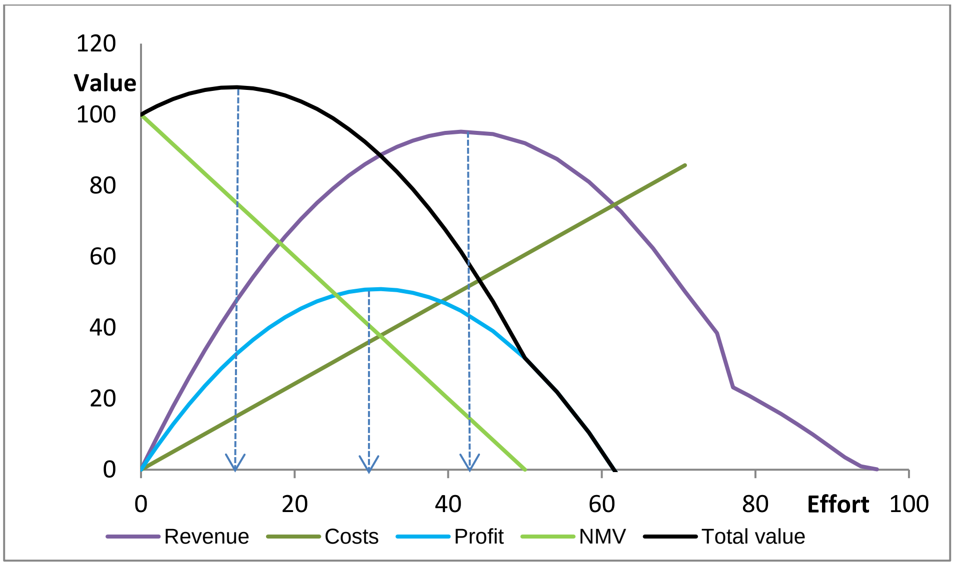


***Figure 10. Economic results with non-market values, three-species model.***

The eight cases presented above represent some of the many potential situations where it could be beneficial to apply a numerical model, which accounts for species interaction and a broader range of ecosystem services. The model used here, is characterized by flexibility and it can accommodate many other different examples.

## 5. Conclusion and Discussion

Ecosystem-based fishery management is expected to become the overall framework that will guide future fishing policies. This will change the objectives of the fisheries management, which at present mainly is based on single-species framework with focus on a few ecosystem services of mainly provisioning character, and aim at the Maximum Sustainable Yield (MSY) or Maximum Economic Yield (MEY) as guiding principles. Ecosystem-based fishery management by contrast will require the establishment of a new set of guiding principles, and therefore a need for assessing the economic effects of this management approach through modelling will be relevant. Such economic analysis should consider several elements: the interrelationship between stocks of different species, all relevant ecosystem services including possible trade-offs between them and the damage by fishing activities to different elements of the ecosystem.

The first stage of the assessment is to analyse the predator-prey model in its most simple form, i.e. without including top predators or forage fish species. In this form, the model includes one predator and one prey, which are both being fished. Depending on the equilibrium values of prey *x* and predator *y*, the system can enter both stable and unstable equilibria, and may have the character of node, focus, saddle point or centre. For a wide range of parameter values, the equilibrium will be stable. However, because analytic solutions cannot be found for more complex models, a numerical model is applied for the different cases, which are assessed here.

The numerical model presented in this paper can conduct an economic analysis that conforms to the criteria mentioned above. The model is flexible because it can include several species at different trophic layers and, hence, simulate a small food web, while at the same time assess the economic effects of fishing on this food web. On the other hand, a disadvantage of the model is that the amount of prey consumed by the predator is not converted directly into predator growth at a certain rate (Berryman 1995b). Therefore, it can be challenging to estimate the direct trade-off between, on one hand, the value of leaving the prey in the sea for predators' consumption and subsequent harvest and, on the other hand, harvesting the prey directly.

The model carries out economic analysis of management interventions under a set of assumptions about species interaction in the food web and the ecosystem effect of fishing. The outcome of the modelling in the present paper should therefore be interpreted as trends rather than concrete results. The results from the numerical analysis show that the inclusion of species interaction and a wider range of ecosystem services than those exclusively linked to commercial fishing will require a change in the conventional management policies. Both the species interaction and the ecosystem services need special attention.

In general, the analyses show that species modelled with interaction can sustain less fishing pressure than if the they are modelled without species interaction. The explanation is that species interaction lowers the carrying capacity and increases predation from species in higher trophic layers or competition for food in the lower tropic layers, which means that less biomass, is available for catches. Also, the optimal level of effort in terms of profit (MEY) and harvest (MSY) is lower as compared to the model without interaction. Hence, if species interaction in its different forms is not taken into consideration when assessing management plans and proposing effort limits, the profitability of the fishery may change and a too high proposed optimal effort level will be the result. Apart from the potentially forgone profits, the excessive use of effort may put stocks in risk of collapse and induce more damage than optimal. The risk of collapse is more pronounced if the lower trophic levels are exploited more intensely than the upper layers and could lead to a sudden and abrupt collapse of the interlinked species. This is partly concluded from the analysis, due to a very simplified food web, where all three species depend on each other and no other species, but it illustrates the fact that the species interaction must be taken into account. The simplified food web leaves out some of the compensatory mechanisms that exist in the ecosystem, such as substitution between predation mortality and other natural mortality (Heithaus et al. 2008, Morissette et al. 2012). The result might be that the effect of species interaction on harvest and profit might be overestimated to some extent.

Besides interaction, the numerical model assesses how the economic result is affected by the inclusion of a broad range of ecosystem services. This is done through the damage cost functions, which depends on effort and reduces the net value, and a set of non-market values, which are functions that depend on the stock of the species. Due to lack of data about the link between fishing effort and the economic results of damage, these functions have been assigned a range of plausible values with a form and a magnitude that will give them sufficient weight to influence the net value. A sharply rising damage function will have a significant influence on the optimal effort level. In particular, there is a large difference between the optimal effort level with damage costs internalised in the decision and the level indicated by a conventional MSY-policy based on a single-species framework if reality involves heavy damage and interaction between species. The MEY and the MSY targets may in some situations not be far apart on the effort-yield curve. In many cases though, a MEY target can accommodate the broader range of ecosystem-based policy goals rather well. However, in an increased damage scenario, a MEY-based policy would also result in a significant loss in net value. Damage may also be disproportional high compared to the profit if the exploitation of the resource is determined by investment behaviour alone. Finally, if fleets cause different degrees of damage then optimal regulation must determine specific targets for each fleet.

The inclusion of non-market values may have a relatively little influence on the optimal effort level in many cases. However, if these values are highly significant and directly related to species that are very sensitive to fishing activities, their value may influence the fishery policy. Such cases of highly valuable and vulnerable species need a policy specifically directed towards this issue, and a solution probably means that effort needs to be reduced very substantially.

The examples shown in this paper suggest that the introduction of ecosystem-based fishery management (EBFM), i.e. the inclusion of a broader range of ecosystem services and species interactions in policy decisions, would require a revision of the conventional management policies. The widely used target of MSY, or the corresponding rate of fishing mortality that a population can sustain, seems less useful in the new context. Besides the problem that the MSY target ignores the costs of fishing and, therefore, is economically unattractive, it is also in contradiction with EBFM as indicated by several cases in the present paper. The MSY concept is generally seen as an integral part of sustainable management of the fisheries (i.e. EBFM) as explained by Richerson et al. (2010). They also point to the MSY as a questionable in this context and suggest that the stock should be higher than the one, which provides MSY. However, the extent to which the fishing mortality should be reduced will depend on the character and value of the other goals in the EBFM. On the other hand, the conventional management policies based on a MEY target will in many cases be close to an optimal policy. There exist ecological conditions – vulnerable species and ecosystems – that require additional policy measures. Such measures or instruments could include requirement of special gear to avoid by-catch or damage to species or structures like reefs and closed areas to protect threatened or sensitive species, or taxes on these damages. Regulation using individual quotas might not provide an optimal solution if fleet segments impact the marine environment differently and should be complemented with other instruments.

The analyses carried out in this paper show the shortcomings of conventional qualitative analytical approaches because of the complexities of marine ecosystems. Numerical models also show shortcomings in particular because specific functional forms are used and data are short in many areas. However, it is shown that much insight can be gained from using such relatively simple models, and a prosperous road for future research seems to be that the numerical models are specifically designed for specific problems and areas in such a way that not least damages and benefits on the ecosystem services from the fishing activity are mapped thoroughly. Therefore, it seems that no uniform measure such as the MSY is desirable.

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## Appendix A. A General Model for Social Optimal Management of a Multiple Species and Multiple Fleet Fisheries with an Ecosystem Approach

The model has been set-up for simulating and assessing the optimal management of a multiple species and multiple fleet fishery, and it captures three main elements; fishing profit, non-fishing values and externalities with respect to fishing. The model could be made spatially explicit if needed. The goal of the fishery management is to maximize the net present social value, *S*, of a multi-species fishery and multiple fleet fisheries by choosing the fishing effort in each period.

Objective function:

$$Max\ S = \max_{ej(t)} \int_0^\infty e^{-\delta t} \left[\sum_{i=1}^{n}\sum_{j=1}^{m} \pi_{ij}(e_j(t), x_i(t)) + v_i(x_i(t)) - d_{ij}(e_j(t))\right] dt\ , \qquad \text{(A1)}$$

s.t. $dx_i/dt = g_i(\underline{x}, d_{ij}) - h_{ij}(e_j, x_i)$ (A2)

$0 \leq e_j \leq e_{max}$

*where*:

the objective function, $\pi_{ij}(e_j(t), x_i(t)) + v_i(x_i(t)) - d_{ij}(e_j(t)$, and the state equations, $dx_i/dt = g_i(\underline{x},) - h_{ij}(e_j, x_i)$, are continuously differentiable functions.

$\pi_{ij}(e_j(t), x_i(t)) = p_i \cdot h_{ij}(e_j, x_i) - c_{ij} \cdot e_j$, = profit (or resource rent) from fishing species *i* for fleet *j* in period *t*.

$v_i(x_i(t)) = GV_i(x_i(t) - DC_i(x_i(t))$, non-fishing net-value of ecosystem services for species *i* in period *t*, e.g. recreation, non-use (existence) value. $v_i$ grows with $x_i$, but at a decreasing rate. $\partial v_i/\partial x_i > 0$. $\partial^2 v_i/\partial x^2_i < 0$. The possible costs of $v_i$ are captured in the profit function as forgone profit and increased costs due to predation on the commercial species or as competition for food resources. The costs can also take the form of a direct damage on catch and gear which is specified in $c_i$.

$GV_i(x_i(t))$ = gross value of ecosystem services for species *i* in period *t*, e.g. value of recreation or existence value. $GV_i(x_i(t)) \geq 0$.

$DC_i(x_i(t))$ = Possible (damage) cost related to maintaining stock of non-commercial species *i* in period *t* (nuisance species or invasive species), e.g. damage to catch by seals or seabirds. $DC_i(x_i(t)) \geq 0$.

$d_{ij}(e_j(t))$ = externality of fishing activities related to species *i* and fleet *j* in period *t*, e.g. damage on sea-floor, discards, activity in fishing communities. In most cases $d_{ij}(e_j(t))$ is a negative externality that reduces the net value, but it can be positive (e.g. activity in fishing communities).

$e_j(t)$ = effort for fleet *j* in period *t*. $e_j(t) \geq 0$.

$x_i(t)$ = stock of species $i$ in period $t$. In tons or numbers. $x_i(t) > 0$.

$\underline{x} = (x_1, x_2, \ldots, x_i)$.

$g_i(\underline{x})$ = growth of species $i$. $g_i \geq 0$.

$h_{ij}(e_j, x_i) = q_{ij}e_jx_i$. Harvest of species $i$ for fleet $j$. $h_{ij}(e_j, x_i) \geq 0$.

$q_{ij}$ = catchability coefficient for species $i$ and fleet $j$.

$p_i$ = price of species $i$. $p_i \geq 0$.

$c_{ij}$ = cost per unit of harvest for species $i$ taken by fleet $j$. $c_{ij} \geq 0$.

$n$ = number of species, $n \in$ N

$m$ = number of fleets, $m \in$ N

$q$ = number of ecosystem services, $q \in$ N

$i$ = species number, $i = 1,\ldots, n$

$j$ = fleet number, $j = 1,\ldots, m$

$t$ = time.

$\delta$ = discount rate. $\delta = \geq 0$.

In order to find an optimal solution the maximum principle must be applied. However, as shown in appendix B even a predator-prey model with one fleet, without damage function and non-market values, is complicated to solve analytically. Hence, in the following a simple version of the model is analysed, consisting of two species without interaction and one fleet, one externality and one non-market value linked to one of the two species (two state variables and one control variable). For simplicity the effect of damage on growth is not considered. The present value Hamiltonian can be expressed as follows:

$$H = \sum_{i=1}^{n}[e^{-\delta t}\ ((\pi_i(e(t), x_i(t))\ +\ v_i(x_i(t))\ - d(e(t))) + \lambda_i(g_i(x) - h_i(e, x_i))] \qquad \text{(A3)}$$

Inserting the relevant expressions, this gives the following.

$$H = e^{-\delta t}\,[p_1 \cdot q_1 \cdot x_1 e + p_2 \cdot q_2 \cdot x_2 e - ce + v_1(x_1) - d(e)] + \lambda_1(g(x_1) - q_1 \cdot e \cdot x_1) + \lambda_2(g(x_2) - q_2 \cdot e \cdot x_2),$$

where $\lambda_i$ are the co-state variable and the shadow price of $x_1$and $x_2$.

From H we get:

The maximum principle: $\partial H/\partial e = 0$

$$\Leftrightarrow e^{-\delta t}\,(p_1 \cdot q_1 \cdot x_1 + p_2 \cdot q_2 \cdot x_2 - c + v_1(x_1(e'(t)) - d'(e)) - \lambda_1(q_1 \cdot x_1) - \lambda_2(q_2 \cdot x_2) = 0 \qquad \text{(A4)}$$

Adjoint equations:

$\partial\lambda_1/\partial t = -\partial H/\partial x_1$ and

$\partial\lambda_2/\partial t == -\partial H/\partial x_2$

$\Leftrightarrow \partial H/\partial x_1 = e^{-\delta t}(p_1 \cdot q_1\, e + v_1'(x_1)) + \lambda_1(g_1' - q_1 \cdot e) = -\dot{\lambda}_1$ (A5)

and $\partial H/\partial x_2 = e^{-\delta t} p_2 \cdot q_2\, e + \lambda_2(g_2' - q_2 \cdot e) = -\dot{\lambda}_2$

<u>Dynamic constraints</u>:

$\partial x_1/\partial t = \dot{x}_1 = g_1 - q_1 \cdot e \cdot x_1$ (A6)

$\partial x_2/\partial t = \dot{x}_2 = g_2 - q_2 \cdot e \cdot x_2$

Following Clark (1990), chapter 10, p. 317-18, and initially ignoring the externality and non-market value, a solution in equilibrium is considered; $\dot{x}_1, \dot{x}_2 = 0$.

Hence, $e = g(x_1)/(q_1 \cdot x_1) = g(x_2)/(q_2 \cdot x_2)$ (A7)

The adjoint equations can be rewritten as:

$\dot{\lambda}_1 - \lambda_1 \gamma_1 = -e^{-\delta t}(p_1 \cdot q_1\, e)$

$\dot{\lambda}_2 - \lambda_2 \gamma_2 = -e^{-\delta t}(p_2 \cdot q_2\, e)$

Where $\gamma_1 = g'(x_1) - g(x_1)/x_1$ and $\gamma_2 = g'(x_2) - g(x_2)/x_2$

Solutions to these equations are (both are constants):

$e^{\delta t} \lambda_1 = \frac{p_1 \cdot q_1\, e}{\gamma_1 + \delta}$

(A8)

$e^{\delta t} \lambda_2 = \frac{p_2 \cdot q_2\, e}{\gamma_2 + \delta}$

Using these results to reorganise the Hamiltonian, the following is obtained:

$$p_1.q_1 \left[x_1 - \frac{g(x_1)}{\gamma_1 + \delta}\right] + p_2.q_2 \left[x_2 - \frac{g(x_2)}{\gamma_2 + \delta}\right] = c \quad \text{(A9)}$$

Equations (A9) together with (A7) determines the optimal equilibrium populations, although it is not possible to obtain a complete solution (Clark 1990).

Adding $v_1'(x_1)$, $v_1(x_1(e'(t))$ and $d'(e)$) complicates the solution, particularly because $v_1(x_1)$ depends on $t$. Hence, there is good reason to apply numerical approaches for the analysis of the more complex settings with more than one interacting species, externalities and non-market values.

# Appendix B. Predator-prey model

## 1. Background

According to Berryman et al. (1995) the general food web equation for the stock of species $\boldsymbol{x_i}$ can be given by:

$$\frac{1}{x_i}\frac{dx_i}{dt} = a_i - b_i x_i - \frac{x_i}{\sum_j c_{ij} x_j} - \frac{\sum_k d_{ik} x_k}{x_i} \qquad \text{(B1)}$$

Where $x_j$ are the stocks of species *j* that $x_i$ consumes, whereas $x_k$ are the stocks of species *k* that prey on $x_i$.

Assuming a simplified food chain with only one predator (*y*) eating one prey (*x*) and including the fishing mortality $F_i(h_{ij}(e_j, x_i))$ we get the following equations[2]. In the following subscript x and y are used to refer to prey and predator respectively:

$$\frac{1}{x}\frac{dx}{dt} = a_x - b_x \cdot x - \frac{d_x \cdot y}{x} - F_x \qquad \text{(prey)} \qquad \text{(B2)}$$

And

$$\frac{1}{y}\frac{dy}{dt} = a_y - b_y \cdot y - \frac{y}{c_y \cdot x} - F_y \qquad \text{(predator)} \qquad \text{(B3)}$$

Or in re-written form:

$$\frac{dx}{dt} = x\,(a_x - b_x \cdot x) - d_x \cdot y - F_x \cdot x \qquad \text{(B4)}$$

$$\frac{dy}{dt} = y\,(a_y - b_y \cdot y) - \frac{y^2}{c_y \cdot x} - F_y \cdot y \qquad \text{(B5)}$$

$a_x$, $a_y$, $b_x$, $b_y$, $c_y$ and $d_x$ are positive parameters. $a_x$ and $a_y$ are related to the intrinsic growth rate, $b_x$ and $b_y$ are related to intraspecific competition for fixed resources and $c_y$ and $d_x$ are concerned with interaction between species. In these equations the terms $x(a_x - b_x \cdot x)$ and $y(a_y - b_y \cdot y)$ can be recognized as the logistic growth equation, including both recruitment and natural mortality other than from predation relationships. The terms $\frac{y^2}{c_y \cdot x}$ and $d_x \cdot y$ describes the predator-prey relationship: when the amount of prey increases, the overall mortality of the predator decreases and vice versa, while the overall mortality of the predator increases when its own stock increases due to increased competition for the resources available. For the prey the overall mortality decreases when the predator density decreases and vice versa.

[2] The model is limited to a two-species predator-prey model in order to handle it analytically. In section 3.3 and appendix C, more species may be added in the numerical version.

At present nothing more is assumed about the fishing mortalities $F_x$ and $F_y$ but in the numerical version they will be split into fleet segment mortalities as a function of segment efforts.

## 2. Equilibriums

Equilibrium of each stock is found when $\dot{x}$ respectively $\dot{y}$ is zero. Equilibrium of the whole system is obtained when $\dot{x}$ and $\dot{y}$ are zero simultaneously.

*Prey: x-isoclines*: $\dot{x}$ equal to zero:

$\dot{x} = x\,(a_x - b_x \cdot x) - d_x \cdot y - F_x \cdot x = 0 \;\Leftrightarrow$

$$y = \frac{a_x x - b_x x^2 - F_x x}{d_x} = \frac{x}{d_x}(a_x - F_x - b_x x), \qquad d_x > 0 \qquad \text{(B6)}$$

$y = \frac{x}{d_x}(a_x - F_x - b_x x) = -\frac{b_x}{d_x}x^2 + \frac{a_x - F_x}{d_x}x$

The isocline crosses the x-axis in 2 points (y = 0)

The equation: $-\frac{b_x}{d_x}x^2 + \frac{a_x - F_x}{d_x}x = 0$ has the solutions:

x = 0 and x = $\frac{a_x - F_x}{b_x}$

and the isocline has a global maximum at x= $\frac{a_x - F_x}{2\,b_x}$ $\quad (a_x \geq F_x)$

*Predator: y-isoclines*: $\dot{y}$ equal to zero:

$\dot{y} = y(a_y - b_y \cdot y) - \frac{y^2}{c_y \cdot x} - F_y \cdot y = 0 \;\Leftrightarrow$

$y(a_y - F_y - b_y y) = \frac{y^2}{c_y \cdot x} \;\Leftrightarrow$

$$x = \frac{y}{c_y\,(a_y - F_y - b_y y)} \qquad \text{(B7)}$$

*x* is non-negative, and for this to be true the following must hold (with $c_y$>0):

$(a_y - F_y - b_y y) > 0 \;\Leftrightarrow$

$0 \leq y < \frac{a_y - F_y}{b_y}(b_y > 0,\; a_x \geq F_x)$

The y-isocline is increasing in x and does only cross the x-axis and y-axis in the point (0,0) and it goes asymptotically towards $\frac{a_y - F_y}{b_y}$ when *x* goes to infinity.

Isoclines cross: $\dot{x}$ and $\dot{y}$ equal to zero, hence where equations (B6) and (B7) cross:

$y = \frac{x}{d}(a_x - F_x - b_x x)$

$x = \frac{y}{c\,(a_y\, - F_y - \,b_y\, y)}$

The value of x is then inserted in the first equation (*c* and *d* for simplicity):

$cd(a_y\, - F_y - \,b_y\, y) - a_x\, + \,F_x\, = -\frac{b_x y}{c\,(a_y\, - F_y - \,b_y\, y)}$

Multiplying with the term $c(a_y\, - F_y - \,b_y\, y)$ and rearranging we get the following quadratic equation:

$H{\cdot}y^2 + I{\cdot}y + G = 0$ (B8)

Where *H*, *I* and *G* are specified as:

$H = db_y^2c^2$

$I = 2F_yb_ydc^2 - 2a_yb_ydc^2 + ca_xb_y - cF_xb_y + b_x$

$G = dc^2(a_y - F_y)^2 - ca_xa_y + ca_xF_y + ca_yF_x - cF_xF_y$

Hence, there may be 0, 1 or 2 solutions depending on the parameter values.

The above evaluations show that there are possibilities of three equilibrium points, in addition to the trivial (x, y) = (0, 0): the point where the x-isocline (equation 6) crosses the x-axis (i.e. when y equals zero, no predator) the point ($\frac{a_x - F_x}{b_x}$, 0), which is a viable point as long $\frac{a_x - F_x}{b_x}$ > 0, and finally one or possibly two inner points where the two isoclines cross each other. The actual character of the inner equilibrium points are derived analytically below.

## 3. Characterization of equilibrium points

The character of the equilibrium points can be determined by the eigenvalues of the below system of ordinary differential equations (ODEs), hence we get the following:

$\dot{x} = x\,(a_x - b_x \cdot x) - d_x \cdot y - F_x \cdot x$ = F(x,y)

$\dot{y} = y(a_y - b_y \cdot y) - \frac{y^2}{c_y \cdot x} - F_y \cdot y$ = y $\left[a_y\, - F_y - \,b_y\, y - \frac{y}{cx}\right]$ = G(x,y)

Matrix A contains the first order differential coefficients from the two equations:

A = $\begin{pmatrix} \partial F/\partial x & \partial F/\partial y \\ \partial G/\partial x & \partial G/\partial y \end{pmatrix}$

Where (in equilibrium),

$\partial F/\partial x = a_x\, - F_x$ - 2 $b_x\, x = \frac{d_x y}{x}$ - $b_x\, x = \alpha_{xx}$

$\partial F/\partial y$ = - $d_x = \alpha_{xy}$

$\partial g/\partial x = \frac{y^2}{cx^2} = \alpha_{yx}$

$\partial g/\partial y = a_y - F_y - 2\, b_y\, y - \frac{2y}{cx} = -\, b_y\, y - \frac{y}{cx} = \alpha_{yy}$ (as $\left[a_y - F_y - b_y\, y - \frac{y}{cx}\right] = 0$)

Depending on the sign of the eigenvalues of matrix A above and whether these are complex number, we can organise the types of equilibrium (Clark 1990).

**Table B1. Types of equilibria**

| Character of equilibrium point | Values of λ | Conditions | |
|---|---|---|---|
| Stable node | $\lambda_1, \lambda_2 < 0$ | $(\alpha_{xx} + \alpha_{yy}) < -\sqrt{D}$ and $(\alpha_{xx} + \alpha_{yy}) < 0$ | $D \geq 0$ |
| Stable focus | $\lambda_1, \lambda_2$ complex, re $\lambda_i < 0$ | $(\alpha_{xx} + \alpha_{yy}) < 0$ | $D < 0$ |
| Saddle point | $\lambda_1 < 0 < \lambda_2$ | $-\sqrt{D} < (\alpha_{xx} + \alpha_{yy}) < \sqrt{D}$ | $D \geq 0$ |
| Unstable node | $\lambda_1, \lambda_2 > 0$ | $(\alpha_{xx} + \alpha_{yy}) > \sqrt{D}$ and $(\alpha_{xx} + \alpha_{yy}) > 0$ | $D \geq 0$ |
| Unstable focus | $\lambda_1, \lambda_2$ complex, re $\lambda_i > 0$ | $(\alpha_{xx} + \alpha_{yy}) > 0$ | $D < 0$ |
| Center | $\lambda_1, \lambda_2$ complex, re $\lambda_i = 0$ | $(\alpha_{xx} + \alpha_{yy}) = 0$ | $D < 0$ |

$\lambda_1$ and $\lambda_2$ are the eigenvalues of matrix A above, which means that $\lambda_1$ and $\lambda_2$ are the roots of the equation:

det(A - $\lambda$I) = $\begin{vmatrix} \alpha_{xx} - \lambda & \alpha_{xy} \\ \alpha_{yx} & \alpha_{yy} - \lambda \end{vmatrix}$ (I is the identity matrix), and determined by:

$(\alpha_{xx} - \lambda)(\alpha_{yy} - \lambda) - \alpha_{yx}\alpha_{xy} = 0$

$= \lambda^2 - \lambda\,(\alpha_{xx} + \alpha_{yy}) + (\alpha_{xx}\alpha_{yy} - \alpha_{yx}\alpha_{xy})$

$D = (\alpha_{xx} + \alpha_{yy})^2 - 4(\alpha_{xx}\alpha_{yy} - \alpha_{yx}\alpha_{xy}) = (\alpha_{xx} - \alpha_{yy})^2 + 4\alpha_{yx}\alpha_{xy}$

$\lambda = ½(\,(\alpha_{xx} + \alpha_{yy}) \pm \sqrt{(\alpha_{xx} - \alpha_{yy})^2 + 4\alpha_{yx}\alpha_{xy}})$ (B9)

In order to obtain the detailed conditions for the different types of equilibrium it is necessary to look closer at the different expressions.

First, we examine the discriminant, D.

$D \geq 0$:

$(\alpha_{xx} - \alpha_{yy})^2 + 4\alpha_{yx}\alpha_{xy} \geq 0$

$\Leftrightarrow (\alpha_{xx} - \alpha_{yy})^2 \geq -4\alpha_{yx}\alpha_{xy}$

$\Leftrightarrow |\alpha_{xx} - \alpha_{yy}| \geq \sqrt{-4\alpha_{yx}\alpha_{xy}} = 2\,\frac{y}{x}\sqrt{\frac{d_x}{c}}$ $(i.e. -4\alpha_{yx}\alpha_{xy} \geq 0$ for all $x, y > 0)$

for $\alpha_{xx} > \alpha_{yy}$:

$\alpha_{xx} - \alpha_{yy} \geq 2\frac{y}{x}\sqrt{\frac{d_x}{c}}$

$\Leftrightarrow \frac{d_x y}{x} - b_x x + b_y y + \frac{y}{cx} \geq 2\frac{y}{x}\sqrt{\frac{d_x}{c}}$

$\Leftrightarrow d_x y - b_x x^2 + b_y y x + \frac{y}{c} - 2y\sqrt{\frac{d_x}{c}} \geq 0$ (as x > 0)

$\Leftrightarrow y(d_x + b_y x + \frac{1}{c} - 2\sqrt{\frac{d_x}{c}}) \geq b_x x^2$

$\Leftrightarrow y \geq \frac{b_x x^2}{A + b_y x}$, $A = (d_x + \frac{1}{c} - 2\sqrt{\frac{d_x}{c}})$ (B10)

for $\alpha_{xx} < \alpha_{yy}$:

$\alpha_{yy} - \alpha_{xx} \geq 2\frac{y}{x}\sqrt{\frac{d_x}{c}}$

$\Leftrightarrow -b_y y - \frac{y}{cx} - \frac{d_x y}{x} + b_x x \geq 2\frac{y}{x}\sqrt{\frac{d_x}{c}}$

$\Leftrightarrow -y(d_x + b_y x + \frac{1}{c} + 2\sqrt{\frac{d_x}{c}}) \geq -b_x x^2$

$\Leftrightarrow y \leq \frac{b_x x^2}{B + b_y x}$, $B = (d_x + \frac{1}{c} + 2\sqrt{\frac{d_x}{c}})$ (B11)

When is $\alpha_{xx} > \alpha_{yy}$:

$\frac{d_x y}{x} - b_x x > -b_y y - \frac{y}{cx}$

$\Leftrightarrow d_x y - b_x x^2 > -b_y y x - \frac{y}{c}$

$\Leftrightarrow$ y $(d_x + b_y x + \frac{1}{c}) > b_x x^2$

$\Leftrightarrow$ y > $\frac{b_x x^2}{b_y x + (d_x + \frac{1}{c})}$

When is $\alpha_{xx} < \alpha_{yy}$

y < $\frac{b_x x^2}{b_y x + (d_x + \frac{1}{c})}$

D < 0, with some adjustments of above we get:

for $\alpha_{xx} \geq \alpha_{yy}$:

$\Leftrightarrow y < \frac{b_x x^2}{A + b_y x}$, $A = (d_x + \frac{1}{c} - 2\sqrt{\frac{d_x}{c}})$ (B12)

for $\alpha_{xx} < \alpha_{yy}$:

$\Leftrightarrow y > \frac{b_x x^2}{B + b_y x}$, $B = (d_x + \frac{1}{c} + 2\sqrt{\frac{d_x}{c}})$ (B13)

**Table B2. Properties of the discriminant**

| Discriminant, D ≥ 0 | Discriminant, D < 0 |
|---|---|
| $y \geq \frac{b_x x^2}{A + b_y x}$ and y > $\frac{b_x x^2}{b_y x + (d_x + \frac{1}{c})}$ ⇔ $y \geq \frac{b_x x^2}{A + b_y x}$ | $y < \frac{b_x x^2}{A + b_y x}$ and y > $\frac{b_x x^2}{b_y x + (d_x + \frac{1}{c})}$ |

| or | or |
|---|---|
| $y \le \frac{b_x x^2}{B+b_y x}$ and y < $\frac{b_x x^2}{b_y x+(d_x+\frac{1}{c})}$ ⇔ $y \le \frac{b_x x^2}{B+b_y x}$ | $y > \frac{b_x x^2}{B+b_y x}$ and y < $\frac{b_x x^2}{b_y x+(d_x+\frac{1}{c})}$ |

A = $(d_x + \frac{1}{c} - 2\sqrt{\frac{d_x}{c}})$, B = $(d_x + \frac{1}{c} + 2\sqrt{\frac{d_x}{c}})$

## 4. Examination of the different types of equilibria points

*Stable node*

i) $(\alpha_{xx} + \alpha_{yy}) < --\sqrt{D}$ , $(\alpha_{xx} + \alpha_{yy}) \le 0$, D ≥ 0

⇔ $|\alpha_{xx} + \alpha_{yy}| > \sqrt{D}$

⇔ $(\alpha_{xx} + \alpha_{yy})^2 > (\alpha_{xx} - \alpha_{yy})^2 + 4\alpha_{yx}\alpha_{xy}$

⇔ $\alpha_{xx}\alpha_{yy} > \alpha_{yx}\alpha_{xy}$

Now inserting the terms from above:

$(\frac{d_x y}{x} - b_x x)(-b_y y - \frac{y}{cx}) > -\frac{d_x y^2}{cx^2}$

⇔ $-\frac{d_x b_y y^2}{x} - \frac{d_x y^2}{cx^2} + b_x b_y xy + \frac{b_x y}{c} > -\frac{d_x y^2}{cx^2}$

⇔ $b_x (x b_y + \frac{1}{c}) > \frac{d_x b_y y}{x}$

⇔ y < $\frac{x b_x}{b_y d_x}(x b_y + \frac{1}{c})$

⇔ y < $\frac{b_x}{d_x}x^2 + \frac{b_x}{d_x b_y c}x$ (B14)

With the roots (0, 0) and $(-\frac{1}{b_y c}$ , 0)

ii) $(\alpha_{xx} + \alpha_{yy}) < 0$

⇔ $\frac{d_x y}{x} - b_x x + (-b_y y - \frac{y}{cx}) < 0$

⇔ $\frac{d_x y}{x} - b_x x - b_y y - \frac{y}{cx} < 0$

⇔ $d_x y - b_x x^2 - b_y y x - \frac{y}{c} < 0$

⇔ $y(d_x - b_y x - \frac{1}{c}) < b_x x^2$

⇔ y < $\frac{b_x x^2}{(-b_y x+C)}$ , for $(-b_y x + C) > 0$ and y > $\frac{b_x x^2}{(-b_y x+C)}$ , for $(-b_y x + C) < 0$ , (B15)

where C = $(d_x - \frac{1}{c})$

*Stable focus*

From above

i) $(\alpha_{xx} + \alpha_{yy})$ < 0 ; and D < 0

⇔ y < $\frac{b_x x^2}{(-b_y x+C)}$ , where C = $(d_x - \frac{1}{c})$ and D < 0

*Saddle point*

Here we look at two separate cases, $(\alpha_{xx} + \alpha_{yy})$ > 0 and $(\alpha_{xx} + \alpha_{yy})$ < 0. In both cases it is assumed that D ≥ 0

i) $(\alpha_{xx} + \alpha_{yy})$ > 0

In this case $(\alpha_{xx} + \alpha_{yy}) + \sqrt{D}$ is trivially >0, but it must be ensured that $(\alpha_{xx} + \alpha_{yy}) - \sqrt{D} <$ 0

$(\alpha_{xx} + \alpha_{yy})$ < $\sqrt{D}$

⇔ $(\alpha_{xx} + \alpha_{yy})^2$ < $D$

⇔ $\alpha_{xx}\alpha_{yy} < \alpha_{yx}\alpha_{xy}$

⇔ y > $\frac{b_x}{d_x}x^2$ + $\frac{b_x}{d_x b_y c}x$ (B16)

or

ii) $(\alpha_{xx} + \alpha_{yy})$ < 0

In this case $(\alpha_{xx} + \alpha_{yy}) - \sqrt{D}$ is trivially <0, but it must be ensured that $(\alpha_{xx} + \alpha_{yy}) + \sqrt{D} >$ 0:

$(\alpha_{xx} + \alpha_{yy})$ > $-\sqrt{D}$ , $D$ ≥ 0

⇔ $(\alpha_{xx} + \alpha_{yy})^2$ < $D$

⇔ y > $\frac{b_x}{d_x}x^2$ + $\frac{b_x}{d_x b_y c}x$ (similar to B16)

*Unstable node*

i) $(\alpha_{xx} + \alpha_{yy})$ > $\sqrt{D}$ , $D$ ≥ 0

⇔ $(\alpha_{xx} + \alpha_{yy})^2$ > $(\alpha_{xx} - \alpha_{yy})^2 + 4\alpha_{yx}\alpha_{xy}$

⇔ $\alpha_{xx}\alpha_{yy} > \alpha_{yx}\alpha_{xy}$

Now inserting the terms from above:

$(\frac{d_x y}{x} - b_x x)(- b_y y - \frac{y}{cx})$ > $-\frac{d_x y^2}{cx^2}$

⇔ $\frac{d_x b_y y^2}{x} - \frac{d_x y^2}{cx^2}$ + $b_x b_y xy$ + $\frac{b_x y}{c}$ > $-\frac{d_x y^2}{cx^2}$

⇔ $b_x (x\, b_y$ + $\frac{1}{c})$ > $\frac{d_x b_y y}{x}$

⇔ y < $\frac{x b_x}{b_y d_x}(x\, b_y + \frac{1}{c})$

⇔ y < $\frac{b_x}{d_x} x^2 + \frac{b_x}{d_x b_y c} x$ (B17)

With the roots (0, 0) and ($\frac{1}{b_y c}$ , 0)

ii) $(\alpha_{xx} + \alpha_{yy})$ > 0

⇔ $\frac{d_x y}{x}$ - $b_x\, x$ + $(-\, b_y\, y - \frac{y}{cx})$ > 0

⇔ $\frac{d_x y}{x} - b_x\, x - b_y\, y - \frac{y}{cx}$ > 0

⇔ $d_x\, y - b_x\, x^2 - b_y\, y\, x - \frac{y}{c}$ > 0

⇔ $y(d_x\, - b_y\, x - \frac{1}{c})$ > $b_x\, x^2$

⇔ y > $\frac{b_x\, x^2}{(-b_y\, x + G)}$ , where G = $(d_x\, - \frac{1}{c})$ (B18)

*Unstable focus*

From above with adjustments

i) $(\alpha_{xx} + \alpha_{yy})$ > 0

⇔ y > $\frac{b_x\, x^2}{(-b_y\, x + C)}$ , where G = $(d_x\, - \frac{1}{c})$ and D < 0

*Center*

From above with adjustments

i) $(\alpha_{xx} + \alpha_{yy})$ = 0

⇔ y = $\frac{b_x\, x^2}{(-b_y\, x + C)}$ , where G = $(d_x\, - \frac{1}{c})$ and D < 0

With the above conditions, we obtain the following specific conditions for the equilibrium points:

**Table B3. Conditions for the equilibrium points.**

| Character of equilibrium point | Specific conditions |
|---|---|
| Stable node | y < $\boldsymbol{\frac{b_x}{d_x} x^2}$ + $\boldsymbol{\frac{b_x}{d_x b_y c} x}$, and y < $\boldsymbol{\frac{b_x\, x^2}{(-b_y\, x + G)}}$ ; D≥ **0** |
| Stable focus | y < $\boldsymbol{\frac{b_x\, x^2}{(-b_y\, x + G)}}$ , D < 0 |
| Saddle point | y > $\boldsymbol{\frac{b_x}{d_x} x^2}$ + $\boldsymbol{\frac{b_x}{d_x b_y c} x}$ , D≥ **0** |
| Unstable node | y < $\boldsymbol{\frac{b_x}{d_x} x^2}$ + $\boldsymbol{\frac{b_x}{d_x b_y c} x}$, and y > $\boldsymbol{\frac{b_x\, x^2}{(-b_y\, x + G)}}$ ; D≥ **0** |

| | |
|---|---|
| Unstable focus | y > $\frac{b_x x^2}{(-b_y x+G)}$ , D < 0 |
| Center | y = $\frac{b_x x^2}{(-b_y x+G)}$ , D < 0 |

G = $(d_x - \frac{1}{c})$

It can be shown that the inner equilibrium point, when only one exists and it occurs to the right of the x-isocline maximum, is stable - a stable node or a stable focus, depending on the values of the ingoing parameters (figure B1).

**Figure B1**

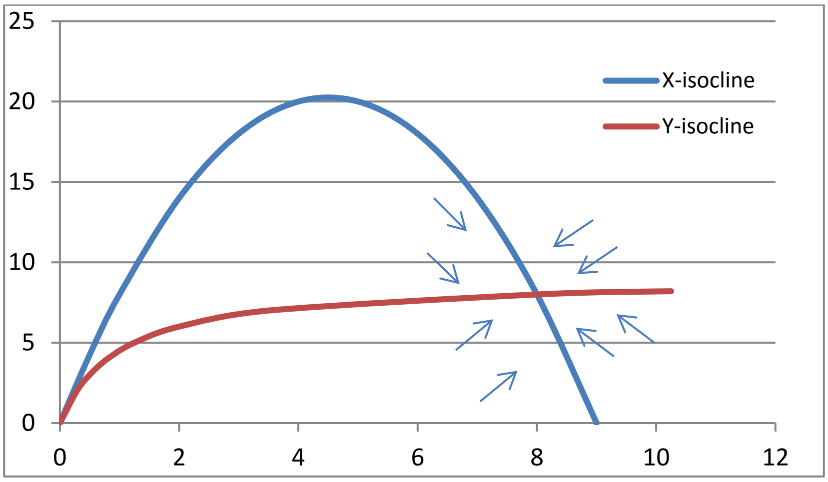
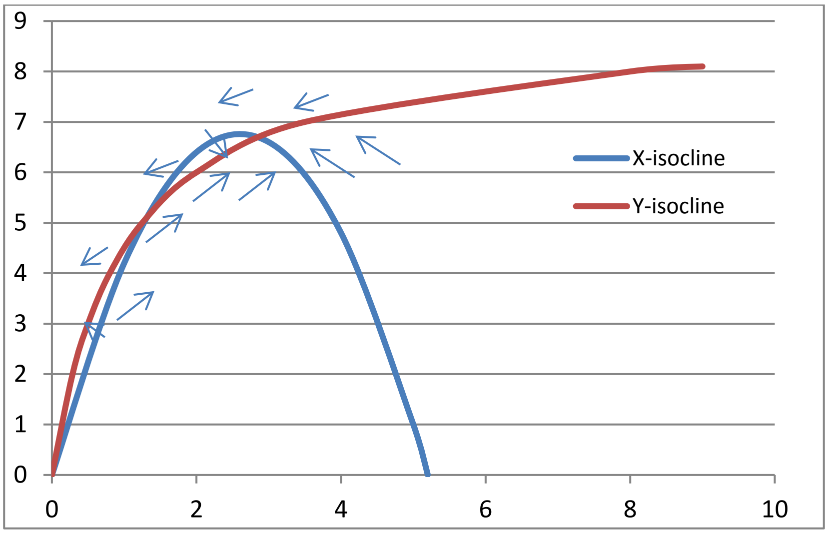
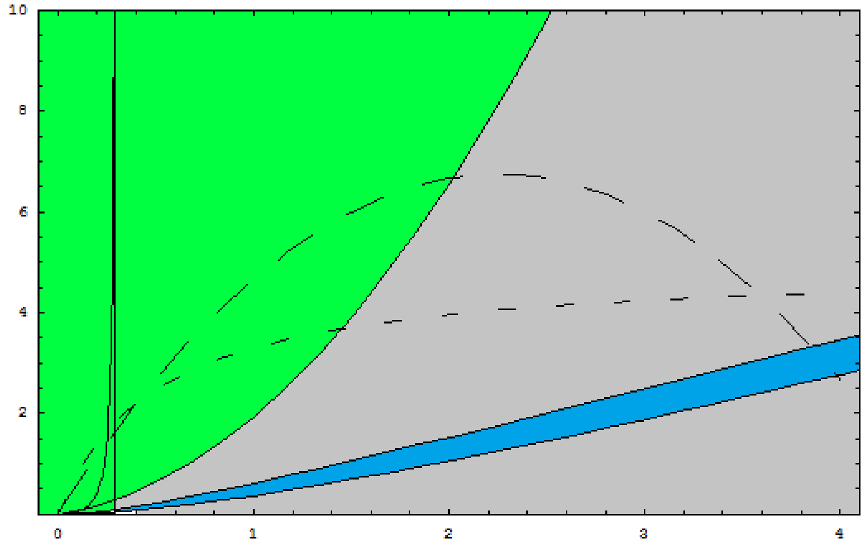



**Figure B2**




When two possible inner points exist, typically one is stable and the other unstable (figure B2). Figure B3 shows the typical distribution of the equilibrium types. It must be notes that also unstable nodes or unstable focus may exist, if both prey and predator stocks are low (B3). The x and y-isoclines shown in figure B3 indicate just one of many possible locations.

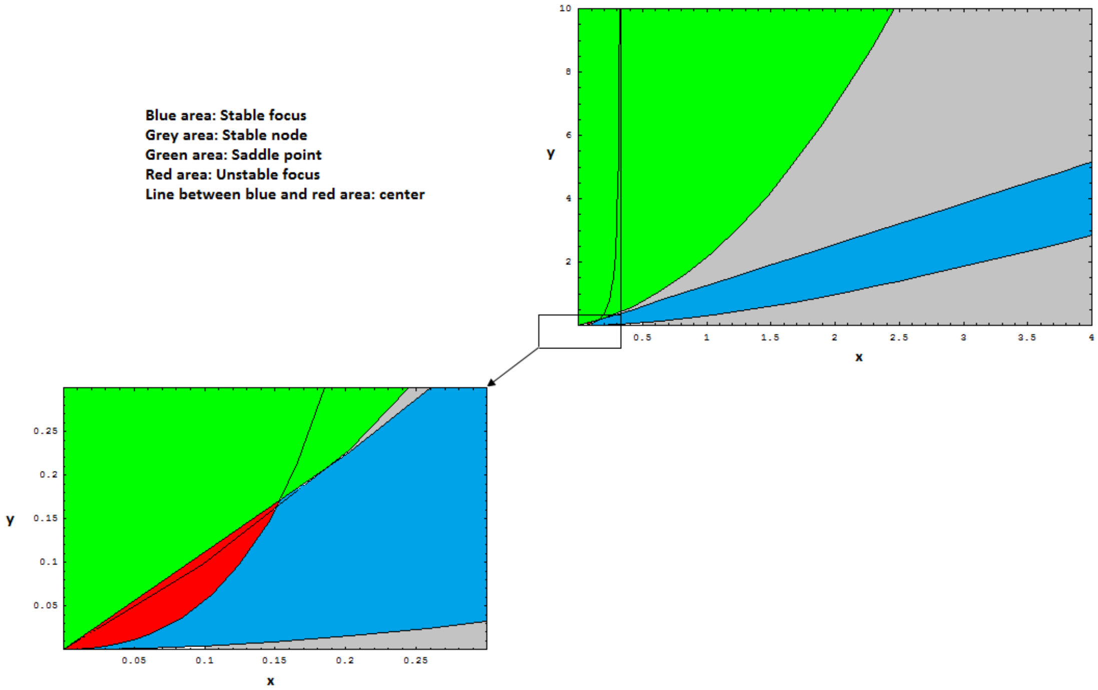
## Figur B3




**Grey area: Stable node**
**Green area: Saddle**

**Big dashed line: X-Isocline**
**Small dashed line: Y-isocline**

## Figur B4



## 5. Bionomic equilibrium

The inner equilibrium $\left(x_{0,}, y_0\right)$ varies when the fishing mortalities of the two species varies. It is – initially – assumed that the species are caught jointly by one fleet, i.e. that equation (4) and (5) are given by:

$$\dot{x} = x\ (a_x - b_x \cdot x) - d_x \cdot y - q_x \cdot E\ x \quad = 0$$

$$\dot{y} = y(a_y - b_y \cdot y) - \frac{y^2}{c_y \cdot x} - q_y \cdot E\ y \ = 0$$

Where $q_x$, $q_y$ are the catchability coefficients.

Thus when there is an inner equilibrium point, the corresponding equilibrium effort is given by:

$$E = \frac{a_x}{q_x} - \frac{b_x\ x_0}{q_x} - \frac{d_x y_0}{q_x \cdot x_0}$$
$$E = \frac{a_y}{q_y} - \frac{b_y\ y_0}{q_y} - \frac{y_0}{q_y \cdot c_y\ x_0} \qquad \text{(B19)}$$

Equating the two parts of equation (19) therefore the equilibrium point as the relationship between $x_0$ and $y_0$ is given by:

$$y_0\ \left(\frac{b_y}{q_y} + \frac{1}{q_y \cdot c_y\ x_0} - \frac{d_x}{q_x \cdot x_0}\right) = \frac{a_y}{q_y} - \frac{a_x}{q_x} + \frac{b_x\ x_0}{q_x} \ \Leftrightarrow$$

$$\boldsymbol{y_0} = \frac{\frac{a_y}{q_y} - \frac{a_x}{q_x} + \frac{b_x\ x_0}{q_x}}{\frac{b_y}{q_y} + \frac{1}{q_y \cdot c_y\ x_0} - \frac{d_x}{q_x \cdot x_0}} \qquad \text{(B20)}$$

A bit of manipulation shows that *y0* is given by:

$$\boldsymbol{y_0} = \frac{x_0 (A + B\, x_0)}{C x_0 + D} \qquad \text{(B21)}$$

where:

$$A = \frac{a_y}{q_y} - \frac{a_x}{q_x}$$

$$B = \frac{b_x}{q_x}$$

$$C = \frac{b_y}{q_y}$$

$$D = \frac{1}{c_y\, q_y} - \frac{d_x}{q_x}$$

Bionomic equilibrium is obtained when the profit $\pi$ is zero whilst the two stocks are in equilibrium. The profit is – simplified – given by:

$$\pi = p_x \cdot q_x \cdot E \cdot x + p_y \cdot q_y \cdot E \cdot y - c \cdot E \qquad \text{(B22)}$$

$\pi$ is non-trivially zero when:

$$y = \frac{c}{p_y \cdot q_y} - \frac{p_x \cdot q_x}{p_y \cdot q_y} \cdot x \qquad \text{(B23)}$$

Hence, setting (20) equal to (23) and a bit of manipulation gives the following conditions for a bionomic equilibrium:

$$x_0^2\left(\mathrm{c_y} q_x^2 b_y \mathrm{p_x} + \mathrm{b_x p_y c_y q_y^2}\right) + x_0\left(p_x q_x^2 + c_y q_x p_y\, a_y q_y - q_x c b_y c_y - q_x\, p_y q_y^2 c_y - d_x p_x q_x q_y c_y\right) + \mathrm{c}\left(d_x q_y c_y + q_x\right) = 0 \qquad \text{(B24)}$$

Jointly with (20) for determination of $y_0$.

## Appendix C. Numerical model

The numerical model is based on the predator-prey model of section 3.2 and appendix B, hence one predator, *y*, eating one prey, *x*. In addition as explained in section 3.3 there can be a 3rd species, either a top predator, $z_{tp}$, preying on both other species and one forage specie, $z_{fs}$, which is eaten by both the prey and the predator. The parameters, *a* and *b* determines recruitment and natural mortality for the individual species, while *c* and *d* denotes the mortality rates inflicted by the species on each other. The biomasses are determined as:

$$x_{n+1} = x_n + x_n(a_x - b_x \cdot x_n) - d_{xy} \cdot y_n - d_{xztp} \cdot z_{tpn} - \frac{{x_n}^2}{c_{xz}\, z_{fsn}} - F_x \cdot x_n \quad \text{(C1)}$$

$$y_{n+1} = y_n + y_n(a_y - b_y \cdot y_n) - d_{yz_{tp}} \cdot z_{tpn} - \frac{{y_n}^2}{c_{yx} \cdot x_n + c_{yz} z_{fsn}} - F_y \cdot y_n \quad \text{(C2)}$$

$$z_{fs\,n+1} = z_{fs\,n} + z_{fs\,n}(a_{zfs} - b_{zfs} \cdot z_{fs\,n}) - d_{zx} \cdot x_n - d_{zy} \cdot y_n \quad \text{(C3)}$$

$$z_{tp\,n+1} = z_{tp\,n} + z_{tp\,n}\left(a_{ztp} - b_{ztp} \cdot z_{tp\,n}\right) - \frac{{z_n}^2}{c_{zx} x_n + c_{zy} \cdot y_n} \quad \text{(C4)}$$

The 3rd species as well as interactions between the predator and prey species can be turned off in order to analyse the species as a set of independent species.

In the economic part of the model, revenue and costs are determined by equations (C5-23). Here *q* represents catchability rates and *V* effort, while *F* is the fishing mortality rate. Harvest is denoted by *H*, and revenue *R* is found using a set of prices *p*. Total cost, *U*, are assumed to be linear in effort. Profit $\pi$ is used as decision variable in optimizations and to determine investments in dynamic simulations. Investment is assumed to be linear in profit (thus positive profits gives positive investment, i.e. increase in effort while negative profit means negative investment, i.e. decrease in effort) and is represented by *I*. $dc_{1,2}$ and $v_{x,y,z}$ represent damage from fleet 1 and fleet 2 and non-market values respectively.

$$F_x = q_{x,1}V_1 + q_{x,2}V_2 \quad \text{(C5)}$$

$$F_y = q_{y,1}V_1 + q_{y,2}V_2 \quad \text{(C6)}$$

$$H_x = F_x x \quad \text{(C7)}$$

$$H_y = F_y y \quad \text{(C8)}$$

$$R_1 = p_{x,1}q_{x,1}V_1 + p_{y,1}q_{y,1}V_1 \quad \text{(C9)}$$

$$R_2 = p_{x,2}q_{x,2}V_2 + p_{y,2}q_{y,2}V_2 \quad \text{(C10)}$$

$$U_1 = u_1V_1 \quad \text{(C11)}$$

$$U_2 = u_2V_2 \quad \text{(C12)}$$

$$\pi_1 = R_1 - u_1V_1 \quad \text{(C13)}$$

$$\pi_2 = R_2 - u_2V_2 \quad \text{(C14)}$$

$$I_1 = v_1\pi_1 \quad \text{(C15)}$$

$$I_2 = v_2\pi_2 \quad \text{(C16)}$$

$$V_{1,t+1} = I_{1,t} + V_{1,t} \quad \text{(C17)}$$

$$V_{2,t+1} = I_{2,t} + V_{2,t} \quad \text{(C18)}$$

$$dc_1 = k_1 V_1^{l_1} \quad \text{(C19)}$$

$$dc_2 = k_2 V_2^{l_2} \quad \text{(C20)}$$

$$v_x = s_x\, x^{r_x} \quad \text{(C21)}$$

$$v_y = s_y\, y^{r_y} \quad \text{(C22)}$$

$$v_z = s_z\, z^{r_z} \quad \text{(C23)}$$

*k*, *l*, *s* and *r* are constants as explained in section 2.