Biodiversity and optimal management of a multi-species ecosystem: Theory and application to Baltic Sea fisheries

May, 2014

Abstract. We analyze optimal multi-species management in a dynamic bio-economic model taking into account both harvesting profit and biodiversity value. Within an analytical model, where we model biomass dynamics of species under different assumptions on ecological interactions, we show that extinction is never optimal when biodiversity value is taken into account, that a stronger preference for species diversity leads to a more even distribution of stock sizes in the optimal steady state, and that a higher value of biodiversity increases steady state stock sizes for all species when species are ecologically independent or in symbiotic ecosystems. For a predator-prey ecosystem, the effects may be positive or negative depending on relative prices and the strength of species interaction. The analytical results are illustrated and extended using an age-structured three-species predator-prey model for the Baltic cod, sprat, and herring fisheries. In this quantitative application we find that using stock biomass or stock numbers as abundance indicators in the biodiversity index may lead to opposite results.

Keywords: Marine biodiversity, fishery economics, Baltic Sea

JEL codes: Q22, Q57

1 Introduction

The goal of implementing ecosystem-based approaches in fisheries management implies that not only economic profits should be maximized but that conservation goals also need to be considered (Pikitch et al., 2004). Consequently, bio-economic models that can be used to derive recommendations for fisheries management should not only include multiple species but also multiple values. Against this background, we reconsider optimal multi-species management in a bio-economic model taking into account both harvesting profit and biodiversity value. More specifically, we analyze how optimal management decisions change when a biodiversity index is introduced in the objective function of a bio-economic dynamic optimization model to capture the value of biodiversity.

The rationale for introducing a biodiversity value into such a model is twofold: Firstly, people can attach a value to in-situ stocks of species simply for their existence. The shadow price of biodiversity could thus be interpreted as a social willingness to pay for species conservation. In our application, this value would not be attributed to a single species but to a biodiversity index that depends on the entire state of the multi-species ecosystem. Secondly, a biodiversity value can serve as a place holder for ecosystem services that are not explicitly modeled via ecological interactions in a bio-economic model. The shadow price of biodiversity could thus also be interpreted as a proxy for the value of some external effects that are too complex to be integrated explicitly in the model.

We consider a biodiversity index that is calculated based on species abundances to represent the biodiversity value. The elements that influence this biodiversity index are the number of different species (species richness), the overall abundance of all species, and the evenness in the distribution of species abundances (Magurran, 2004). There are a range of ecological indices used to aggregate abundances to

represent biodiversity, e.g. the Simpson-Index or the Shannon-Index. It is possible to use either biomass or the number of individuals to compute these indices. Different weightings for different species are also possible (Buckland et al., 2005).

Buckland et al. (2005) state axioms that an index based on abundances should fulfill if it was used for monitoring biodiversity developments over time. These axioms include the requirement that the index value should decrease if overall abundance is decreasing while the number of species as well as species evenness stay constant. Neither the Simpson-Index nor the Shannon-Index fulfill this axiom. Here, we consider the class of constant-elasticity-of-substitution (CES) functions to aggregate single stocks into one index. CES-functions fulfill the axioms[1] stated in Buckland et al. (2005) and thus seem well-suited to track biodiversity developments over time. Moreover, the class of CES-functions are frequently used and a well-studied specification to describe production processes or consumer preferences in economics.

The literature on renewable resources and bio-economic modeling has dealt with the inclusion of existence values before, but mostly considering single-species models. For example, Alexander (2000) includes existence values in a one-species model and derives implications for the potential optimality of extinction. More recent papers also include existence values in multi-species models. Kellner et al. (2010) introduce an existence value for each single species in a multi-species predator-prey model but they do not aggregate the values into one index. Voss et al. (2013) also consider a multi-species predator-prey model, but the existence value they introduce only applies to the sprat stock. With a slightly different focus, Quaas and Requate (2013) include a CES-function in a bio-economic model, but preferences for diversity are attached to the consumption of fish, not to the biodiversity of the ecosystem. Finally, Noack et al. (2010) use a biodiversity index similar to the one we are using in this paper, but they do not consider the context of fisheries management and, more

[1]More specifically, a CES-function fulfills the first four axioms mentioned in Buckland et al. (2005). Axiom 5 and 6 refer to characteristics of the biodiversity measures related to their empirical estimation, which is not relevant in the theoretical context of this paper.

importantly, do not investigate the effects of the introduction of this index on the single species stocks captured by the index.

Since multi-species applications are increasingly prominent in bio-economic modeling and biodiversity remains an important topic, we think that it is important to investigate the properties of a bio-economic model when an aggregate biodiversity index is included to capture biodiversity values. We thus explore the effects of introducing such an index on the optimal stocks of the single species, which has, to our knowledge, not been investigated before. In addition, we exemplify the effects in a more complex age-structured model applied to the example of a predator-prey system of three Baltic Sea fish species (cod, sprat, and herring). We illustrate the effects of switching from an index calculated using biomasses to an index calculated using number of individuals. We also illustrate the role of the elasticity of substitution for optimal management. Both parameters crucially influence optimal management, which is important knowledge for applying such an index.

The remainder of the paper is structured as follows: Section 2 presents a dynamic biomass model and compares optimal multi-species management without biodiversity value to optimal multi-species management with biodiversity value using a CES-function to construct a biodiversity index based on the biomasses of the different species. We analytically show the effects of changes in the shadow price of biodiversity, in market prices, and in the elasticity of substitution between species in the biodiversity index on optimal steady state stocks for different kinds of ecological interactions. Section 3 introduces a state-of-the-art age-structured model and simulates the effects of changing the shadow price of biodiversity and of changing the elasticity of substitution on steady state stocks, profits and biodiversity levels for the example of a three-species predator-prey ecosystem in the Baltic Sea. We also compare the effects when switching from a biodiversity index with biomass to an index using the number of individuals. Section 4 discusses the results and concludes.

2 Dynamic model of optimal multi-species ecosystem management

2.1 Measuring biodiversity

One of the most established ways to measure species-level biodiversity is to calculate a diversity index based on individual species abundances. The elements that influence such a biodiversity index are the number of different species (species richness), and the evenness in the distribution of species abundances. A large number of such indices exist and they are widely used in ecology to measure species-level biodiversity (Magurran, 2004). Buckland et al. (2005) state axioms that such a biodiversity index should fulfill if it was used for monitoring biodiversity over time. These axioms are:[2]

> 1.) For a system that has a constant number of species, overall abundance and species evenness, but with varying abundance of individual species, the index should show no trend.
>
> 2.) If overall abundance is decreasing, but number of species and species evenness are constant, the index should decrease.
>
> 3.) If species evenness is decreasing, but number of species and overall abundance are constant, the index should decrease.
>
> 4.) If number of species is decreasing, but overall abundance and species evenness are constant, the index should decrease.

Ecological indices such as the Simpson-Index or the Shannon-Index are constructed using relative abundances. Even though these indices are common in ecology, they do not allow a consistent comparison of biodiversity levels over time because they do not fulfill the second axiom (Buckland et al., 2005). We thus use absolute abundances x_{it}

[2]These are the first four axioms mentioned in Buckland et al. (2005); the last two axioms refer to sampling and empirical estimation of the indices and are thus not relevant in the theoretical context of this paper.

for the in-situ stock of species $i = 1, \ldots, n$ at time t for calculating the biodiversity of a multi-species ecosystem with n in-situ stocks. Specifically, we measure biodiversity by using the following class of functions

$$B_t = B_t(x_{1t}, ..., x_{nt}) = \left(\frac{1}{n} \sum_{i=1}^{n} x_{it}^{\frac{\omega-1}{\omega}} \right)^{\frac{\omega}{\omega-1}} . \tag{1}$$

This index satisfies the following conditions (using subscripts to denote partial derivatives with respect to the corresponding variables):

$$B_{x_i} > 0 \text{ and } B_{x_i x_i} < 0 \text{ and } B_{x_i x_j} > 0 \ \forall \ i, j \tag{2}$$

The functional form (1) with a constant elasticity of substitution (CES) does not only fulfill the axiomatic conditions specified in Buckland et al. (2005) for functions that can be used to measure and compare biodiversity levels over time. It is also a common form for production functions (Arrow et al., 1961) or utility functions (Dixit and Stiglitz, 1977) in economics.

The axioms stated in Buckland et al. (2005) do not restrict the functional forms of potential biodiversity indices regarding the structure of the exponent outside the brackets in (1). Any monotone transformation of the CES-function in (1) would fulfill the axioms as well. Here, we assume a structure of the exponent such that the resulting index is linear homogeneous. This is different from the structural form of the exponent used in the ecological indices that are based on relative abundances. Our specification implies that the index value is measured in terms of species abundances, just as the abundances for the individual species, which alleviates its interpretation. In the following, we analyze this special functional form and its implications for optimal management.

The index (1) may be interpreted as a generalized mean of species abundances. In economic terms, the parameter $\omega > 0$ measures the elasticity of substitution between the stocks of the n species. For $\omega \to 0$, the elasticity of substitution would

be zero and the stocks would be perfect complements. For $\omega \to \infty$, the elasticity of substitution would be infinitely large and the stocks would be perfect substitutes. In this case, the index (1) simply gives the arithmetic mean of species. For $\omega \to 1$, the index (1) becomes the geometric mean of species abundances.

Ceteris paribus, the value of the biodiversity index B_t increases as ω increases; only for equal abundances of all stocks, the value of B_t is not affected by a change in ω. For $\omega < 1$, the biodiversity index, B_t, approaches zero if the stock x_i of any species i, is driven towards zero. The marginal biodiversity values, B_{x_j}, of the other species $j \neq i$ also go to zero if $x_i \to 0$. Substituting a species stock, x_i, by another stock, x_j, thus becomes less acceptable, the smaller the stock of species i already is. For $\omega > 1$, substitution between the species is more easily possible, i.e. the biodiversity index would continuously increase with an increasing stock of at least one species even if all other species are driven towards zero or go extinct. More formally, both B_t and B_{x_j} are finite and stay positive for $x_i \to 0$, as long as there is at least one other species $j \neq i$ with a positive stock size $x_j > 0$.

For the case $\omega \leq 1$, Axiom 4 can not be applied because in this case the index is defined only for a constant number of species, and not defined if the abundance of any one species becomes zero. Considering the different species as complements, $\omega \leq 1$, is thus only reasonable for issues where species extinction is out of scope, such as the three-species fishery in the Baltic, considered in section 3.3 below. Consequently, for biodiversity considerations where species richness can vary, an index of the form (1) can be applied under the restriction that different species are substitutes, i.e. under the assumption $\omega > 1$. Also in this case the weight of the abundances of the single species in the CES-function $(1/n)$ needs to be determined once based on the initial number of species and may not be changed afterwards even if the number of species changes, e.g. due to extinction. Changing the weight when measuring biodiversity over time would violate the axioms stated in Buckland et al. (2005) which a valid biodiversity index needs to satisfy.

2.2 Model framework and optimal management

In this section, we introduce an analytical biomass model and compare optimal management solutions with biodiversity value to optimal management solutions without biodiversity value. We also show the effects of parameter changes on optimal steady states, differentiating between cases with and without ecological interactions.

We use a general set-up with n species and possible ecological interactions. In addition, we use a CES-function (1) aggregating the biomasses of the different species to capture the value of biodiversity in the objective function.

There are n species ($i = 1, ..., n$). The dynamics of each stock x_{it} are determined by its natural growth (G_{it}) and the biomass harvested (h_{it}):

$$\dot{x}_{it} = G_{it}(x_{1t}, ..., x_{nt}) - h_{it} \quad \text{for} \quad \forall\, i, t \tag{3}$$

We assume perfectly selective harvesting, i.e. harvest of species i does not directly affect the dynamics of any other resource stock $j \neq i$. Species may interact ecologically, which is captured by the dependency of species i's growth function $G_i(\cdot)$ on the other species' stock sizes x_j. For some parts of the analysis, we will however reduce the complexity of the model by assuming that species are ecologically independent, i.e. we impose the following assumption

$$G_{ix_j} \equiv 0 \quad \forall \quad j \neq i. \tag{4}$$

Time subscripts are dropped for notational clarity from now on unless needed to avoid confusion. Furthermore, we use the vector notation $\mathbf{x} \equiv (x_1, ..., x_n)$ and $\mathbf{h} \equiv (h_1, ..., h_n)$.

We now consider socially optimal multi-species management. An ecosystem manager simultaneously chooses harvest quantities for all species over time such that the present value of benefits, i.e. the sum of net benefits from harvest plus biodiversity

value, is maximized:

$$\max_{\mathbf{h}} \int_0^\infty e^{-\rho t} \Big[\Pi(\mathbf{h}, \mathbf{x}) + v\, B(\mathbf{x}) \Big] dt \tag{5}$$

subject to the stock growth equations (3) and given the initial stock sizes x_{i0} for all species i. Here, we use ρ to denote the social discount rate and $\Pi(\mathbf{h}, \mathbf{x})$ to denote the economic net benefit derived from harvesting the multi-species ecosystem at time t. The net benefit is allowed to depend on the stock size to capture possibly stock-dependent harvesting costs. The parameter v measures the marginal value of biodiversity relative to harvest benefits in the objective function.

A couple of remarks are in place to discuss the meaning of using the biodiversity index (1) in the objective function (5). Firstly, we interprete the parameter v, as the shadow price of biodiversity. It converts biodiversity into monetary units. As (1) is linear homogeneous, biodiversity is measured in units of species abundance. Thus, v is measured in monetary units per species abundance (tons of biomass, for example). As discussed above, however, the value of the biodiversity index (1) changes with ω. Thus, it must be kept in mind that v has to be adjusted when using different values of ω in the objective function.

Secondly, the assumption of linear homogeneity of the biodiversity index (1) carries economic meaning. Specifically, the particular specification of the exponent outside the brackets in (1) becomes important becuase it determines (a) the elasticity of *intertemporal* substitution between the abundances of species, and (b) the elasticity of substitution between biodiversity and (monetary) income. In both respects, more general specifications of biodiversity are conceivable, but we think that the linear homogeneous index (1) is a simple and appealing specification. Thus we focus on analyzing the implications of using this particular index in the objective function (5).

Using a CES-function to aggregate the stocks implies that the marginal biodiversity value of one species depends not only on the own stock but also on the stocks

of the other species. This introduces an interdependency between the species on the management side. Hence, species have to be managed jointly even in a case where species are ecologically independent, i.e. when equation (4) holds. This is in contrast to Kellner et al. (2010), where marginal biodiversity or non-fishing values are non-linear but only depend on the own resource stock, corresponding to the assumption $\omega \to \infty$ in our set-up.

To derive the conditions for optimal multi-species management, we set up the current-value Hamiltonian

$$H^c = \Pi(\mathbf{h}, \mathbf{x}) + v\, B(\mathbf{x}) + \sum_{i=1}^{n} \lambda_i (G_i(\cdot) - h_i). \tag{6}$$

Applying the maximum principle, the necessary conditions for optimal management are

$$\frac{\partial H^c}{\partial h_i} = 0 \qquad \Leftrightarrow \qquad \Pi_{h_i} = \lambda_i \tag{7a}$$

$$-\frac{\partial H^c}{\partial x_i} = \dot{\lambda}_i - \rho\lambda_i \qquad \Leftrightarrow \qquad \rho = \frac{\dot{\lambda}_i}{\lambda_i} + G_{ix_i} + \sum_{j \neq i} \frac{\lambda_j}{\lambda_i} G_{jx_i} + \frac{\Pi_{x_i}}{\lambda_i} + v\, \frac{B_{x_i}}{\lambda_i} \tag{7b}$$

for all $i = 1, \ldots, n$. The first condition states that the marginal net benefit of harvesting species i should equal the marginal opportunity costs of reducing stock i, captured by the shadow price of this stock, λ_i. This shadow price is determined by condition (7b). We have a closer look at the different terms in that condition when discussing the optimal steady state, i.e. the long-run optimal stock sizes and harvest levels for the multi-species ecosystem. The steady state conditions are obtained by using (7a) and the conditions $\dot{x}_i = 0$ in (3) and $\dot{\lambda}_i = 0$ in (7b):

$$G_i(\bar{\mathbf{x}}) = \bar{h}_i \tag{8a}$$

$$\rho = G_{i\bar{x}_i} + \sum_{j \neq i} \frac{\Pi_{\bar{h}_j}}{\Pi_{\bar{h}_i}} G_{j\bar{x}_i} + \frac{\Pi_{\bar{x}_i}}{\Pi_{\bar{h}_i}} + \frac{v\, B_{\bar{x}_i}}{\Pi_{\bar{h}_i}} \tag{8b}$$

both for all $i = 1, \ldots, n$.

When taking species interactions into account, corner solutions to the dynamic optimization problem (5) may become possible. Here we focus on interior solutions described by the necessary conditions (7). To this end, we assume that species interactions are such that the maximized Hamiltonian is concave in the stock variables, i.e. the sufficiency conditions for the dynamic optimization problem are fulfilled (Arrow and Kurz, 1970).[3]

Condition (8b) states that in the optimal steady state the social discount rate, ρ, has to equal the interest rate earned on a marginal increase of each stock x_i. This own interest rate is composed of the marginal stock growth of the species itself, of the marginal increase of stock growth of all other species $j \neq i$, of the value of the marginal stock effect of reducing future harvesting costs, and of the marginal contribution to biodiversity value.

To shed some light on the implications of (8b) for the optimal steady-state stock size, consider the case of ecologically independent species, i.e. impose (4). In this case without ecological interactions between the species the second term in (8b) would vanish. Note that even in this case the right-hand side (RHS) of equation (8b) does not only depend on the stock of species i but also on the stocks of the other species $j \neq i$ if biodiversity values are considered in addition to harvesting values. Thus, the biodiversity value modeled as a CES-function introduces an interdependency in steady state conditions even if the species are ecologically independent.

If the economic benefits of harvest were independent of stock size, $\Pi_{x_i} = 0$, and if there was no biodiversity value, $v = 0$, the optimal steady-state stock sizes would be below the maximum-sustainable-yield stock sizes $x_{i,\mathrm{MSY}}$ defined by $G_{ix_i}(x_{i,\mathrm{MSY}}) = 0$ for all species i. This is the well-known result of applying a positive discount rate $\rho > 0$. The two effects of stock-dependent harvesting costs, $\Pi_{x_i} > 0$, and of biodiversity value, $v > 0$, both tend to increase optimal steady-state stock sizes.

[3]It is straightforward to verify that the sufficiency conditions are always fulfilled in the absence of species interactions, i.e. if assumption (4) holds, and if the biomass growth functions are concave.

If these effects are strong enough, the optimal steady-state stock sizes in absence of biological interactions will all be larger than $x_{i,\mathrm{MSY}}$. Thus, taking into account biodiversity values with a positive weight, $v > 0$, has a similar effect to stock-dependent harvesting costs and implies a positive differential between ρ and $G_{i\bar{x}_i}$, i.e. $\rho > G_{i\bar{x}_i}$ in optimal steady state with $v > 0$.

This result still holds in the case of ecological interactions as long as all other species j depend positively on the stock of species i, i.e. $G_{j\bar{x}_i} > 0 \; \forall \; j \neq i$, such that there is an additional positive external effect of the stock x_i. Negative ecological interactions, i.e. $G_{j\bar{x}_i} < 0$, can imply a negative differential between ρ and $G_{i\bar{x}_i}$, which would imply that steady state stocks of species i are lower. See, e.g., Brown et al. (2005) for this effect in a predator-prey model without biodiversity values. In all cases, steady state stocks with biodiversity value c.p. are larger than steady state stocks without considering biodiversity value.

Slightly rearranging (8b), multiplying with x_i and summing over all species i leads to the following condition:

$$\sum_{i=1}^{n} \left((\rho - G_{i\bar{x}_i})\, \Pi_{\bar{h}_i} - \Pi_{\bar{x}_i} - \sum_{j \neq i} G_{j\bar{x}_i}\, \Pi_{\bar{h}_j} \right) \bar{x}_i = v \sum_{i=1}^{n} \bar{x}_i B_{\bar{x}_i} = v\, B \tag{9}$$

The RHS of equation (9) is the weighted value of biodiversity in steady state, i.e. the total biodiversity value attached to aggregate steady state stock levels. The LHS of equation (9) represents the opportunity costs connected to introducing biodiversity values and increasing steady state stock levels such that a higher share of fish remains unfished. These opportunity costs are given by the sum of the economic net benefits of each steady state stock multiplied with the differential between the social discount rate and the marginal growth rate. These opportunity costs are reduced by the positive effect of larger stocks on harvesting costs and further affected by the effect of increased stock sizes of species i on the other species due to ecological interdependencies.

To proceed with the theoretical analysis, we will focus on the effect of biodiversity value and simplify the analysis by neglecting harvesting costs, i.e. we impose the following assumption

$$\Pi(\mathbf{h}, \mathbf{x}) = \mathbf{p}\,\mathbf{h} = \sum_{i=1}^{n} p_i\, h_i. \tag{10}$$

For the case without biodiversity value, $v = 0$, and in the case of ecologically independent species (assumption (4) holds), extinction may be optimal for species with $G_{ix_i}(0) \leq \rho$ (Clark, 1973).

Proposition 1

Assume (4), (10), $\omega > 1$, and positive biodiversity value $v > 0$. Then, extinction is never optimal, i.e. $x_i > 0$ for all $i = 1, \ldots, n$.

Proof. See Appendix A. □

Thus, extinction is never optimal when a biodiversity value specified as above is part of the objective function, and for $\omega > 1$, i.e. the specification of the biodiversity index that is applicable with a changing number of species. The reason for this result is that the marginal biodiversity value, B_{x_i}, diverges to infinity if the stock x_i approaches zero. Extinction can be optimal if the substitution elasticity is infinitely large, i.e. in the case of perfect substitutes $\omega = \infty$, but only for a species with $G_{ix_i}(0) < \rho - \frac{v\,n}{p_i}$.

2.3 Comparative statics with respect to v

We now analyze how changes in the shadow price of biodiversity, v, influence optimal steady state stocks in a two-species ecosystem. Under Assumption (10), but with

ecological interactions, we derive the following conditions:

$$\frac{d\bar{x}_1}{dv} = \frac{1}{\Delta}\left(B_{\bar{x}_2}\left(p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} + v\, B_{\bar{x}_1\bar{x}_2}\right) - B_{\bar{x}_1}\left(p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2}\right)\right) \tag{11}$$

$$\frac{d\bar{x}_2}{dv} = \frac{1}{\Delta}\left(B_{\bar{x}_1}\left(p_1\, G_{1\bar{x}_2\bar{x}_1} + p_2\, G_{2\bar{x}_2\bar{x}_1} + v\, B_{\bar{x}_2\bar{x}_1}\right) - B_{\bar{x}_2}\left(p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1}\right)\right) \tag{12}$$

We assume $\Delta > 0$, which holds if sufficient conditions for optimality are met. See Appendix B for the derivation and the definition of Δ.

Proposition 2

The optimal steady-state stock $\bar{x}_i$ of species i increases with v,

$$\frac{d\bar{x}_i}{dv} > 0 \tag{13}$$

if (a) species j and i are ecologically independent, i.e. if $G_{i\bar{x}_i\bar{x}_j} = 0$, or if (b) species i and j have a symbiotic relationship, i.e. if $G_{i\bar{x}_j\bar{x}_i} > 0 \;\; \forall \;\; i, j \;\; \text{with} \;\; i \neq j$.

Proof. See Appendix C. □

In the case of ecologically independent species and in the case of symbiosis, the term $p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2}$ is unambiguously positive such that the effect of v on steady state stocks can be unambiguously determined. In a competitive system, the effect of v on both steady state stocks is ambiguous as $p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} < 0$.

In a predator-prey system, the sign of $p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2}$ is ambiguous and depends on the relative prices and the predation relationship between the species. Consider the example of a Lotka-Volterra predator-prey relationship such that the term modifies to $p_1\, \alpha_1 + p_2\, \alpha_2$, with constants α_1 and α_2. Assume without loss of generality that species 1 is the predator ($\alpha_1 > 0$) and species 2 is the prey ($\alpha_2 < 0$). The term $p_1\, \alpha_1 + p_2\, \alpha_2$ would now only be positive if the predator is sufficiently more valuable than the prey or if the predation coefficient α_1 is sufficiently larger than

α_2 in absolute terms. In this case, again, the effect of v on both predator and prey stocks would be positive in steady state.

2.4 Comparative statics with respect to p

We now analyze how changes in the market prices of the two species, p_i, influence optimal steady state stocks in a two-species ecosystem. Under Assumption (10), but with ecological interactions, we derive the following conditions:

$$\frac{d\bar{x}_1}{dp_1} = \frac{1}{\Delta}\left(-G_{1\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} + v\, B_{\bar{x}_1\bar{x}_2}\right) + \right.$$
$$\left. + \left(\rho - G_{1\bar{x}_1}\right)\ \left(p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2}\right)\right) \quad (14)$$

$$\frac{d\bar{x}_2}{dp_1} = \frac{1}{\Delta}\left(-\left(\rho - G_{1\bar{x}_1}\right)\ \left(p_1\, G_{1\bar{x}_2\bar{x}_1} + p_2\, G_{2\bar{x}_2\bar{x}_1} + v\, B_{\bar{x}_2\bar{x}_1}\right) + \right.$$
$$\left. + G_{1\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1}\right)\right) \quad (15)$$

with $\Delta > 0$ as above. See Appendix D for the derivation.

Proposition 3

The optimal steady state stocks $\bar{x}_j$ of species $j = 1, 2$ decrease with p_i,

$$\frac{d\bar{x}_j}{dp_i} < 0 \quad (16)$$

if (a) species j and i are ecologically independent, i.e. if $G_{i\bar{x}_j} = 0$ and $G_{i\bar{x}_i\bar{x}_j} = 0$, or if (b) species j and i have a symbiotic relationship, i.e. if $G_{i\bar{x}_j} > 0$ and $G_{i\bar{x}_j\bar{x}_i} > 0\ \forall\ i, j\ \text{ with }\ i \neq j$.

Proof. See Appendix E. □

In the case of ecologically independent species and in the case of symbiosis, the

term $p_1\, G_{1\bar{x}_1\bar{x}_2}+p_2\, G_{2\bar{x}_1\bar{x}_2}$ is unambiguously positive such that the effect of p on steady state stocks can be unambiguously determined. The negative effect on steady state stocks is in contrast to a model of independent species when there is no biodiversity value in the model, i.e. $v = 0$. In such a case, the effect of price changes on steady state stocks would be zero. In a competitive system, the effect of p on both steady state stocks is ambiguous as $p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} < 0$.

For a predator-prey system, the effect depends on the relative prices and the predation relationship between the two species. Consider, again, the example of a Lotka-Volterra model with species 1 being the predator and species 2 being the prey, such that $p_1\, \alpha_1 + p_2\, \alpha_2$ is the decisive term. If the predator is sufficiently more valuable than the prey or if the predation coefficient α_1 is sufficiently larger than α_2 in absolute terms, the effect of changes in the price of the predator species is negative on both predator and prey. The effect of price changes of the prey species is still ambiguous in this case.

2.5 Comparative statics with respect to ω

We now analyze how changes in the elasticity of substitution between the two species, ω, influence optimal steady state stocks in a two-species ecosystem. Under Assumption (10), and with ecologically independent growth functions of the two species, we derive the following conditions:

$$\frac{d\bar{x}_1}{d\omega} = \frac{v}{\Delta}\left(\frac{\partial B_{\bar{x}_2}}{\partial \omega}\, v\, B_{\bar{x}_1\bar{x}_2} - \frac{\partial B_{\bar{x}_1}}{\partial \omega}\, \left(p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2}\right)\right) \tag{17}$$

$$\frac{d\bar{x}_2}{d\omega} = \frac{v}{\Delta}\left(\frac{\partial B_{\bar{x}_1}}{\partial \omega}\, v\, B_{\bar{x}_2\bar{x}_1} - \frac{\partial B_{\bar{x}_2}}{\partial \omega}\, \left(p_1\, G_{1\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1}\right)\right) \tag{18}$$

We have (using the notation $\hat{x} = x_1/x_2$)

$$\frac{\partial B_{x_1}}{\partial \omega} = \frac{B_{x_1}}{\omega^2\,(1-\omega)\left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right)}\left(\omega^2\left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right)\ln\left(2\,B_{x_1}\right) + \hat{x}^{\frac{1-\omega}{\omega}}\ln\hat{x}\right). \tag{19}$$

For the following proposition, we use $\hat{\omega}$ to denote the solution of $\hat{\omega}+\ln(\hat{\omega}-1)=0$, which is $\hat{\omega} \approx 1.28$.

Proposition 4

(a) If $\omega \geq \hat{\omega}$, the smaller stock decreases with ω.

(b) If $\omega < \hat{\omega}$, it exists a $0 \leq \underline{\hat{x}} < 1$ such that the smaller stock decreases with ω for all $\hat{x} \in (\underline{\hat{x}}, 1)$.

Proof. See Appendix F. □

The intuition behind this result is that a larger elasticity of substitution allows a larger divergence between optimal stock sizes in steady state. Consequently, the smaller stock decreases with ω in steady state.

3 Application to Baltic Sea fisheries

3.1 Baltic Sea fisheries

The marine ecosystem in the central Baltic Sea is dominated by three fish species: cod, herring and sprat, which also form the basis of the economically most important fisheries in the Baltic Sea. These fish stocks are closely connected by strong ecological inter-connections between species (Köster and Möllmann, 2000), as cod preys on both herring and sprat. In economic terms, the cod fishery used to be the most important of the three. Overfishing has caused a decline in the cod stock during the last decades, and only recently the introduction of a long-term management plan has led to some signs of stock recovery again.

The upper panel in Figure 1 shows the development of the stock sizes of cod, sprat and herring from 1974 to 2012 measured in units of spawning stock biomass, i.e. the biomass of all fish in spawning age. The lower panel shows the corresponding levels of the biodiversity index (1) using spawning stock biomasses as abundance

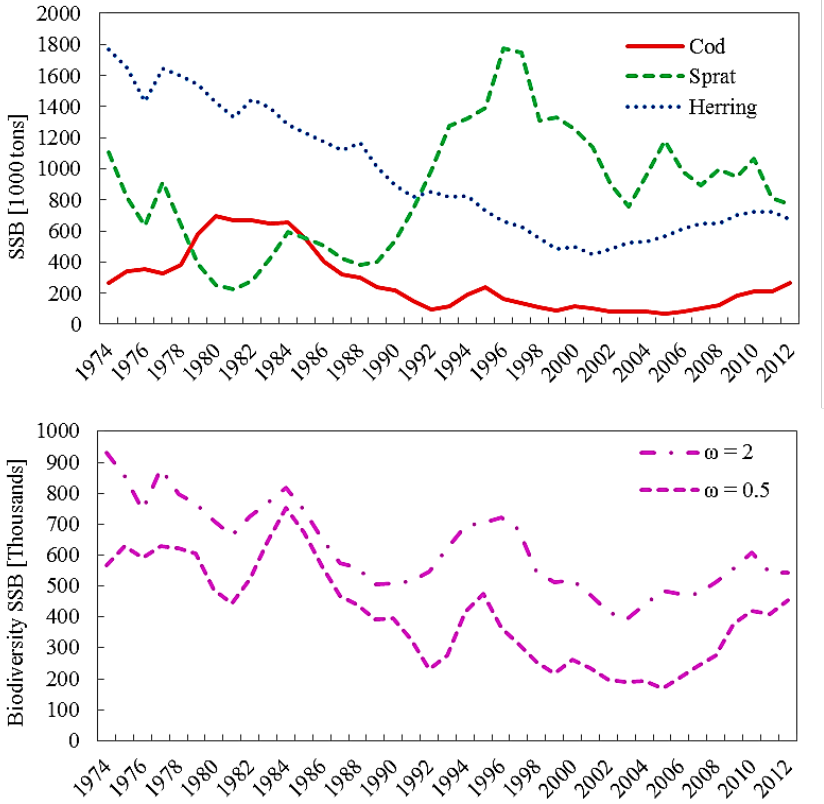

Figure 1: Historic development of spawning stock biomasses and levels of the biodiversity index using spawning stock biomasses as abundance indicators for sprat, herring, and cod in the Baltic Sea.

indicators for a relatively large elasticity of substitution ($\omega = 2$) and for a relatively low elasticity of substitution ($\omega = 0.5$).

3.2 Description of the age-structured model

For the application to the Baltic sea fisheries, we replace the biomass model of resource dynamics (equation 3) by a state-of-the-art age-structured population model, building on Voss et al. (2014), who provide a bio-economic fishery model for the Baltic cod, herring, and sprat fisheries, taking the predator-prey relationship between cod and the two other species into account. This model is an extension of a single-species age-structured fishery model (Tahvonen, 2009; Tahvonen et al., 2013).

A second deviation from the model used in the previous section is that we consider a discrete-time, discrete age-structured setting for the quantitative application here.

In the following we use x_{ist} to denote the number of fish of species $i \in \{C, S, H\}$, where C stands for cod, S for sprat, and H for herring, in age group $s = 1, \ldots, S$ and at the beginning of period $t = 0, 1, \ldots$. Using the indices $i \in \{C, S, H\}$ for the species, and $s = 1, \ldots, S$ for the age group, where $S > 1$ is the oldest age group considered in the model, we use $\alpha_{is} > 0$ to denote age specific survival rates, $\gamma_{is} > 0$ to denote age specific proportions of mature individuals and w_{is} to denote the mean weights (in kilograms). For cod, all of these parameters are assumed to be constant (Tahvonen, 2009), and as in the standard biological stock assessments for the Eastern Baltic cod (ICES, 2012). For sprat and herring, we assume that proportions of mature individuals and weights are constant, but the survival rates of sprat depend on cod spawning stock biomass. We use the specification

$$\alpha_{is} = \exp\left(-M_{2is} - \delta_{is}\, x_{C0t}\right), \tag{20}$$

where M_{2is} is instantaneous natural mortality of sprat ($i = S$) and herring ($i = H$) cohort s in the absence of cod, and $\delta_{is} > 0$ is a parameter that measures the dependency of instantaneous natural mortality of sprat ($i = S$) and herring ($i = H$) cohort s on cod spawning stock biomass, x_{C0t}. Denoting the recruitment function for species i by $\varphi_i(\cdot)$ and the spawning biomass by x_{i0t}, the age structured population model with harvesting activity can be summarized as

$$x_{i0t} = \sum_{s=1}^{S} \gamma_{is}\, w_{is}\, x_{ist} \tag{21a}$$

$$x_{i1,t+1} = \varphi_i(x_{i0t}) \tag{21b}$$

$$x_{i,s+1,t+1} = \alpha_{is}\ (x_{ist} - h_{ist}) \qquad \text{for } s = 1, \ldots, S-2 \tag{21c}$$

$$x_{i,S,t+1} = \alpha_{i,S-1}\ (x_{i,S-1,t} - h_{i,S-1,t}) + \alpha_{iS}\ (x_{iSt} - h_{iSt}) \tag{21d}$$

Here, we use h_{ist} to denote the number of fish harvested from cohort s of species i in period t. We maintain the assumption of perfect selectivity with respect to the species, which is a reasonable assumption for the Baltic, as different species are caught by different fleets. Aggregate instantaneous fishing mortality F_{it} for species i in year t translates into age-specific fishing mortalities, captured by the constant, age-specific catchability coefficients $q_{is} \geq 0$, such that

$$h_{ist} = q_{is}\, x_{ist}\, \left(1 - \exp\left(-F_{it}\right)\right). \tag{22}$$

For cod and herring we assume stock-recruitment functions of the Ricker (1954) type (Quaas et al., 2013), i.e. we assume

$$\varphi_i(x_{i0t}) = \phi_{i1}\, x_{i0t}\, \exp\left(-\frac{x_{i0t}}{\phi_{i2}}\right). \tag{23}$$

with $\phi_{i1}, \phi_{i2} > 0$. For sprat we assume a Beverton-Holt type (Tahvonen et al., 2013), i.e. we assume

$$\varphi_S(x_{S0t}) = \frac{\phi_{S1}\, x_{S0t}}{1 + \frac{x_{S0t}}{\phi_{S2}}} \tag{24}$$

with $\phi_{S1}, \phi_{S2} > 0$. For modeling the profits of the cod fishery, we use the specification from Quaas et al. (2012) with age-specific prices and a cost function of the Spence-type (Spence, 1974). Thus, profits of the cod fishery in year t are

$$\pi_{Ct} = \sum_{s=1}^{S} p_{Cs}\, w_{Cs}\, h_{Cst} - c_C\, F_{Ct}, \tag{25}$$

where p_{Cs} are prices for cod in age group s, and instantaneous fishing mortality F_{Ct} equals instantaneous effort, and c_C is the unit effort cost for the cod fishery. Sprat and herring are modeled as schooling fisheries (Tahvonen et al., 2013), where the market price p_i is assumed to be independent of age. The profits in the sprat and

herring fisheries thus is

$$\pi_{it} = (p_i - c_i) \sum_{s=1}^{S} p_{is}\, w_{is}\, h_{ist}. \tag{26}$$

With analogous interpretations for the symbols as for the cod fishery. The values for the parameters of the population model and for prices and harvesting costs are taken from Voss et al. (2014) and can be found in Appendix G.

As for the harvesting benefits $\Pi(\mathbf{h}, \mathbf{x})$, we assume that the fishery manager has some aversion against income inequality across fishery, and specify

$$\Pi(\mathbf{h}, \mathbf{x}) = \left(\frac{1}{3}\pi_{Ct}^{1-\eta} + \frac{1}{3}\pi_{St}^{1-\eta} + \frac{1}{3}\pi_{Ht}^{1-\eta} \right)^{\frac{1}{1-\eta}}. \tag{27}$$

In our simulations, we use $\eta = 0.25$.

We assume that the aim is to maximize (5) with harvesting benefits (27) and taking a biodiversity value into account. Here, we use two versions of the biodiversity index: in one version, we use the total stock numbers, $\sum_{s=1}^{S} x_{ist}$ as the abundance index for species i, in the other one, we use the spawning stock biomass x_{i0t} as the abundance index. We vary the marginal willingness to pay for biodiversity, v, and use a discount rate of zero, $\rho = 0$, in the numerical optimization.

The numerical optimization is performed using Knitro (version 8.1) with AMPL.

3.3 Numerical optimization results

The results of our numerical optimization show the effects of changes in the shadow price of biodiversity, v, on the optimal steady state stocks of cod, sprat, and herring as well as on optimal profits of the three fisheries and on optimal biodiversity levels. We report optimal stocks and optimal biodiversity levels both in terms of biomass and in terms of number of individuals, showing the sensitivity of the results to the shadow price of biodiversity, v, for a relatively low elasticity of substitution ($\omega = 0.5$) and

for a relatively high elasticity of substitution ($\omega = 2$), and we do so for formulating the biodiversity index in terms of biomass and in terms of number of individuals.

Before interpreting the simulation results in more detail, we would like to point out that the relatively scarce predator species cod crucially influences the system. In particular, increasing the cod stock has two opposing effects. Firstly, there is a negative effect on the stock, and, hence, on long-run fishing profits, of the prey species: Increasing cod stocks leads to decreasing stocks of sprat and herring, which tends to reduce total stock biomass or number of individuals and reduces profits from the sprat and herring fisheries. Secondly, there is a positive scarcity or diversity effect: Cod is a relatively scarce species; in terms of number of individuals, it even is the scarcest species among the three species in the Baltic ecosystem considered here. Thus, increasing cod stocks is good for biodiversity as it increases the evenness of the species distribution. Increasing the prey stocks has no such ambiguous effects. Stock effect and scarcity effect are positive for both prey species. Increasing prey stocks increases aggregate stocks and evenness because this would also imply increases in cod stocks.

Now turn to Figure (2), which shows the results for $\omega = 2$. The optimal stocks of the prey species sprat and herring increase with v while the optimal stock of the predator species cod decreases with v. This holds for optimal stocks measured in biomass (first row) and for optimal stocks measured in numbers (second row). This shows that the species interaction makes a qualitative difference. As our theoretical results derived in section 2.3 have shown, the effect of v on optimal steady state stocks would be unambiguously positive if there was no ecological interactions between the species.

The results for $\omega = 2.0$ are quite similar when comparing whether the objective is to maximize biodiversity in terms of biomass (left panel) or in terms of numbers (right panel). The reason for this is the relatively large elasticity of substitution, ω, in the biodiversity index. Initial stock sizes of the three species are quite similar measured

Objective: biodiversity in biomass

Objective: biodiversity in numbers

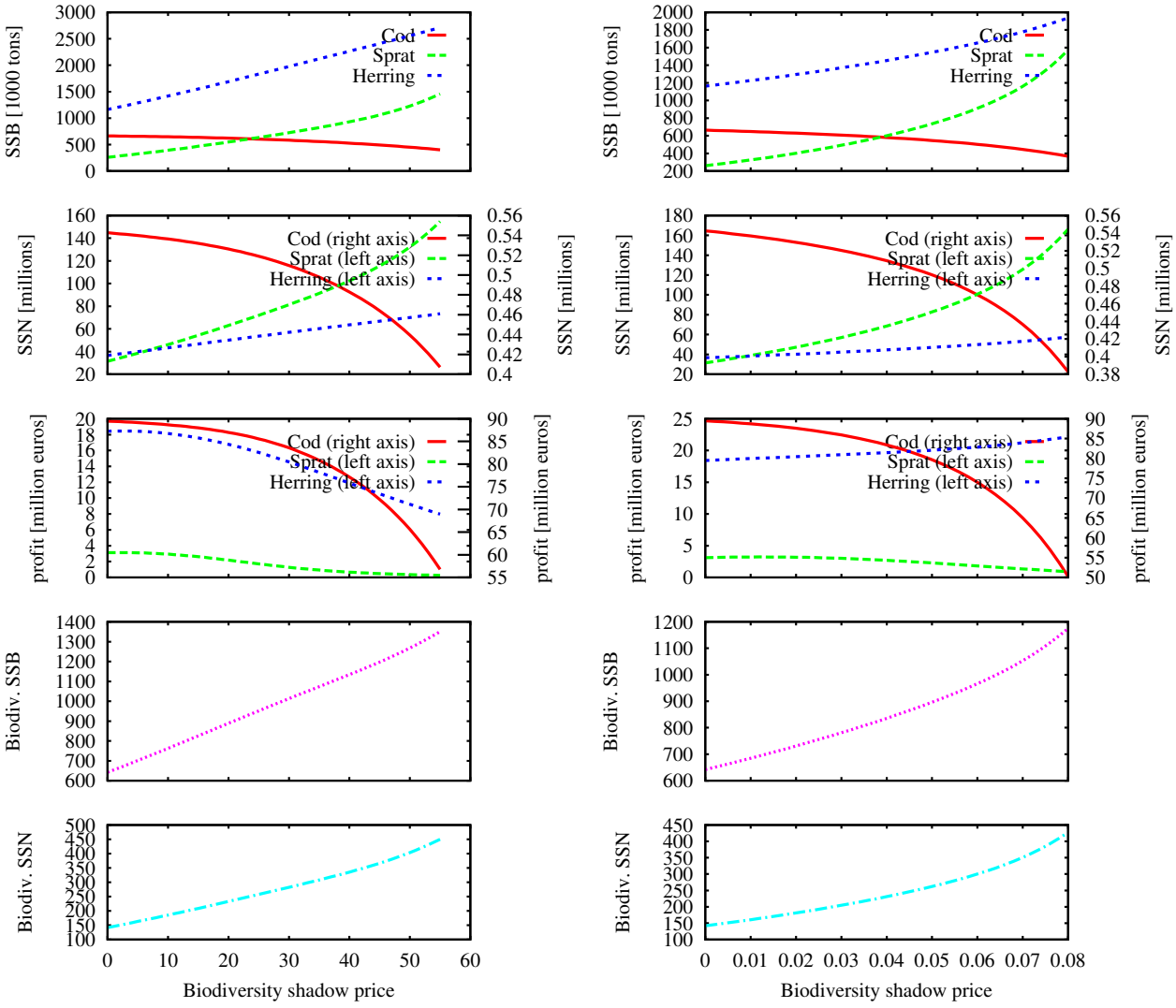

Figure 2: $\omega = 2.0$

Objective: biodiversity in biomass

Objective: biodiversity in numbers

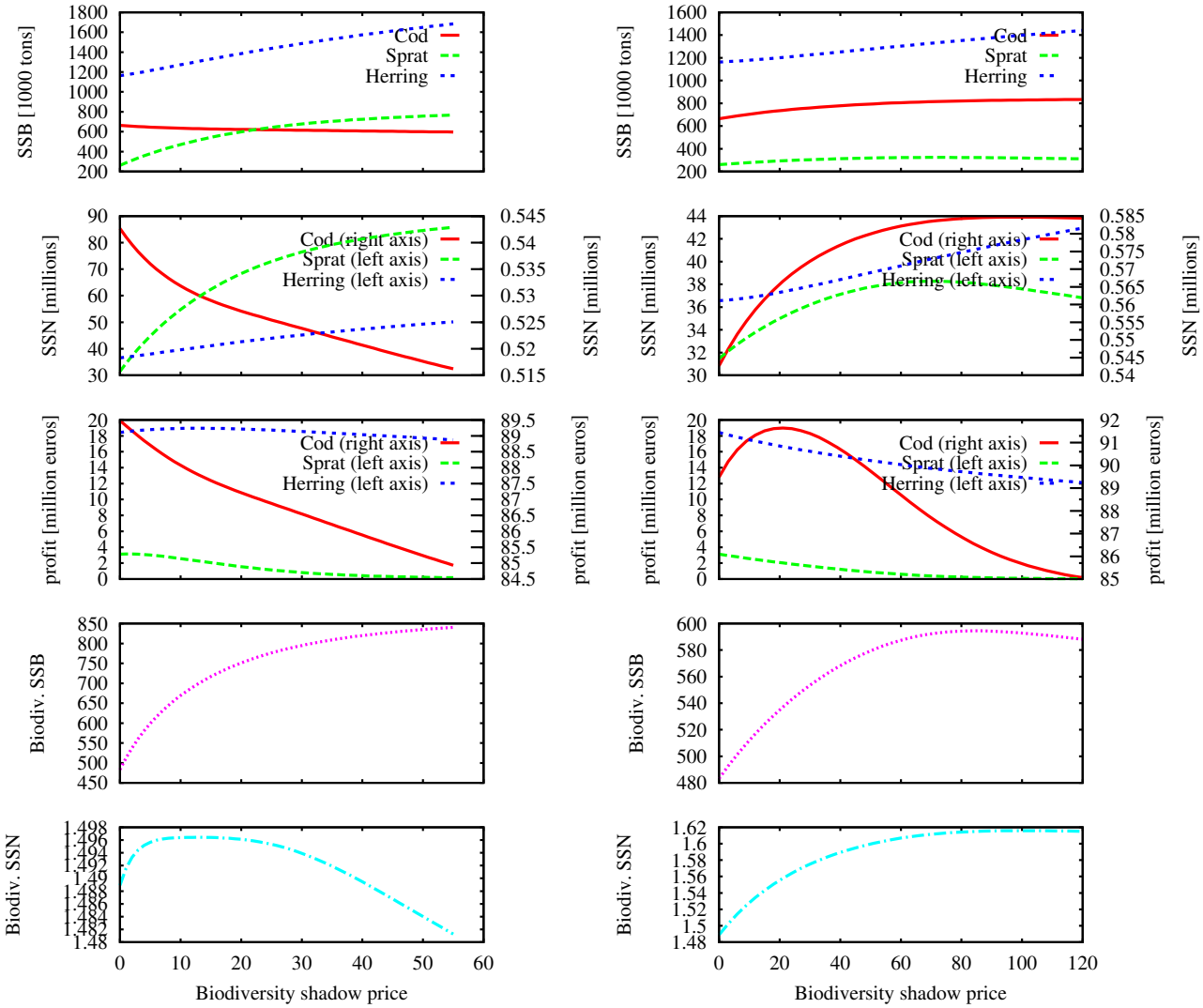

Figure 3: $\omega = 0.5$

in terms of biomass. Measured in terms of numbers, the stock size of cod is about two orders of magnitude smaller than the stock sizes of sprat and herring. The evenness of the species distribution measured in terms of numbers is thus considerably smaller than the one measured in terms of biomass. The large elasticity of substitution, however, implies that an even distribution of species abundances is relatively less important than the absolute aggregate biomass or number of individuals.

Figure 3, in turn, which shows the results for $\omega = 0.5$, reveals interesting differences between the objective to maximize biodiversity in terms of biomass and in terms of numbers. For the objective biodiversity in numbers, the optimal stock of cod now increases while the optimal stock of sprat first increases and then decreases with v. For this case, the scarcity of cod is particularly pronounced in the objective function and evenness plays a relatively larger role than in the other three cases. Consequently, the scarcity effect dominates the stock effect such that the cod stock increases with v. In addition, for $\omega = 0.5$, we observe a smaller divergence of stocks than for $\omega = 2.0$, even for the same objective. The reason for this is that an increase in the elasticity of substitution, ω, increases the dominance of the stock effect over the scarcity effect.

For $\omega = 0.5$ we also find a trade-off between the two types of biodiversity measures (biomass vs. numbers) for large values of the biodiversity shadow price. The left panel of Figure 3, where the biodiversity objective is formulated in biomass, shows that the biodiversity index in terms of biomass unambiguously increases with the shadow price, as expected. If we measure the biodiversity outcome in terms of numbers of individuals, however, we observe a *decline* in biodiversity when the shadow price of biodiversity increases beyond a level of about 20 euros per ton of spawning stock biomass. Looking at the right-hand panel of Figure 3, we find the reverse pattern for biodiversity shadow prices beyond about 100 euros/million fish: while the biodiversity index in terms of numbers (the one included in the objective function in this case) continues to slightly increase with v, biodiversity measured in

terms of biomass decreases with the shadow price of (number) biodiversity.

The reason is that in terms of biomass the unevenness between the three stock sizes is by far not as pronounced as in terms of numbers of individual fish. Thus, when caring for biodiversity in terms of biomass the desire for an overall larger abundance of fish dominates the desire for evenness, and one tends to slightly decrease the cod stock in order to build up the other two stocks. Measuring biodiversity in terms of numbers, however, this implies that the unevenness increases so strongly that the biodiversity index decreases despite an overall increasing abundance of fish. This effect is reversed if the fishery manager cares for biodiversity measured in terms of numbers of individual fish (right-hand panel of Figure 3), in this case leading to a decrease in the biomass-biodiversity index when the shadow price for biodiversity in numbers increases beyond a certain value.

As discussed in section 2.2, the shadow price of biodiversity, v, is not independent of the elasticity of substitution, ω, and the index value, B, which is also reflected in the numerical optimization results. Comparing Figure 2 and Figure 3, it becomes obvious that for the same objective and the same stock sizes, the value of B is lower for $\omega = 0.5$ than for $\omega = 2.0$. This is particularly pronounced for biodiversity in terms of numbers for the case $\omega = 0.5$, for which the unevenness is highest and (number) biodiversity is two orders of magnitudes smaller than for $\omega = 2.0$. In addition, we observe that for the case $\omega = 2.0$ and the objective biodiversity in numbers, a much smaller change in the shadow price, v, brings about similar changes in optimal stock sizes than for the case $\omega = 0.5$.

Comparing optimal biodiversity levels and stock sizes to historic ones (see Figure 1), we observe that current biodiversity levels measured in biomass are below the optimal levels, even if one considers $v = 0$. The same applies to current stocks of herring and cod, which are also below optimal levels. Both results hold for $\omega = 0.5$ and for $\omega = 2.0$. Current stocks of sprat, in contrast, are above optimal levels for low values of v. In the case of $\omega = 0.5$ and when biodiversity in terms of numbers

is the objective, current sprat stocks are higher than optimal levels for a large range of values for v. Comparing optimal biodiversity levels to historically high levels, we observe that historically high levels are in the range of optimal levels for all cases except the one in which $\omega = 0.5$ and the objective is to maximize biodiversity in terms of numbers.

The effects of v on fishing profit are mostly negative, and aggregate profits always fall with the introduction of biodiversity values. Increasing the shadow price of biodiversity v has this negative effect for profits as harvested amounts of fish go down in order to increase the standing stocks. For $\omega = 2$, a positive effect of v on profits only occurs for the herring fishery when the objective is to maximize biodiversity in numbers. The reason is that the concern for biodiversity leads to a decreasing cod stock, thus alleviating predation pressure on herring. The resulting larger steady-state stock size of herring enables a more profitable fishery.

For $\omega = 0.5$, and small values of the biodiversity shadow price, we also see an increase in cod profits with v. The reason is the following: Without biodiversity value, it is optimal to reduce the cod stock below the single-species optimal steady-state stock size (i.e. the steady-state stock size that would result when neglecting the predation effect on the two other species), in order to reduce fishing pressure on the two prey species. As cod is the scarcest species among the three in terms of stock numbers, increasing the biodiversity value leads to an increased cod stock size in steady-state. Thus, the cod stock approaches its single-species optimal stock size and profit increases. For still higher biodiversity shadow price, also the cod stock is built up beyond the single-species profit-maximizing stock level and profits decrease again.

4 Discussion and conclusions

In this paper we have studied how the consideration of a biodiversity value affects optimal management of a multi-species ecosystem with and without ecological interactions.

The biodiversity index used in this paper fulfills all axioms of Buckland et al. (2005) so it seems well-suited to monitor developments of biodiversity over time. Still, our analyses show that optimal management decisions would strongly depend on the parameters and objectives chosen. Specifying the substitution elasticity to a value below or equal to one, $\omega \leq 1$, is sensible only for situations where extinction is out of scope because the biodiversity index would be undefined in that case. Using the index with an elasticity of substitution larger than one is sensible also in situations with changing number of species. Our analysis shows, however, that extinction would never be optimal in that case.

We have shown analytically that species extinction is never optimal when biodiversity, as measured by a constant-elasticity-of-substitution function of in-situ species abundances, plays a role in the objective function. This is in contrast to prior findings such as by Alexander (2000), where non-fishing values made extinction less likely but not impossible in optimal steady states. The reason for this finding is that for the case of imperfect substitutes, $\omega > 1$, the marginal contribution of a species to the biodiversity value goes to infinity if its stock size approaches zero.

How strongly conservation goals are weighted in the objective function can be controlled by choosing the shadow price of biodiversity, v. Without ecological interactions, increasing the biodiversity value v unequivocally increases the steady-state stock sizes of all species in the system. With predator-prey interactions, some steady state stocks may decrease. A quantitative application to the three-species fishery in the Baltic Sea has shown that the steady state stock of a relatively scarce predator species may decrease with the biodiversity shadow price. This is the case if substitutability between the species is relatively high such that the stock effect dominates

the scarcity effect.

We also show how the specification of the substitution elasticity, ω, between species and the choice of abundance indicators in the biodiversity index crucially influence optimal management solutions. The larger the elasticity of substitution, ω, between the species, the more valuable it is to increase aggregate abundance compared to ensuring an even distribution of species abundances. In the case of the Baltic fisheries, cod is significantly less abundant than sprat and herring. This relative scarcity of cod is particularly pronounced when species abundance is measured in terms of numbers, as individual cod are much larger than individual sprat or herring. Consequently, optimal cod stocks increase with the shadow price of biodiversity, v, when the objective is to maximize biodiversity in numbers and ω is relatively small. In all other cases, the negative stock effect of cod, the predator species, dominates the scarcity effect so that optimal cod stocks decrease with v while optimal stocks of herring and sprat increase with v.

These results show that the exact specification of the biodiversity index has important implications for the conclusions on optimal management. Results can change qualitatively when the indicator of species abundance or the value for the elasticity of substitution is changed. One conclusion, however, seems to be robust: as long as species diversity (as measured by the CES-function) plays a role in the objective function, species extinction is never optimal.

A Proof of proposition 1

Under the given assumptions, the condition for the optimal steady state simplifies to

$$(\rho - G_{ix_i})\, p_i = v\, B_{x_i} \tag{A.1}$$

for all $i = 1, \ldots, n$. Here,

$$B_{x_i} = \frac{1}{n}\, x_i^{-\frac{1}{\omega}} \left(\frac{1}{n} \sum_{j=1}^{n} x_j^{\frac{\omega-1}{\omega}} \right)^{\frac{\omega}{\omega-1}-1} = n^{\frac{\omega}{1-\omega}} \left(1 + \sum_{j \neq i}^{n} \left(\frac{x_i}{x_j} \right)^{\frac{1-\omega}{\omega}} \right)^{\frac{1}{\omega-1}}$$

For $x_i \to 0$ and $\omega \geq 1$, B_{x_i} diverges to infinity. Thus, the RHS of equation (A.1) diverges to infinity while the LHS of equation (A.1) is positive but finite. Equation (A.1) will thus never be balanced for $x_i \to 0$.

B Comparative statics w.r.t. v

Under Assumption (10), but with ecological interactions, condition (8b) simplifies to

$$\left(\rho - \sum_{j=1}^{n} \frac{p_j}{p_i}\, G_{jx_i} \right) p_i = v\, B_{x_i} \tag{B.2}$$

Differentiating (B.2) with respect to v, we obtain

$$-\left(p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1}\right) \frac{d\bar{x}_1}{dv} - \left(p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} + v\, B_{\bar{x}_1\bar{x}_2}\right) \frac{d\bar{x}_2}{dv} = B_{\bar{x}_1} \tag{B.3}$$

$$-\left(p_1\, G_{1\bar{x}_2\bar{x}_1} + p_2\, G_{2\bar{x}_2\bar{x}_1} + v\, B_{\bar{x}_2\bar{x}_1}\right) \frac{d\bar{x}_1}{dv} - \left(p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2}\right) \frac{d\bar{x}_2}{dv} = B_{\bar{x}_2} \tag{B.4}$$

Solving yields

$$\frac{d\bar{x}_1}{dv} = \frac{1}{\Delta}\ \left(B_{\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} + v\, B_{\bar{x}_1\bar{x}_2}\right) - B_{\bar{x}_1}\ \left(p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2}\right)\right) \tag{B.5}$$

$$\frac{d\bar{x}_2}{dv} = \frac{1}{\Delta}\ \left(B_{\bar{x}_1}\ \left(p_1\, G_{1\bar{x}_2\bar{x}_1} + p_2\, G_{2\bar{x}_2\bar{x}_1} + v\, B_{\bar{x}_2\bar{x}_1}\right) - B_{\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1}\right)\right) \tag{B.6}$$

with

$$\begin{aligned}
\Delta = {} & p_1^2\ \left(G_{1\bar{x}_1\bar{x}_1}\, G_{1\bar{x}_2\bar{x}_2} - G_{1\bar{x}_1\bar{x}_2}^2\right) + p_2^2\ \left(G_{2\bar{x}_1\bar{x}_1}\, G_{2\bar{x}_2\bar{x}_2} - G_{2\bar{x}_1\bar{x}_2}^2\right) \\
& + p_1\, p_2\ \left(G_{1\bar{x}_1\bar{x}_1}\, G_{2\bar{x}_2\bar{x}_2} + G_{2\bar{x}_1\bar{x}_1}\, G_{1\bar{x}_2\bar{x}_2} + 2\, G_{1\bar{x}_1\bar{x}_2}\, G_{2\bar{x}_1\bar{x}_2}\right) \\
& + v\left(B_{\bar{x}_1\bar{x}_1}\ \left(p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2}\right) + B_{\bar{x}_2\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1}\right)\right. \\
& \qquad \left. - 2\, B_{\bar{x}_1\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2}\right)\right) \\
& + v^2\ \left(B_{\bar{x}_1\bar{x}_1}\, B_{\bar{x}_2\bar{x}_2} - B_{\bar{x}_1\bar{x}_2}^2\right) > 0 \\
= {} & p_1^2\ \left(G_{1\bar{x}_1\bar{x}_1}\, G_{1\bar{x}_2\bar{x}_2} - G_{1\bar{x}_1\bar{x}_2}^2\right) + p_2^2\ \left(G_{2\bar{x}_1\bar{x}_1}\, G_{2\bar{x}_2\bar{x}_2} - G_{2\bar{x}_1\bar{x}_2}^2\right) \\
& + p_1\, p_2\ \left(G_{1\bar{x}_1\bar{x}_1}\, G_{2\bar{x}_2\bar{x}_2} + G_{2\bar{x}_1\bar{x}_1}\, G_{1\bar{x}_2\bar{x}_2} + 2\, G_{1\bar{x}_1\bar{x}_2}\, G_{2\bar{x}_1\bar{x}_2}\right) \\
& + v\left(B_{\bar{x}_1\bar{x}_1}\ \left(p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2}\right) + B_{\bar{x}_2\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1}\right)\right. \\
& \qquad \left. - 2\, B_{\bar{x}_1\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2}\right)\right) > 0
\end{aligned} \tag{B.7}$$

C Proof of proposition 2

For $G_{i\bar{x}_i\bar{x}_j} = 0$, the expressions (11) and (12) simplify to

$$\frac{d\bar{x}_1}{dv} = \frac{1}{\Delta}\ \left(B_{\bar{x}_2}\, v\, B_{\bar{x}_1\bar{x}_2} - B_{\bar{x}_1}\ \left(p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2}\right)\right) > 0 \tag{C.8}$$

$$\frac{d\bar{x}_2}{dv} = \frac{1}{\Delta}\ \left(B_{\bar{x}_1}\, v\, B_{\bar{x}_2\bar{x}_1} - B_{\bar{x}_2}\ \left(p_1\, G_{1\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1}\right)\right) > 0 \tag{C.9}$$

with

$$\Delta = p_1\, p_2\, G_{1\bar{x}_1\bar{x}_1}\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_1\bar{x}_1}\, p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2}\, p_1\, G_{1\bar{x}_1\bar{x}_1} > 0. \tag{C.10}$$

This concludes the proof of part (a) of the proposition.

For $G_{i\bar{x}_i\bar{x}_j} > 0$, $p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} > 0$ such that the RHS of (11) and (12) are positive. This concludes the proof of part (b) of the proposition.

D Comparative statics w.r.t. p

Differentiating (B.2) with respect to p_1 for $i = 1, 2$ we obtain

$$(\rho - G_{1\bar{x}_1}) - (p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1})\, \frac{d\bar{x}_1}{dp_1} - (p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} + v\, B_{\bar{x}_1\bar{x}_2})\, \frac{d\bar{x}_2}{dp_1} = 0 \quad \text{(D.11)}$$

$$- G_{1\bar{x}_2} - (p_1\, G_{1\bar{x}_2\bar{x}_1} + p_2\, G_{2\bar{x}_2\bar{x}_1} + v\, B_{\bar{x}_2\bar{x}_1})\, \frac{d\bar{x}_1}{dp_1} - (p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2})\, \frac{d\bar{x}_2}{dp_1} = 0 \quad \text{(D.12)}$$

Solving yields

$$\frac{d\bar{x}_1}{dp_1} = \frac{1}{\Delta}\,((-G_{1\bar{x}_2}\ (p_1\, G_{1\bar{x}_1\bar{x}_2} + p_2\, G_{2\bar{x}_1\bar{x}_2} + v\, B_{\bar{x}_1\bar{x}_2}) + (\rho - G_{1\bar{x}_1})\ (p_1\, G_{1\bar{x}_2\bar{x}_2} + p_2\, G_{2\bar{x}_2\bar{x}_2} + v\, B_{\bar{x}_2\bar{x}_2})) \quad \text{(D.13)}$$

$$\frac{d\bar{x}_2}{dp_1} = \frac{1}{\Delta}\,(-(\rho - G_{1\bar{x}_1})\ (p_1\, G_{1\bar{x}_2\bar{x}_1} + p_2\, G_{2\bar{x}_2\bar{x}_1} + v\, B_{\bar{x}_2\bar{x}_1}) + G_{1\bar{x}_2}\ (p_1\, G_{1\bar{x}_1\bar{x}_1} + p_2\, G_{2\bar{x}_1\bar{x}_1} + v\, B_{\bar{x}_1\bar{x}_1})) \quad \text{(D.14)}$$

with Δ as above.

E Proof of proposition 3

For $G_{i\bar{x}_j} = 0$ and $G_{i\bar{x}_i\bar{x}_j} = 0$, the expressions (14) and (15) simplify to

$$\frac{d\bar{x}_1}{dp_1} = \frac{1}{\Delta}\,(\rho - G_{1\bar{x}_1})(p_2\,G_{2\bar{x}_2\bar{x}_2} + v\,B_{\bar{x}_2\bar{x}_2}) < 0 \tag{E.15}$$

$$\frac{d\bar{x}_2}{dp_1} = \frac{-1}{\Delta}\,(\rho - G_{1\bar{x}_1})v\,B_{\bar{x}_2\bar{x}_1} < 0 \tag{E.16}$$

with

$$\Delta = p_1\,p_2\,G_{1\bar{x}_1\bar{x}_1}\,G_{2\bar{x}_2\bar{x}_2} + v\,B_{\bar{x}_1\bar{x}_1}\,p_2\,G_{2\bar{x}_2\bar{x}_2} + v\,B_{\bar{x}_2\bar{x}_2}\,p_1\,G_{1\bar{x}_1\bar{x}_1} > 0. \tag{E.17}$$

This concludes the proof of part (a) of the proposition.

For $G_{i\bar{x}_j} > 0$ and $G_{i\bar{x}_j\bar{x}_i} > 0$, $p_1\,G_{1\bar{x}_1\bar{x}_2} + p_2\,G_{2\bar{x}_1\bar{x}_2} > 0$ and $(\rho - G_{1\bar{x}_1}) > 0$ such that the RHS of (14) and (15) are positive. This concludes the proof of part (b) of the proposition.

F Proof of Proposition 4

We first determine the sign of the following term in (17)

$$\begin{aligned}
&\frac{\partial B_{\bar{x}_2}}{\partial\omega}\,B_{\bar{x}_1\bar{x}_2} - \frac{\partial B_{\bar{x}_1}}{\partial\omega}\,B_{\bar{x}_2\bar{x}_2} \\
&= -2^{-2\,\frac{\omega}{\omega-1}}\,\frac{\hat{x}^{\frac{1}{\omega}}\left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right)^{\frac{2}{\omega-1}}}{x_2\,\omega^2}\,\underbrace{\frac{1}{1-\omega}\left(\frac{\hat{x}^{\frac{1-\omega}{\omega}}}{1+\hat{x}^{\frac{1-\omega}{\omega}}}\,\ln(\hat{x}) + \ln\left(\frac{1+\hat{x}^{\frac{1-\omega}{\omega}}}{2}\right)^{\frac{\omega}{\omega-1}}\right)}_{\equiv\Omega} \le 0
\end{aligned} \tag{F.18}$$

Lemma 1

$\Omega \ge 0$ with $\Omega = 0$ only for $\hat{x} = 1$.

Proof. Ω has a global minimum $\Omega = 0$ at $\hat{x} = 1$, as

$$\frac{d\Omega}{d\hat{x}} = \frac{\hat{x}^{\frac{1-\omega}{\omega}}\,\ln(\hat{x})}{\omega\,\hat{x}\left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right)^2} \tag{F.19}$$

is zero if and only if $\hat{x} = 1$; negative for all $\hat{x} < 1$ and positive for all $\hat{x} > 1$. □

Lemma 1 implies that $d\bar{x}_1/d\omega < 0$ if $\frac{\partial B_{x_1}}{\partial \omega} < 0$. To determine the sign of this last expression, we define

$$\Gamma \equiv \frac{1}{1-\omega} \left(\frac{\hat{x}^{\frac{1-\omega}{\omega}}}{1+\hat{x}^{\frac{1-\omega}{\omega}}} \ln(\hat{x}) + \omega \ln \left(\frac{1+\hat{x}^{\frac{1-\omega}{\omega}}}{2} \right)^{\frac{\omega}{\omega-1}} \right). \tag{F.20}$$

Note that $\frac{\partial B_{x_1}}{\partial \omega} \lesseqgtr 0$ if and only if $\Gamma \lesseqgtr 0$.

We have $\Gamma = 0$ for $\hat{x} = 1$, and furthermore

$$\frac{d\Gamma}{d\hat{x}} = \frac{d\Omega}{d\hat{x}} + \frac{\hat{x}^{\frac{1-\omega}{\omega}}}{\hat{x}\left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right)} = \frac{\hat{x}^{\frac{1-\omega}{\omega}}}{\omega\,\hat{x}\left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right)^2} \left(\ln(\hat{x}) + \omega \left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right) \right) \tag{F.21}$$

Thus, for $\hat{x} \geq 1$, $d\Gamma/d\hat{x} > 0$. Thus, $\Gamma > 0$ for all $\hat{x} > 1$. This shows that for the larger stock, the effect of ω on $\bar{x}$ is ambiguous.

If x_1 is the smaller stock, i.e. $\hat{x} < 1$, the situation is more complicated. For the following lemma, we use $\hat{\omega}$ to denote the solution of $\hat{\omega} + \ln(\hat{\omega} - 1) = 0$, which is $\hat{\omega} \approx 1.28$.

Lemma 2

(a) If $\omega \geq \hat{\omega}$, $\Gamma < 0$ for all $0 < \hat{x} < 1$.

(b) If $\omega < \hat{\omega}$, it exists an $0 \leq \underline{\hat{x}} < 1$ such that $\Gamma < 0$ for all $\hat{x} \in (\underline{\hat{x}}, 1)$.

Proof. In the following we show that for $\omega \geq \hat{\omega}$, $d\Gamma/d\hat{x} > 0$ for all $\hat{x} > 0$, and that for $\omega < \hat{\omega}$, Γ has a unique minimum where it assumes some negative value.

To this end, we consider the expression $\Sigma \equiv \ln(\hat{x}) + \omega \left(1+\hat{x}^{\frac{1-\omega}{\omega}}\right)$, which determines the sign of $d\Gamma/d\hat{x}$, i.e. $d\Gamma/d\hat{x} \gtreqless 0$ if and only if $\Sigma \gtreqless 0$. We show that the equation $\Sigma = 0$ has no solution (i.e. Γ is monotonic) if $\omega > \hat{\omega}$, and (at least) one solution if $\omega \leq \hat{\omega}$.

Note that for $\hat{x} = 1$, $\Sigma = 2\,\omega > 0$, and $\lim_{\hat{x}\to 0} \Sigma = +\infty$ for $\omega > 1$, as

$$\lim_{\hat{x}\to 0} \frac{\ln(\hat{x})}{1+\hat{x}^{\frac{1-\omega}{\omega}}} = \lim_{\hat{x}\to 0} \frac{\frac{1}{\hat{x}}}{\frac{1-\omega}{\omega}\,\hat{x}^{\frac{1-\omega}{\omega}-1}} = \lim_{\hat{x}\to 0} \frac{\omega}{1-\omega}\,\hat{x}^{\frac{\omega-1}{\omega}} = 0. \tag{F.22}$$

Furthermore,

$$\frac{d\Sigma}{d\hat{x}} = \frac{1}{\hat{x}} \left(1 - (\omega-1)\,\hat{x}^{\frac{1-\omega}{\omega}}\right) \tag{F.23}$$

Case $\omega \geq \hat{\omega}$: Σ has a minimum $\Sigma^* = \frac{\omega}{\omega-1}\,(\omega + \ln(\omega-1))$ at $\hat{x}^\star = (\omega-1)^{\frac{\omega}{\omega-1}}$. This minimum is non-negative if $\omega \geq \hat{\omega}$ and thus $\Sigma \geq 0$ for all $\hat{x} < 1$ in this case. This implies that Γ monotonically increases with $\hat{x}$ if $\omega \geq \hat{\omega}$. Since $\Gamma = 0$ for $\hat{x} = 1$, this implies that $\Gamma < 0$ for all $0 < \hat{x} < 1$. This concludes the proof of part (a) of the lemma.

Case $\omega < \hat{\omega}$: The minimum of Σ is negative, $\Sigma^\star < 0$. As $\Sigma = 2\omega > 0$ for $\hat{x} = 1$, this implies that there exist a value $\underline{\hat{x}} > \hat{x}^\star$ where $\Sigma = 0$. At $\underline{\hat{x}}$, Γ assumes a minimum, i.e. for values of $\hat{x} < \underline{\hat{x}}$, Γ decreases with $\hat{x}$. Depending on the value of $\omega < \hat{\omega}$, Γ may or may not intersect with zero for some value $\hat{x} < \underline{\hat{x}}$. Let $\underline{x}$ be the maximum of that value of $\hat{x}$ where $\Gamma = 0$ and zero. This concludes the proof of part (b) of the lemma. □

G Parameter values for the age-structured bio-economic model

age	maturity γ_{is}			weight w_{is} [g]			catchability q_{is}			mortality M_2			δ_{is} $[10^{-4}]$		price p_{Cs}
	C	H	S	C	H	S	C	H	S	C	H	S	H	S	C
1	0.00	0.0	0.17	80	11	52	0.00	0.28	0.27	0.0	0.170	0.132	3.32	8.74	0.00
2	0.13	0.7	0.93	179	20	84	0.11	0.44	0.49	0.2	0.173	0.137	2.31	7.08	0.35
3	0.36	0.9	1.0	511	25	96	0.42	0.66	0.79	0.2	0.178	0.132	0.45	6.74	0.35
4	0.83	1.0	1.0	838	31	105	0.81	0.82	0.85	0.2	0.188	0.132	0.45	6.74	0.35
5	0.94	1.0	1.0	1204	37	111	1.00	0.97	1.00	0.2	0.188	0.132	0.45	6.74	0.48
6	0.96	1.0	1.0	1796	43	113	1.00	0.96	1.00	0.2	0.188	0.132	0.45	6.74	0.48
7	0.96	1.0	1.0	2596	48	111	1.00	1.00	1.00	0.2	0.188	0.132	0.45	6.74	0.64
8	0.98	1.0	1.0	4068	53	113	1.00	1.00	1.00	0.2	0.188	0.132	0.45	6.74	0.73

$c_C = 55.2$ million euros. $p_S - c_S = 0.039$ euros/kg, and $p_H - c_H = 0.100$ euros/kg.

		ϕ_{i1}	ϕ_{i2}
cod	Ricker	1.7	549
herring	Ricker	30.33	2156
sprat	Beverton-Holt	104.2	503.2

References

Alexander, R. (2000). Modelling species extinction: the case for non-consumptive values. *Ecological Economics*, 35:259–269.

Arrow, K. J., Chenery, H., Minhas, B. S., and Solow, R. M. (1961). Capital-labor substitution and economic efficiency. *The Review of Economics and Statistics*, 43(3):225–250.

Arrow, K. J. and Kurz, M. (1970). *Public Investment, The Rate of Return, and Optimal Fiscal Policy*. Resources for the Future, John Hopkins Press, Baltimore.

Brown, G., Berger, B., and Ikiara, M. (2005). A predator-prey model with an application to lake victoria fisheries. *Marine Resource Economics*, 20(3):221–248.

Buckland, S., Magurran, A., Green, R., and Fewster, R. (2005). Monitoring change in biodiversity through composite indices. *Philosophical Transactions of the Royal Society B*, 360:243–254.

Clark, C. (1973). Profit maximization and the extinction of animal species. *The Journal of Political Economy*, 81(4):950–961.

Dixit, A. K. and Stiglitz, J. E. (1977). Monopolistic competition and optimum product diversity. *American Economic Review*, 67(3):297–308.

ICES (2012). Report of the Baltic fisheries assessment working group (WGBFAS). ICES, Copenhagen.

Kellner, J., Sanchirico, J., Hastings, A., and Mumby, P. (2010). Optimizing for multiple species and multiple values: tradeoffs inherent in ecosystem-based fisheries management. *Conservation Letters*, 00:1–10.

Köster, F. W. and Möllmann, C. (2000). Trophodynamic control by clupeid predators on recruitment success in baltic cod? *ICES Journal of Marine Science*, 57:310–323.

Magurran, A. (2004). *Measuring Biological Diversity*. Blackwell Publishing, Malden, USA, Oxford, UK, and Victoria, Australia.

Noack, F., Manthey, M., Ruitenbeek, J., and Mohadjer, M. (2010). Separate or mixed production of timber, livestock and biodiversity in the caspian forest. *Ecological Economics*, 70:67–76.

Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E., Link, J., Livingston, P., Mangel, M., McAllister, M., Pope, J., and Sainsbury, K. (2004). Ecosystem-based fishery management. *Science*, 305(5682):346–347.

Quaas, M. and Requate, T. (2013). Sushi or fish fingers - seafood diversity, collapsing fish stocks, and multispecies fishery management. *The Scandinavian Journal of Economics*, 155(2):381–422.

Quaas, M., Requate, T., Ruckes, K., Skonhoft, A., Vestergaard, N., and Voss, R. (2013). Incentives for optimal management of age-structured fish populations. *Resource and Energy Economics*, 35(2):113–134.

Quaas, M. F., Froese, R., Herwartz, H., Requate, T., Schmidt, J. O., and Voss, R. (2012). Fishing industry borrows from natural capital at high shadow interest rates. *Ecological Economics*, 82:45–52.

Ricker, W. E. (1954). Stock and recruitment. *Journal of the Fisheries Research Board of Canada*, 11:559–623.

Spence, A. M. (1974). Blue whales and applied control theory. In Gottinger, H. W., editor, *System Approaches and Environmental Problems*, pages 97–124. Vandenhoeck and Ruprecht, Göttingen.

Tahvonen, O. (2009). Economics of harvesting age-structured fish populations. *Journal of Environmental Economics and Management*, 58(3):281–299.

Tahvonen, O., Quaas, M., Schmidt, J., and Voss, R. (2013). Optimal harvesting of an age-structured schooling fishery. *Environmental and Resource Economics*, 54(1):21–39.

Voss, R., Quaas, M., Schmidt, J., and Hoffmann, J. (2014). Regional trade-offs from multi-species maximum sustainable yield (MMSY) management options. *Marine Ecology Progress Series*, 498:1–12.