Title: Ecologically Sustainable Exploitation Rates – A multispecies approach for fisheries management

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ABSTRACT

Fisheries management is slowly evolving from its traditional single species focus to a more holistic ecosystem based approach. Yet, limits for exploitation are almost always set based on single species models, treating species as isolated entities. This is problematic since the sustainability of a fishery hinges on its effects on the exploited community as a whole. Here, we develop a novel analytical approach of estimating exploitation rates that are sustainable with respect to the state of whole fish communities. Our approach simultaneously addresses species interactions, environmental covariates and natural variability of population sizes, yet it is framed around a simple and accessible objective. We derive Ecologically Sustainable Exploitation Rates, i.e. exploitation rates associated with a maximum acceptable probability (determined by management) that any interacting species decreases to an unacceptably low population size. Using models fitted to an exploited fish community we show how accounting for species interactions constrains the possibilities for ecologically sustainable exploitation. The conventional omission of species interactions may thus result in overestimated exploitation limits. Moreover, our application rendered a counterintuitive result: it suggests that the exploitation of one species should increase, as compared to mean historical levels, for the purpose of conservation of the community as a whole. Such insights could impossibly be gained using single species approaches, illustrating the need to adopt multispecies models in fisheries management. Analytical derivation of Ecologically Sustainable Exploitation Rates offers a mean to do so.

Keywords: Multispecies exploitation; Multispecies objective; Reference points; Stock assessment; Viability modeling; Statistical modeling.

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INTRODUCTION

Reference points for fisheries management have traditionally been set based on a single species perspective, and are most often still derived using such an approach (Collie et al., 2014; Holsman, Ianelli, Aydin, Punt, & Moffitt, 2016; Skern-Mauritzen et al., 2016; Möllmann et al., 2014). However, selective fishing also indirectly affects non-target, ecologically interlinked species (Baum & Worm, 2009; Cury et al., 2011; Smith et al., 2011). In the worst case this might even lead to extinctions of other dependent species (Matsuda & Abrams, 2006; Säterberg, Sellman, & Ebenman, 2013), thus questioning the viability of a single species approach in fisheries management. Moreover, limits for exploitation rates based on single- and multispecies approaches can differ substantially (EC, 2012; Gislason, 1999; Gårdmark et al., 2013; Holsmann, Ianelli, Aydin, Punt, & Moffitt, 2016; May, Beddington, Clark, Holt, & Laws, 1979; Tyrell, Link, & Moustahfid, 2011), because species interactions govern how populations respond to fishing (Gårdmark et al., 2013). Increased fishing of forage fish might, for example, decrease the sustainable fishing limit of their predators due to food-shortage. Fishing on predators may instead lead to increased sustainable fishing limits of their prey fish when they are released from predation (Gislason, 1999; May, Beddington, Clark, Holt, & Laws, 1979; but see Huss, de Roos, Van Leeuwen, & Gårdmark, 2014). A successful management of exploitation of interacting species therefore requires a multispecies approach.

However, population dynamics and thus exploitation limits of fish populations are also affected by other factors besides species interactions and exploitation. Population dynamics of fish species result from stochastic processes, and environmental conditions affect fish productivity (Lindegren, Möllmann, Nielsen, & Stenseth, 2009). Moreover, uncertainty about any biotic or abiotic process propagates to uncertain fishing limits (Thorpe, Le Quesne, Luxford, Collie, & Jennings, 2015). Therefore, to set sustainable and precautionary limits for exploitation, approaches should not only be multispecies, but also account for exogenous environmental variables (Gårdmark et al., 2013; Lindegren, Möllmann, Nielsen, & Stenseth, 2009), uncertainty in parameter estimates (Link et al., 2012; Thorpe, Le Quesne, Luxford, Collie, & Jennings, 2015) and natural variability of population sizes (Lindegren, Möllmann, Nielsen, & Stenseth, 2009; Link et al., 2012).

Although it is desirable to address biotic, abiotic as well as statistical factors when estimating exploitation limits in a multispecies context, accounting for such factors may lead to complex modeling outcomes (Collie et al., 2014). Conventional reference points derived from statistical multispecies models are, for example, highly uncertain (Holsman, Ianelli, Aydin, Punt, & Moffitt, 2016) and contingent on exploitation exerted on all species in a community (Gislason, 1999; May, Beddington, Clark, Holt, & Laws, 1979). Basing management actions on such reference points may thus be a difficult task (but see Norrström, Casini, & Holmgren, 2017). However, viability modeling offers an alternative procedure (Cury, Mullon, Garcia, & Shannon, 2005; Doyen et al., 2012). This modeling framework infers that all trajectories of a dynamical system under uncertainty remain within predefined boundaries of its state variables. Thus, rather than estimating uncertain reference points that depend on exploitation exerted on all species in a community, viability modelling can be used to estimate ranges of exploitation rates leading to a viable status of the community as a whole.

Multispecies models are needed when estimating sustainable exploitation rates in communities of interacting species. Yet, designing such models is difficult, since knowing which specific ecological processes are at work in a large ecosystem is intricate (Planque, 2016). Most modern statistical multispecies models are therefore to some extent dependent on assumptions of ecological processes and preset parameter values (Plagányi et al., 2014). However, an alternative is to statistically fit all parameters of a stochastic multispecies model with no prerequisite assumptions about parameter values (Ives, Dennis, Cottingham, & Carpenter, 2003). This has been argued as the preferable approach for tactical fisheries management advice (Plagányi et al., 2014), because species interactions can completely determine both qualitative and quantitative effects of fishing (Gårdmark et al., 2013). Fully statistically fitted stochastic multispecies models may further be preferable for assessing communities' long-term responses to exploitation, since the net effects of species on each other are then based solely on observation data. Thus, it is somewhat surprising that fully statistically fitted stochastic multispecies models have not, at least to our knowledge, been used for estimating long-term exploitation rates associated with a viable status of fish communities (cf. Lindegren, Möllmann, Nielsen, & Stenseth, 2009).

Here we introduce a novel analytical time series approach of estimating exploitation levels associated with a viable status of communities of interacting fish species (see Methods). The approach relies entirely on statistically fitted model parameters and it can handle both environmental covariates and natural variability of fish populations. We derive Ecologically Sustainable Exploitation Rates, i.e. exploitation rates associated with a low probability (lower than a predefined maximum acceptable probability) that any interacting species in a community goes below its predefined critical biomass limit. We show how such Ecologically Sustainable Exploitation Rates can be analytically derived from purely statistically fitted models, and demonstrate the approach using models fitted to long-term observation data for the fish populations dominating the fisheries in the Baltic Sea.

RESULTS AND DISCUSSION

Estimating Ecologically Sustainable Exploitation Rates

An ecologically sustainable exploitation rate (hereafter ESER) can quantitatively be defined as a mean exploitation rate associated with a low probability (lower than a predefined maximum acceptable probability) that any fish population goes below its critical biomass limit (here we use Blim; a biomass limit below which a fish population's productivity risks being impaired [ICES, 2015]). ESERs are thus related to a quantitative and probabilistically well-defined objective at the community level. They require three inputs before application: (i) a statistical multivariate model fitted to time series of interacting fish populations, exploitation rates and potentially important environmental covariates; (ii) biological information on critical biomass limits for the interacting fish populations; and (iii) a maximum probability a manager is willing to accept. Further, in contrast to how conventional reference points previously have been derived using statistical multispecies models, i.e. through extensive computer simulations, ESERs can be derived analytically (see Methods; Figs. 1 & S1).

Example of Ecologically Sustainable Exploitation Rates

To exemplify the ESER approach we use multivariate autoregressive (MAR-) models fitted to survey data for the three commercially most important fish populations in the Baltic Sea: cod, sprat and herring (see "Baltic Sea application" & "MAR-model assumptions" in SI for details; Table S2). Limits for ESERs based on the final model, following model selection (Table S1 & S3; Figs. 1-2 & S2-S4), suggest that it may be beneficial for the viability of the fish community to increase sprat exploitation rate somewhat compared to mean historical levels (1988-2014). This is because a small increase in sprat exploitation rate would decrease the probability that any species declines below its critical biomass limit (Fig. 1d), and because the upper limit to sprat ESER (0.62 [0.39 1.16]; Fig. 1c) is more disconnected from mean historical exploitation levels (i.e. zero anomaly) than sprat's lower limit (-0.53 [-1.75 -0.25]; Fig. 1a). Exploitation rate of sprat would thus be at maximum distance from its two ESER limits if increased slightly above mean historical levels. The reason for this seemingly counterintuitive result is the negative effect of sprat on both cod and herring found in the final model (Table S1). As a result, increased exploitation of sprat decreases the likelihood that cod and herring populations decline below their critical biomass limits (Table S4). For cod and herring, however, ESER limits suggest that lowering exploitation below mean historical levels is always a beneficial management strategy (cod upper limit: 0.84 [0.61 1.49]; herring upper limit: 0.39 [0.24 0.79]; herring lower limit: -1.64 [-6.65 -0.79]), across all models investigated (Table S3; see also Table S5). Overall, the ESER limits illustrate the importance of a multispecies approach to fisheries management since an increased exploitation of a given species may in fact - due to species interactions - be beneficial for conservation of a community as a whole; a result that impossibly can be rendered using a single species model (Fig. S5).

When exploitation is concurrently varied for all populations in the final model, species interactions constrain the ranges of ESERs (Fig. 3) compared to the single species case (Fig. S5). Further, the more interactions that are included in the model, the smaller the range of ESERs (Fig. 3 vs. Fig. S6). Thus, due to interdependence among fish populations and uncertainties in these, narrow ranges of exploitation rate combinations are needed to attain the multispecies objective in multispecies models (Figs. 3 & S6). In contrast, ESERs derived from the corresponding single species models have much wider ranges (Fig. S5) and they show that decreased exploitation is always beneficial for the community. Thus, if species interactions and accompanying interdependencies of different fisheries are not accounted for when estimating ESERs, the range of ESERs will be overestimated and misleadingly large.

The multispecies objective may be differently sensitive to exploitation of different fish populations. In our example, the multispecies objective is more sensitive to changes in exploitation of sprat than of the other species (Fig. 3a-c & g-i). This specific result stems, in our example, from three factors: (i) compared to mean historical exploitation rate for each species during 1988-2014, a change in the exploitation rate of sprat causes an almost twice as large effect on the ln(biomass) of sprat than what a change in the exploitation rate of cod or herring causes on their respective ln(biomasses) (diagonal in Table S4); (ii) the variability of mean biomass responses of all species to changes in sprat exploitation rate is larger than that of the responses to changes in exploitation of the other species (CI ranges in Table S4); (iii) the initial probability that a population declines below its Blim is initially higher for both cod and herring than for sprat (Fig. 1b), such that a relatively small decrease in sprat exploitation rate indirectly causes cod and herring to decrease below their Blims. Overall, sensitivity of the multispecies objective to changes in exploitation of a given fish population thus depends on the sensitivity of the targeted population, inter- and intra-specific interactions among exploited species, natural variability of fish populations, parameter uncertainty, and how close populations initially are to their critical biomass limits.

Implications of the ESER approach

The analytical approach of estimating reference levels for exploitation in fish communities we present can simultaneously addresses natural variability among fish populations, environmental covariates, species interactions as well as resulting interdependencies of different fisheries. Although similar multispecies models have been developed (Collie et al., 2014, Plagányi et al., 2014), very few have been applied when setting reference points for management (Collie et al., 2014; Möllmann et al., 2014; Plagányi et al., 2014; Skern-Mauritzen et al., 2016). One potential reason is that multispecies models often give less conservative estimates of exploitation targets associated with maximum sustainable yield, i.e. higher estimates of fishing mortality, than single species models (e.g. EC, 2012; Gislason, 1999; Holsman, Ianelli, Aydin, Punt, & Moffitt, 2016; Norrström, Casini, & Holmgren, 2017). Such permissive multispecies targets lead to unsustainably low population biomasses that are particularly sensitive to stochastic perturbations (EC, 2012; Holsman, Ianelli, Aydin, Punt, & Moffitt, 2016; Norrström, Casini, & Holmgren, 2017). It has therefore been suggested that critical biomass limits of fish populations should be introduced when setting target levels for exploitation using multispecies models, resulting in lower recommended target catches (Holsman, Ianelli, Aydin, Punt, & Moffitt, 2016). Thus, if conservation of fish populations is of concern, target reference setting based solely on maximizing yield will not suffice in a multispecies context. Here, as opposed to target reference point setting, we have derived an approach with a single conservation objective: ESERs are associated with a low probability (lower than a predefined maximum acceptable probability) that any fish population goes below its critical biomass limit. The boundaries for the ranges of ESERs (Fig. 3) should therefore be seen as exploitation limits, and if exploitation targets based on other objectives (e.g. maximum sustainable yield) are not within these limits they could be defined as ecologically unsustainable. In a broad sense, the ESER approach could thus potentially act as a complement to traditional single species stock assessment, and exploitation rates derived from single species stock assessments could readily be evaluated for ecological sustainability, using the ESER approach.

The ranges of ESERs depend on four factors: (i) sensitivity of fish populations to exploitation and environmental covariates; (ii) species interactions; (iii) different types of uncertainty (i.e. process error, parameter uncertainty and uncertainty in covariate projections); and (iv) the multispecies objective. The first two combined determine mean biomass responses of fish populations to changes in mean values of extrinsic variables (i.e. exploitation rates and environmental covariates); the third factor determines the variability of these fish stock projections; and the last determines how ESERs are probabilistically bounded by species' critical biomass limits. Thus, an increase in any type of uncertainty will increase the variability of fish population projections. This increases the probability that any fish population declines below its critical biomass limit, leading to a smaller range of ESERs. Correspondingly, reduced uncertainty will instead increase the range of ESERs. Thus, if uncertainty of any type increases, the statistical support for exploiting a given multispecies community in an ecologically sustainable way decreases. Exploitation rate combinations suggested by the ESER approach are therefore strongly contingent on the quality of input data (e.g. precision and time series length).

The range of ESERs inevitably depends on the multispecies objective, i.e. on the predefined maximum acceptable probability, the critical biomass limits, as well as the number of species it accounts for. If a manager is willing to accept a large risk (i.e. a high probability that any population declines to the extent that its productivity is impaired) or low critical biomass limits, a wide range of exploitation rates would be accepted (Figs. S7 & S8 vs. Fig. 3, respectively). Further, similar to viability models, where the viability kernel shrinks with an increasing number of boundaries of its state variables (Cury, Mullon, Garcia, & Shannon, 2005; see Doyen et al., 2012 for an example), the range of ESERs decreases with the number of species' critical biomass limits incorporated in the multispecies objective. This result is an inherent property of the multispecies objective, and for a fixed maximum acceptable probability, an increasing number of species included in the analysis will eventually lead to no support for ecologically sustainable exploitation. Yet, for diverse ecosystems, it may be just as important to consider conservation of the ecological functions inherent in a system as it is to consider conservation of the populations of all species (e.g. Bozec, O'Farrell, Bruggemann, Luckhurst, & Mumby, 2016; Cury et al., 2011). To this end, the ESER approach could be extended by redefining the multispecies objective as a probability lower than a maximum acceptable probability that either (i) the total biomass of any functional group goes below a predefined group specific critical biomass limit, or (ii) that any species within each functional group goes below its critical biomass limit (see "ESERs in specious systems" in SI). The former means that limits for exploitation are associated with conservation of the total biomass of each functional group, whereas in the latter case they are associated with a maximum acceptable probability that any species, in the most sensitive functional group, decreases below its critical biomass limit. Thus, if the mere conservation of ecosystem functions is of concern the former approach could be used, whereas if conservation of individual species is also of concern the latter should be used. Importantly, any of these modifications makes it possible to derive ESERs also in specious ecosystems.

The ESER approach is not only useful for deriving quantitative exploitation limits; it also has an important qualitative application in management. It can be used to single out species of specific management concern for the conservation of the community as a whole. A species may be pinpointed because it induces strong indirect effects in a community of interacting fish species, or due to uncertainty in how these effects are induced, given data at hand. For such species it may be especially important to keep exploitation rate within ecologically safe limits, since changes in exploitation may have a strong effect on the rest of the community, or, because the magnitude of these effects are statistically uncertain. Both of these aspects are probabilistically captured and quantifiable when estimating ESERs.

As with any modelling approach, the ESER approach is strongly dependent on the underlying mathematical model. This relates both to the variables included in the model and to the model structure itself. Although any multivariate model can be used to estimate ESERs, we have here used a MAR-model to allow for analytically derivation of ESERs. This model assumes that time series are stationary and interactions are linear on a ln-scale, and this is indeed a simplifying assumption since interactions (e.g. feeding relationships) among species are often non-linear (Jeschke, Kopp, & Tollrian, 2004). However, the model can be seen as a first order linear approximation to other non-linear stochastic processes around an equilibrium (Ives, Dennis, Cottingham, & Carpenter, 2003), and could thus provide a good starting point even for somewhat non-linear dynamics.

Final remarks

The ESER approach demonstrates how species interactions, and a multispecies objective, set narrow bounds for sustainable exploitation in communities of naturally fluctuating fish populations. This novel analytical approach for deriving sustainable exploitation limits can simultaneously address important statistical properties as well as abiotic and biotic factors affecting community dynamics. Yet, it is framed around a simple and applicable multispecies objective, which can easily be extended in various ways (see “future directions” in SI). Our example application to the Baltic Sea further demonstrated a seemingly counterintuitive result: the exploitation rate of one population is suggested to increase, as compared to mean historical levels, for the purpose of conservation of the community of interacting fish populations as a whole. Due to the ubiquity of interactions among exploited species, such management strategies are likely applicable also in other systems. Yet, using conventional single species assessment models, it is inherently impossible to obtain this type of insights. Our results thus illustrate the need to adopt multispecies approaches in fisheries management, and that for precautionary applications, natural variability of fish populations, parameter uncertainty and influential environmental drivers should also explicitly be addressed. The ESER approach probabilistically addresses all of these, and may therefore be a useful tool for setting exploitation limits at the community level - an important part of ecosystem based fisheries management.

METHODS

MAR-models

We use mean-adjusted multivariate autoregressive models (MAR-models) with exogenous variables (Ives, Dennis, Cottingham, & Carpenter, 2003) in order to analytically derive ESERs:

$$\mathbf{X}_t = \mathbf{B}\mathbf{X}_{t-1} + \mathbf{C}\mathbf{U}_t + \mathbf{D}\mathbf{F}_t + \mathbf{E}_t \qquad (1)$$

Here $\mathbf{X}_t$ is a m x 1 vector with ln(biomasses) of species at time t, **B** is a m x m interaction matrix with elements (i, j) giving the per ln(biomass) effect of species j on the per unit ln(biomass) rate of change of species i, **C** is a S x m matrix with elements (i, j) giving the per unit effect of environmental covariate j on the per unit ln(biomass) rate of change of species i, $\mathbf{U}_t$ is a m x 1 vector with environmental covariates at time t, **D** is a S x S diagonal matrix with the per unit effect of exploitation rate on species' rates of change in ln(biomass), $\mathbf{F}_t$ is a S x 1 vector with yearly exploitation rates at time t, and $\mathbf{E}_t$ is a m x 1 vector of process errors that has a multivariate normal distribution with mean **0** covariance matrix $\sum_{\mathrm{E}}$.

Conditional on $\mathbf{U}_t$ and $\mathbf{F}_t$, the endogenous part, $\mathbf{X}_t$, is a stationary process provided that all eigenvalues of the interaction matrix **B** lie within the unit circle (Ives, Dennis, Cottingham, & Carpenter, 2003; Tsay, 2014). The mean and covariance of the stationary distribution, $\mathbf{X}_\infty$, with environmental covariates and exploitation rates held at their mean values, is given by:

$$\boldsymbol{\mu}_{\mathrm{X}} = (\mathbf{I} - \mathbf{B})^{-1}(\mathbf{C}\boldsymbol{\mu}_{\mathrm{U}} + \mathbf{D}\boldsymbol{\mu}_{\mathrm{F}}) \tag{2}$$

$$\mathrm{Vec}(\mathbf{V}_{\mathrm{X}}) = (\mathbf{I} - \mathbf{B} \otimes \mathbf{B})^{-1} Vec(\textstyle\sum_{\mathrm{E}} + \mathbf{C}\sum_{\mathrm{U}}\mathbf{C}^{T}),$$

where $\boldsymbol{\mu}_{\mathrm{X}}$ is the mean vector of the stationary distribution, $\mathbf{V}_{\mathrm{X}}$ is the covariance matrix of the stationary distribution, **I**, is the identity matrix, $\otimes$ refers to the tensor product and "Vec" is the vector form of a matrix in which columns of the matrix are packed on top of each other, with the first column of the matrix on top. $\boldsymbol{\mu}_{\mathrm{U}}$ and $\boldsymbol{\mu}_{\mathrm{F}}$ refers to the mean of environmental covariates and exploitation rates, respectively. If environmental covariates are included in an analysis they can be assumed to affect the stationary covariance by the term $\mathbf{C}\sum_{\mathrm{U}}\mathbf{C}^{\mathrm{T}}$, in which $\sum_{\mathrm{U}}$ is the covariance of the environmental covariates. Exploitation rate is something that is under control and is therefore assumed not to affect the covariance of the stationary distribution.

Estimating Ecologically Sustainable Exploitation Rates

Eq. 2 can be used to predict changes in mean ln(biomasses), $\boldsymbol{\mu}_{\mathrm{X}}$, from changes in exploitation rates, $\boldsymbol{\mu}_{\mathrm{F}}$. Further, if it is assumed that: (i) the variance-covariance, $\mathbf{V}_{\mathrm{X}}$, is an estimate of the variance-covariance that would occur if exogenous variables, i.e. $\boldsymbol{\mu}_{\mathbf{F}}$ and $\boldsymbol{\mu}_{\mathrm{U}}$, were held constant (Ives, Dennis, Cottingham, & Carpenter, 2003; Tsay, 2014); and (ii) the process errors and environmental covariates are normally distributed and temporarily uncorrelated, the stationary distribution (eq. 2) can be used to analytically estimate the probability that any population declines below its Blim, $P(\boldsymbol{\mu}_{\mathrm{F}})$, for a given set of mean exploitation rates, $\boldsymbol{\mu}_{\mathrm{F}}$ (see Fig. 1). This probability thus changes depending on the mean exploitation rate subjected to each species in a community. To derive ESERs we then define a multispecies objective function:

$$\varphi(\boldsymbol{\mu}_{\mathrm{F}}) = \alpha - P(\boldsymbol{\mu}_{\mathrm{F}}), \tag{3}$$

where α is a constant giving a predefined maximum acceptable probability (set by management) that any population declines below its Blim, and $P(\boldsymbol{\mu}_{\mathrm{F}})$ is the probability that any species does so, given a vector of mean exploitation rates, $\boldsymbol{\mu}_{\mathrm{F}}$. Mean exploitation rates associated with positive values of the multispecies objective function (eq. 3) are referred to as ESERs, since the predefined maximum acceptable probability, α, is then larger than the probability $P(\boldsymbol{\mu}_{\mathrm{F}})$ that any species is below Blim. Negative values of the multispecies objective function (eq. 3), in contrast, infer that a given exploitation rate is not ecologically sustainable. Limits for ESER are given by zero of the multispecies objective function; that is, when α equals $P(\boldsymbol{\mu}_{\mathrm{F}})$.

The probability that any population declines below its Blim for a given mean exploitation rate, $P(\boldsymbol{\mu}_{\mathrm{F}})$, can mathematically be defined as:

$$P(\boldsymbol{\mu}_{\mathrm{F}}) = P\left(\bigcup_{i=1}^{n}\left(x_{\infty,i}(\boldsymbol{\mu}_{\mathrm{F}}) \leq Blim_i\right)\right), \tag{4}$$

where $x_{\infty,i}(\boldsymbol{\mu}_{\mathrm{F}})$ is the marginal stationary distribution of species *i*, given by the stationary distribution (eq. 2). The probability $P(\boldsymbol{\mu}_{\mathrm{F}})$ is found using the inclusion-exclusion principle (Toufik, 2013), i.e. $P(\boldsymbol{\mu}_{\mathrm{F}}) = \sum_{k=1}^{n}\left((-1)^{k-1}\sum_{\substack{I\subset\{1,\dots,n\}\\|I|=k}} P(A_I)\right)$, where the last sum is for all the subsets *I* of the set, *{1,…,n}*, which contain k elements, and $A_I \coloneqq \bigcap_{i\in I}(x_{\infty,i}(\boldsymbol{\mu}_{\mathrm{F}}) \leq Blim_i)$ represents the intersection where all species in subset *I* cross their associated thresholds. $P(A_I)$ are found numerically (Genz et al., 2013) using the marginal distribution for the species in set *I*. It follows from the properties of the multivariate normal distribution that these marginal distributions are found by dropping rows and columns in the variance-covariance matrix and elements in the mean vector (eq. 2) for the species that are not included in subset *I*.

It should be noted that the variance of mean prediction errors of a MAR-model converges to the stationary covariance over infinite time (Lütkepohl, 2007). ESERs estimated using this method should therefore be seen as conservative reference levels for exploitation rates.

Analyses

In the example, limits for ESERs were first estimated by changing the exploitation rate of single focal species in the community, in the final model found after model selection (see "Model fitting and model selection" in SI & final model Table S1) while maintaining the other non-focal species at their mean historical exploitation rates (for 1988-2014). A root finding algorithm ("uniroot" implemented in R [R Core Team, 2017]) was used to find these ESER limits, i.e. the zero root of the multispecies objective function (eq. 3), one for each species in the community. Innovation bootstrapping (Ives, Dennis, Cottingham, & Carpenter, 2003) was used to account for uncertainties in parameter estimates and thus to create confidence intervals for ESERs. The mean of the stationary distribution (eq. 2) plus the direct effect of exploitation rates at the initial time step were used as initial point when creating the bootstrapped parameter sets. This is a preferred initial point when creating bootstrapped parameter sets for relatively unstable MAR-models ($0.5<\max(\lambda_B) < 1$) (Ives, Dennis, Cottingham, & Carpenter, 2003).

We investigated how much the mean exploitation rates of all species in the community could simultaneously be changed while still fulfilling the multispecies objective function. This was done by creating a (2 x 2) grid of mean exploitation rates for two species, with the third species held at a constant exploitation rate, representing a half standard deviation above the historical levels (original scale: cod=827 tons/kg*h^{-1}, sprat=0.28 kg*kg^{-1}, herring=0.16 kg*kg^{-1}, see “Data description” in SI), at mean historical level (original scale: cod=622 tons/kg*h^{-1}, sprat=0.23 kg*kg^{-1}, herring=0.13 kg*kg^{-1}) or at a half standard deviation below the observed historical level (original scale: cod=417 tons/kg*h^{-1}, sprat=0.18 kg*kg^{-1}, herring=0.10 kg*kg^{-1}). The procedure was repeated for all subsets of the three species. The objective function (eq. 3) was thereafter evaluated for all of these exploitation rate combinations. A positive value of the objective function infers that the objective was met (coded as 1), and a negative value infers that the objective was not met (coded as 0). The same grids were numerically investigated for 500 bootstrap parameter sets, thus creating a probability landscape with ranges of simultaneous ESERs for all the fish species.

For all analyses we assumed a maximum acceptable probability that any species goes below its Blim, α, of 10%.

All analyses were conducted in the R programming language version 3.4.3 (R Core Team, 2017). Computer code and data will be made publically available at github if this paper gets published.

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FIGURES

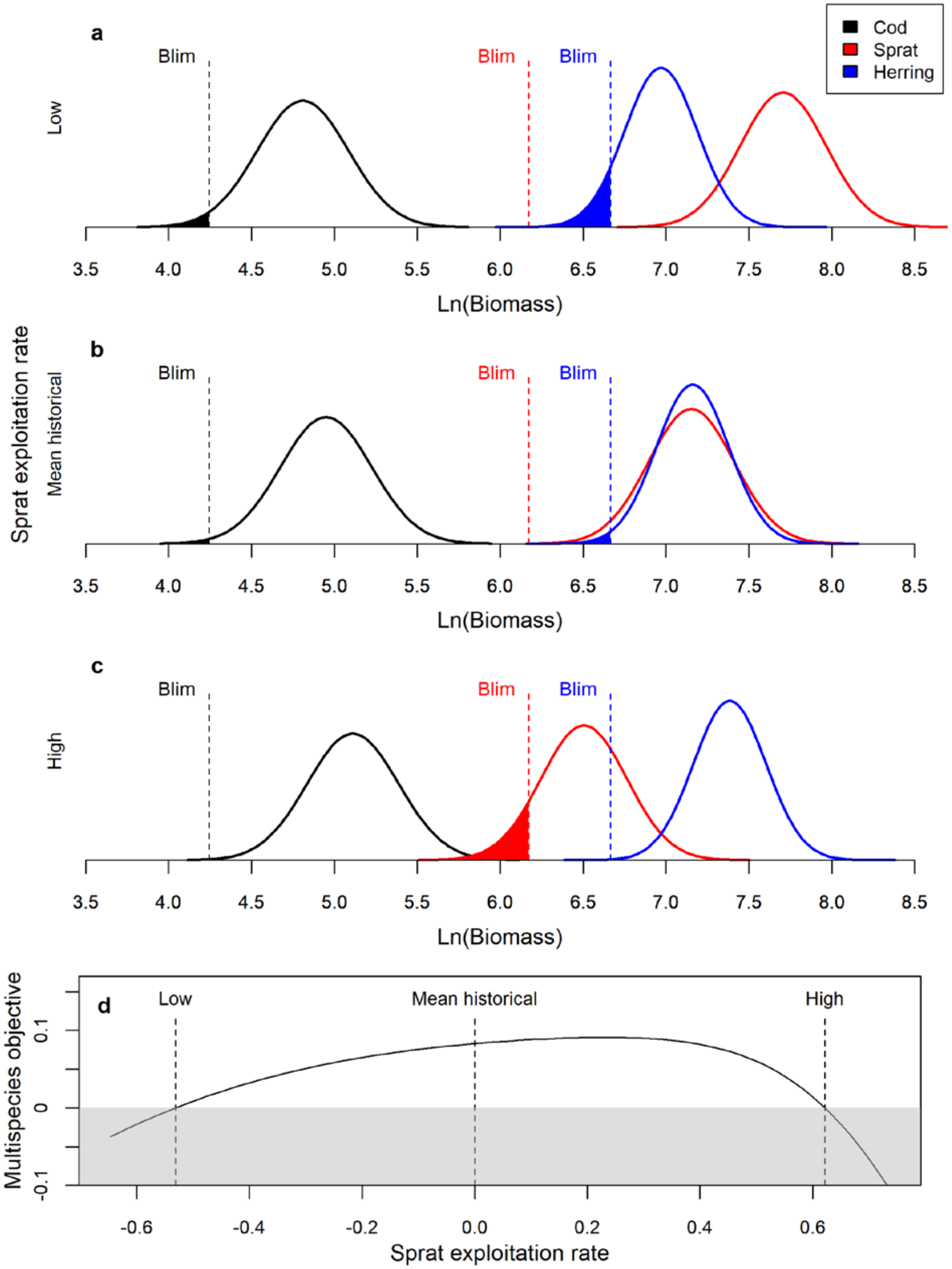

Figure 1. An illustration of the methodological approach of estimating Ecologically Sustainable Exploitation Rates (ESERs). Panels (**a**), (**b**) and (**c**) illustrate marginal stationary

distributions of a multivariate autoregressive model of biomasses of the interacting fish species cod (*Gadus morhua*, Gadidae), sprat (*Sprattus sprattus*, Clupeidae) and herring (*Clupea harengus,* Clupeidae) (see Final model in Table S2 for model parameters), subjected to (**a**) low, (**b**) mean historical or (**c**) high mean exploitation rates on sprat, and mean historical exploitation on cod and herring. The filled areas in (**a**)-(**c**) represent the marginal probability that a species biomass goes below its critical biomass limit (Blim). These marginal probabilities make up the core of the multispecies objective function shown in (**d**). The y-axis in (**d**) represents the difference between a predefined maximum acceptable probability that any species goes below its Blim, and the probability for this to occur given a set of mean exploitation rates. Exploitation rates associated with positive values of the objective function represents Ecologically Sustainable Exploitation Rates; that is, exploitation rates associated with a low probability (lower than the maximum acceptable probability) that any species goes below its Blim, whereas exploitation rates associated with negative values of the objective function can be categorized as ecologically unsustainable. The lower (**a**) and upper (**c**) limits for ESER, i.e. where the multispecies objective function is zero, are indicated by (Low) and (High) sprat exploitation rate in panel (**d**), respectively. Exploitation rates are represented as anomalies, i.e. as the number of standard deviations above or below mean historical levels (here 1988-2014).

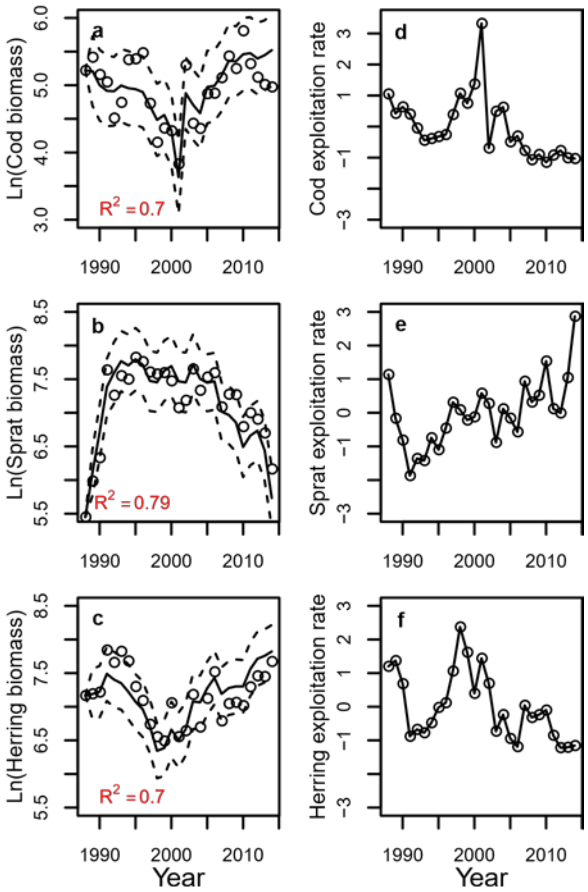

Figure 2. Observations of biomasses of the fish populations dominating the fisheries in the Baltic Sea (circles) are well explained by the final model (predictions as black lines, 95% bootstrapped prediction bounds as dashed lines) used as a basis for deriving Ecologically Sustainable Exploitation Rates (ESERs) in the example application of the method. (**a**) Cod, (**b**) sprat and (**c**) herring. The model accounts for pairwise net relationships ('interactions') among species and exploitation rates (see Final model in Table S2 for estimated parameter values). The standardized time series of exploitation rate have a direct impact on cod (**d**), sprat (**e**) and herring (**f**).

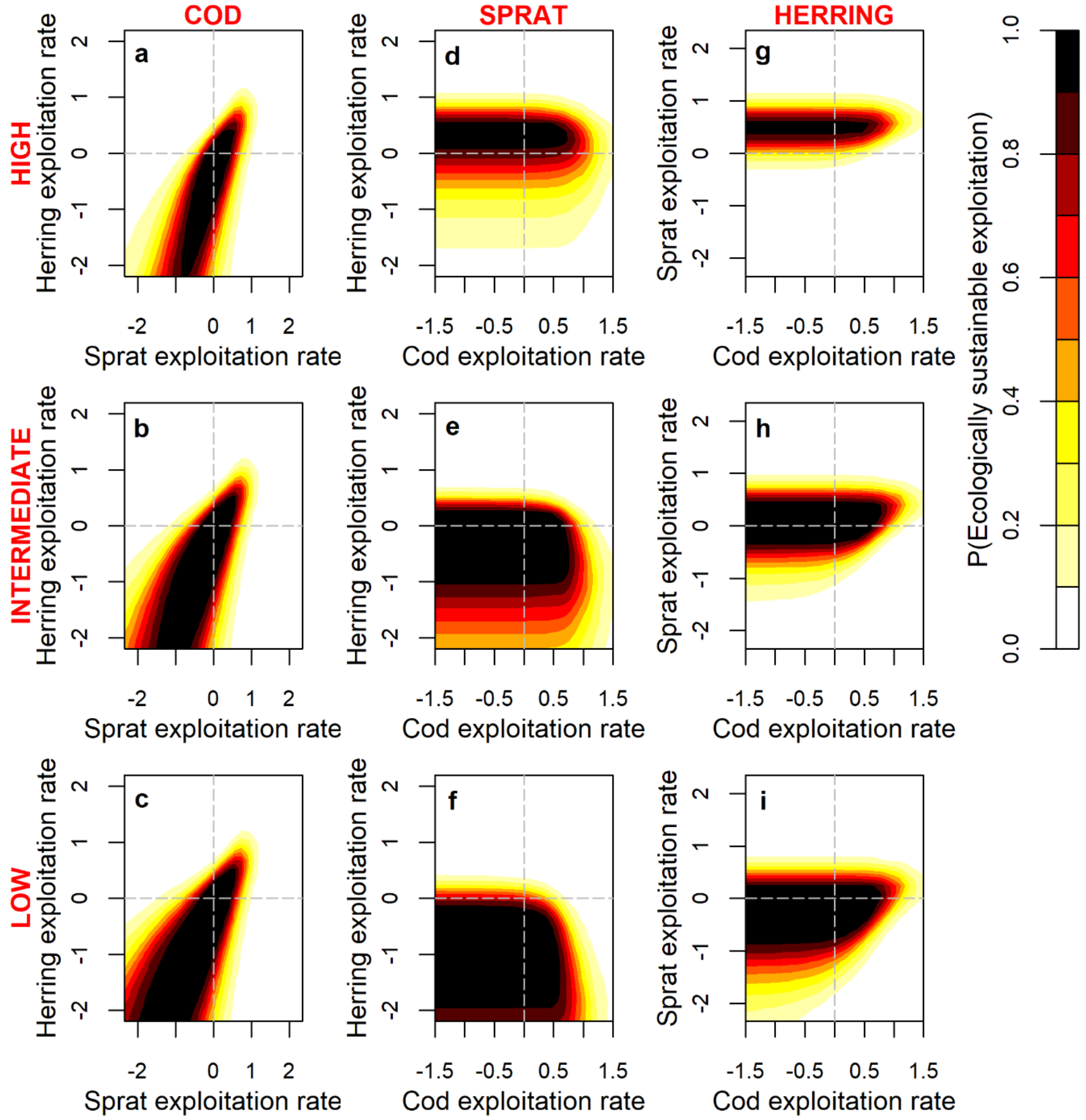

Figure 3. Ranges of Ecologically Sustainable Exploitation Rates. This figure shows the probability of ecologically sustainable exploitation as a function of exploitation rates, in a community of three interacting fish species. The probabilities are numerically found by evaluating if a specific exploitation rate combination is associated with a low probability (lower than a predefined maximum acceptable probability) that any interacting species in the community goes below its critical biomass limit (Blim), across 500 bootstrapped parameter sets. Top panels: (**a**), (**d**) and (**g**); middle panels: (**b**), (**e**) and (**h**); and bottom panels: (**c**), (**f**) and (**i**) show cases where exploitation rate of the species represented in each column (left:

cod, middle: sprat, right: herring) is held at a fixed high (0.5), intermediate (0) or low (-0.5) level, respectively. Exploitation rates are represented as anomalies, i.e. as the number of standard deviations above or below mean historical levels (for 1988-2014). Dashed grey lines represent mean historical exploitation rates.