Appendix: complete model description

Size spectrum model

Size spectrum models have emerged as a conceptually simple way to model a large community of fish based on the size of individuals. There is now a growing literature describing different types of size spectrum models (Benoît and Rochet, 2004; Andersen and Beyer, 2006; Andersen et al., 2008b; Law et al., 2008; Hartvig et al., 2011; Hartvig, 2011) and their application to understand how marine communities are organised (Andersen and Beyer, 2006; Andersen et al., 2008a; Blanchard et al., 2009) and, in particular, how they respond to fishing (Andersen and Pedersen, 2010; Andersen and Rice, 2010; Jacobsen et al., 2014). The advantage of the models is that they are based on a few simple and generally accepted assumptions, they respect mass-conservation in the community, and they are fast to simulate on a computer. The size spectrum modelling framework exists in three versions of increasing complexity: the *community* size spectrum model (Benoît and Rochet, 2004; Maury et al., 2007; Blanchard et al., 2009; Law et al., 2008), the *trait-based* size spectrum model (Andersen and Beyer, 2006; Andersen and Pedersen, 2010), and the *food-web* spectrum model (Hartvig et al., 2011). The model which is applied here is the trait-based size-spectrum model. A web-based version of the model is available on http://130.226.135.24/SSC.

The aim of the trait-based size-spectrum model is to calculate the abundance of individuals $N(w, W)$ as a function of the size of individuals w and the asymptotic (maximum) size that the individual may reach W (see Table 2 for list of variables). The representation of the trait W as a continuous function replace the need to represent specific species. The diversity of the fish community is therefore characterized by the abundance of individuals as a function of the trait. All parameters in the size spectrum models are related to individual weight, which makes it possible to formulate the model with a small set of general parameters (Table A2), which has prompted the label "charmingly simple" to the model framework (Pope et al., 2006). In the following the models equations (Table A1) and parameters (Table A2) are described.

The model framework is based on two central assumptions and a number of lesser standard assumptions. The first central assumption is that an individual can be characterized by its weight w and asymptotic weight W only. The aim of the model is to calculate the size- and trait-spectrum $\mathcal{N}(w, W)$ which is the density of individuals where $\mathcal{N}(w, W)dw\, dW$ is the number of individuals in the interval $[w : w + dw]$ and $[W : W + dW]$. In practice the trait-direction is discretized in a number of trait group or size spectra, each representing individuals within a range of trait values $N_i(w, W)$. The dimensions of each trait group is numbers per weight

Table A1: Model equations

Scaling:

$$\frac{\partial N_i}{\partial t} + \frac{\partial g N_i}{\partial w} = -\mu_i N_i \tag{M1}$$

$$N_c(w) = \sum_i N_i(w) + N_R(w) \tag{M2}$$

Food encounter and consumption:

$$\phi(w_p/w) = \exp\left[(-(\ln(w/(w_p\beta)))^2/(2\sigma^2)\right] \tag{M3}$$

$$E_e(w) = \gamma w^q \int N_c(w)\phi(w_p/w)w\,dw_p \tag{M4}$$

$$f(w) = E_e/(E_e + hw^n) \tag{M5}$$

Growth:

$$\psi(w, W) = \left[1 + (w/(\eta W))^{-10}\right]^{-1} (w/W)^{1-n} \tag{M6}$$

$$g(w, W) = (\alpha f(w)hw^n - k_s w^p)(1 - \psi(w, W)) \tag{M7}$$

Reproduction:

$$R_{p.i} = \frac{\epsilon}{2w_0} \int N_i(w)(\alpha f(w)hw^n - k_s w^p)\psi(w, W)\,dw \tag{M8}$$

$$R_i = R_{\max.i}R_{p.i}/(R_{p.i} + R_{\max.i}) \tag{M9}$$

$$R_{\max.i} = \kappa(\alpha f_0 hw_0^n - k_s w_0^p)W_i^{2n-q-3+a}\Delta W_i \tag{M10}$$

$$a = f_0 h\beta^{2n-q-1} \exp[(2n(q-1) - q^2 + 1)\sigma^2/2]/(\alpha f_0 h - k_s) \tag{M11}$$

Mortality:

$$\mu_p(w_p) = \int \phi(w_p/w)(1 - f(w))\gamma w^q N_c(w)\,dw \tag{M12}$$

$$\mu_{b.i} = \mu_0 W^{n-1} \tag{M13}$$

per volume. Scaling from individual-level processes of growth and mortality to the size spectrum of each trait group is achieved by means of the McKendrik-von Foerster equation which is simply a conservation equation (M1) where individual growth $g(w, W)$ and mortality $\mu(w, W)$ are both determined by the availability of food and predation from the community size spectrum, which is the sum of all trait groups (M2). The conservation equation is supplemented by a boundary condition at the right boundary at weight w_0 where the flux of individuals (numbers per time) $g(w_0)N_i(w_0)$ is determined by the reproduction of offspring by mature individuals in the trait group R_i (M3).

The second central assumption is that the preference of food is only determined by individual weight, not by the trait-value or species identity of prey. The preference for prey weight is described by the log-normal selection model (Ursin, 1973) which prescribes prey preference in terms of the ratio between the weight of predators and prey of weight w and w_p respectively (M4) where β is the preferred predator-prey mass ratio and σ the width of the weight selection function.

The remaining formulation of the model rests "standard" assumptions from ecology and fisheries science about how encounters between predators and prey leads to growth $g(w, W)$ and recruitment R_i of the predators, and mortality of the

2

Table A2: Variables and parameters in the system. For a detailed explanation of the determination of the values see (Hartvig et al., 2011, App. E).

Variables			
w		g	Weight of an individual
W		g	Asymptotic weight of an individual
$\mathcal{N}$		number/g	Size spectrum
N_i		number/g	Size spectrum of asymptotic size group i
R_i		number/time	Recruitment
Resource spectrum			
κ_R	$5 \cdot 10^{-3}$	$g^{\lambda-1}/m^3$	Magnitude of the resource spectrum
λ	2.05	-	Exponent of resource spectrum $(= 2 - n + q)$
r_0	4	g^{1-p}/yr	Constant for regeneration rate of resources
w_{cut}	0.5	g	Upper weight limit of the resource spectrum
Individual growth			
f_0	0.6	-	Initial feeding level
α	0.6	-	Assimilation efficiency
h	$40^\dagger$	g^{1-n}/yr	Constant for max. food intake
n	0.75	-	Exponent for max. food intake
k_s	$4.8^\dagger$	g^{1-p}/yr	Constant for std. metabolism and activity
p	0.75	-	Exponent of standard metabolism*
β	100	-	Preferred predator-prey mass ratio
σ	$1.3^\P$	-	Width of size selection function
γ	1500	g^{-q}/yr	Constant for clearance rate
q	$0.8^\S$	-	Exponent for clearance rate
Mortality			
ξ	0.1	-	Fraction of body weight containing reserves
μ_0	$3^\dagger$	g^{1-n}/yr	Constant for background mortality
Reproduction and recruitment			
w_0	0.5	mg	Offspring weight
η	0.25	-	Weight at maturation divided by W
ϵ	0.1	-	Efficiency of offspring production
κ	$50^\ddagger$	-	Factor for maximum recruitment.

*Laboratory experiments on fish indicate that the exponent of standard metabolism should be higher, around $p = 0.86$ (Winberg, 1956; Killen et al., 2007). The practical implication of choosing $p > n$ is that a maximum weight for individuals at which all energy, even if $f = 1$, is used for standard metabolism at $W_+ = [(\alpha h)/k_s]^{1/(p-n)}$ (Andersen et al., 2008b, Eq. 8). Here a value of $p = n$ is used to make the analysis of the model output easier. In this case there is no maximum weight since $W_+ = \infty$.

†Adjusted to a different value than in (Hartvig et al., 2011) to give growth rates similar to growth rates of species in the North Sea.

¶The width of the selection function is chosen to be larger in the trait-based model than in the species-based model (Hartvig et al., 2011) to emulate the diversity in prey-preferences of the species within a trait-class (Pope et al., 2006). The practical implication of enlarging σ is that the model is more stable (fewer oscillations) (Datta et al., 2010; Zhang et al., 2013).

‡This value should be a little higher but it has been lowered to give a stable output which will facilitate analysis of model output.

§ Andersen and Beyer (2006)

prey $\mu(w)$.

The available food (mass per volume) for a predator of weight w is determined by integrating over the community size spectrum weighted by the size selection function (M4): $\int N_c(w)\phi(w_p/w)w\,dw_p$. The food actually encountered E_e (mass per time) depends on the clearance rate (volume per time) which is assumed to scale with individual weight as γw^q (M5). Note that the encounter between predators and prey is only determined by the relative individual weights, not by the trait W. This means that a 100 g cod will consume the same food as a 100 g herring.

The encountered food is consumed subjected to a standard Holling functional response type II to represent satiation. This determines the *feeding level $f(w)$* which is a dimensionless number between 0 (no food) and 1 (fully satiated) (M6) where hw^n is the maximum consumption rate.

The consumed food $f(w)hw^n$ is assimilated by an efficiency α and used to fuel the needs for standard metabolism and activity $k_s w^p$. The remaining available energy, $\alpha f(w)hw^n - k_s w^p$, is divided between growth and reproduction by a function of weight changing between zero around the weight of maturation to one at the asymptotic weight where all available energy is used for reproduction (M7), leading to an equation for growth (M8). The form of the allocation function is chosen such that the growth curve approximate a von Bertalanffy growth curve if the feeding level is constant (see (Hartvig et al., 2011) for details about the derivation). The actual emerging growth curves from the model will depend on the amount of food available.

Recruitment of new fish is determined from the food-dependent egg production and density-dependent regulation. The total production of eggs R_p (numbers per time) is found by integrating the energy allocated to reproduction over all individuals (M8). Density dependence in the recruitment is modelled as a compensation on the egg production such that the recruitment flux R_i (numbers per time) is lowered towards a maximum recruitment as the egg production increases. The compensation is modelled as a "Beverton-Holt" type of stock-recruitment function (M9) where the maximum recruitment flux $R_{\max.i}$ is given by (M10+M11).

The mortality rate of an individual $\mu(w)$ has two sources: predation mortality $\mu_p(w)$ and a constant background mortality $\mu_{b.i}(w)$. Predation mortality is calculated such that all consumption translates into corresponding predation mortalities on the ingested prey individuals (M12; see (Hartvig et al., 2011, App. A) for derivation). When food supply does not cover metabolic requirements $k_s w^p$, growth stops, e.i. no negative growth, and the individual is subjected to a starvation mortality. Starvation mortality is assumed proportional to the energy deficiency $k_s w^p - \alpha f(w)hw^n$, and inversely proportional to lipid reserves, which are assumed proportional to body weight. Starvation is not an important process in the simulations presented here.
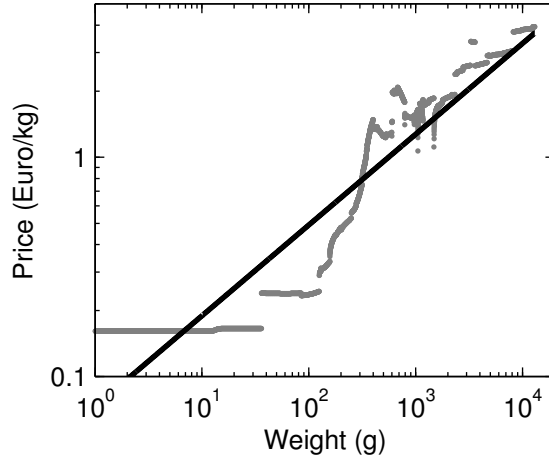
Figure A1: The price of individual fish caught in the North Sea as a function of their weight (grey dots) fitted to a power-law function with exponent 0.41 (black line).

Mortality from other sources than predation is assumed constant within a species and inversely proportional to generation time (Peters, 1983) (M13). The background mortality is needed to remove the largest individuals, which do not experience predation mortality.

Food items for the smallest individuals (smaller than βw_0) is represented by a resource spectrum $N_R(w)$. The temporal evolution of each size group in the resource spectrum is described using semi-chemostatic growth (M14) where $r_0 w^{p-1}$ is the population regeneration rate (Fenchel, 1974; Savage et al., 2004) and $\kappa_R w^{-\lambda} = \kappa_R w^{-2-q+n}$ the carrying capacity.

Parameter values are determined from physiological studies and cross-species analyses of fish stocks; see Table A2).

Bioeconomic model

The bioeconomic model contains a description of how price $p(w)$ varies as a function of individual weight and how cost C_i depends on the abundance, fishing effort and trait of the stock.

The price function was based on Danish landing statistics 2006–10 provided by the Danish Ministry of Food, Agriculture and Fisheries (Fig. A1). Denmark is, with respect to fish, highly integrated in the world market; the prices in Denmark therefore reflect demand on the world market. We included all landings which
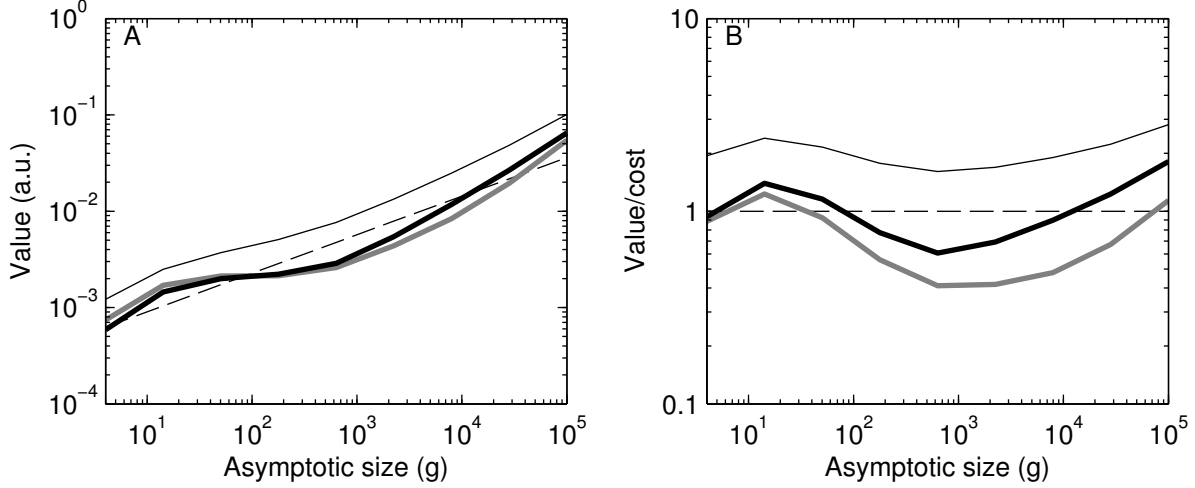
Figure A2: Rent (thick), cost (dashed) and income (thin) for a fishing pattern where all species are fished with $F = 0.7$ yr^{-1}. B) Measured relative to the cost. The fishing pattern is a reasonable approximation of the fishing pattern in the North Sea today.

have size information in the landing statistics. For forage fish we used the size distribution of sand eel (Jensen et al., 2011). We used the method described in Ravn-Jonsen et al. (2012, appendix B) to fit a power function to the prices: $p(w) = a_p w^{b_p}$ with $a_p = 0.073$ $^{1-b}$/g and $b_p = 0.41$ ($r^2 = 0.89$).

Cost in the fishery depends on the management of the fishery. We assume a cost effective fishery with a fleet adapted to the current yield. We can therefore assume that the cost is only dependent on the abundance of the fished part of the stock N_{fsa}. The total cost, that is operation cost and capital cost, can then be written as being proportional to the fishing effort F_i: $C_i = A_i F_i N_{fsa.i}^{b_c}$. The value of the exponent b_c depends on the behaviour of the fished stocks. There are two extreme cases:

1. The stock is distributed evenly in space such that the spatial density is proportional to the abundance. This is often assumed for pelagic species (e.g. Bjørndal, 1987). In this case the cost depend on the amount of fishing hours, which is proportional to the fishing effort, so $b_c = 0$.

2. The spatial distribution of the stock varies with abundance but where the stock occurs the spatial density is constant. In this case the cost depends is proportional to the fished stock abundance so $b_c = 1$. This is the "classic"

catch-per-unit effort assumption (e.g. Schaefer, 1954).

We have explored three cases of the exponent: $b_c = 0$, 0.5 and 1. In each case the value of the parameters have been calibrated as explained in the main text, and shown for case 1 in Figure A2.

The impact of varying the cost function on the fishing pattern which maximizes rent is surprisingly small (Fig. A3) and we therefore conclude that the results of rent maximization are insensitive to the exponent b_c.
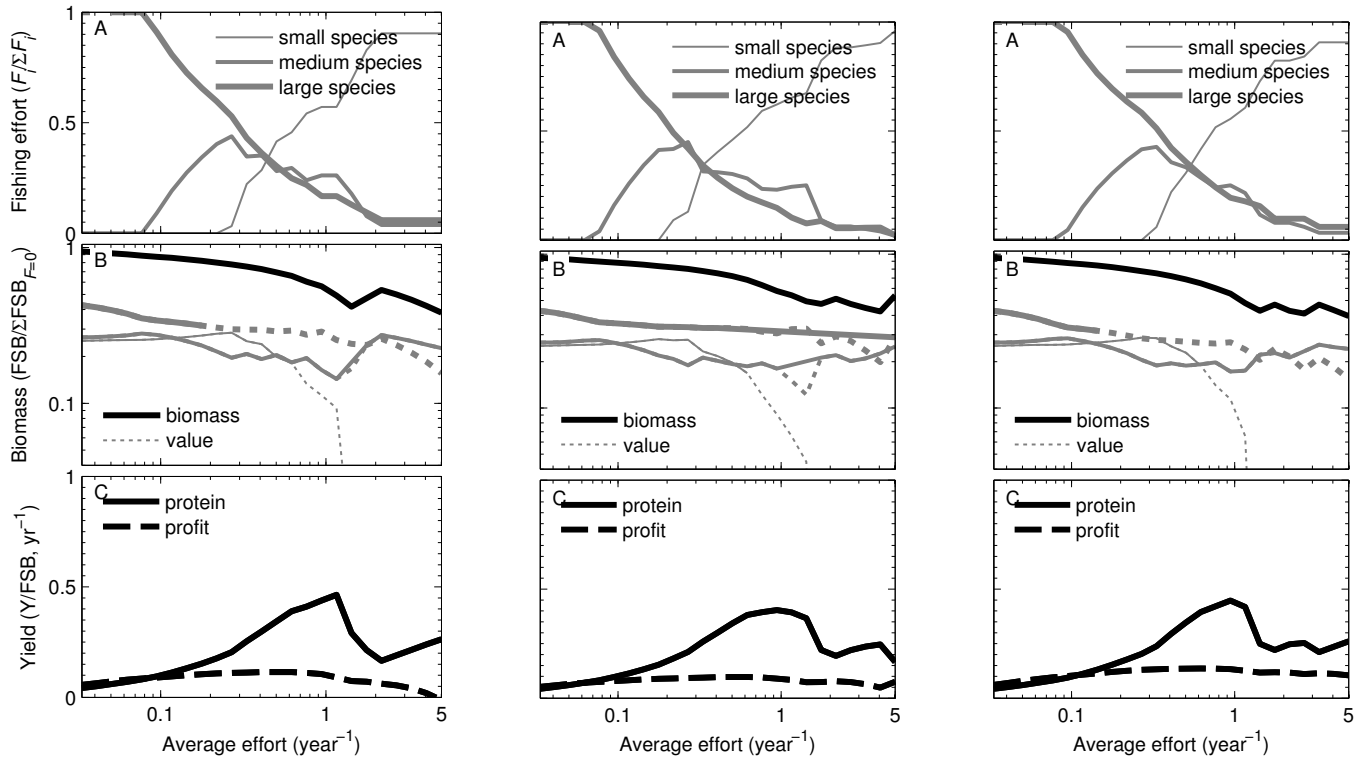
Figure A3: Results from maximizing rent, shown as a function of the total effort for the three fisheries. A) Fishing effort in the three fisheries, B) Total biomass (black) and value of the stock targeted by each fishery (grey lines). Dashed lines is when one stock in a fishery has dropped below 20%. C) Yield in terms of protein (catch) or rent. Left column: maximizing with cost proportional to the fishing mortality. Middle column: Maximizing using a cost function which is proportional to the effort multiplied by the square-root of the fished stock abundance. Right column: using a cost function proportional to the yield.
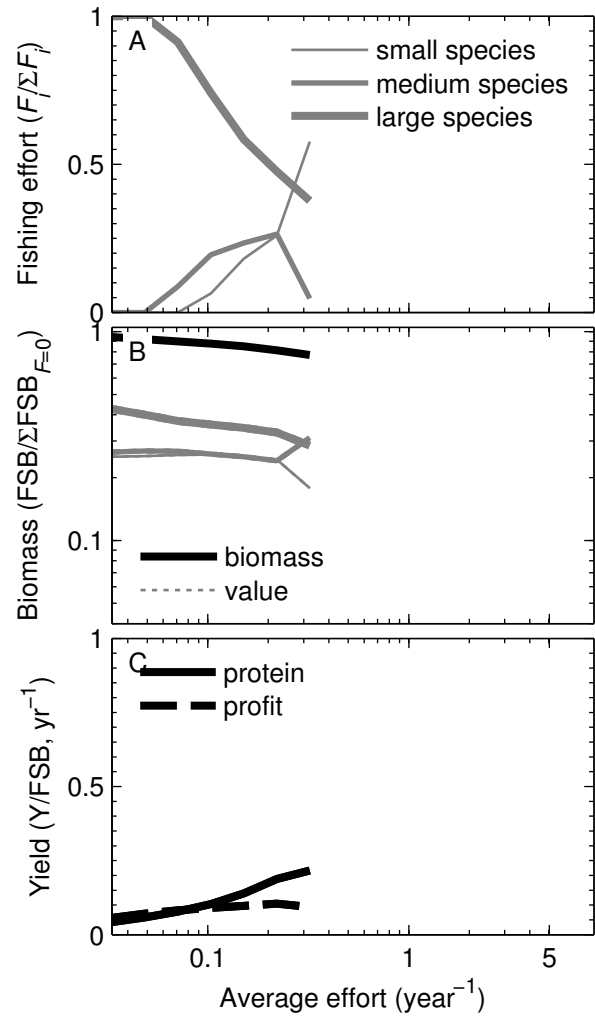
Figure A4: Maximizing catch while respecting the conservation constraint.

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