Direct and indirect community effects of rebuilding plans

Ken H. Andersen and Jake C. Rice

Many fish communities are heavily exploited and rebuilding plans need to be implemented for depleted species. Within an ecosystem approach to management, development of rebuilding plans should include consideration of the expected consequences of the rebuilding of the target species on the rest of the marine community. Using size- and trait-based single-species and community models, a general assessment is made of the direct and indirect ecological consequences of a rebuilding plan based on a reduction in fishing mortality. If fishing mortality is sufficiently reduced, the time-scale of rebuilding is in the order of the time to reach maturation of an individual, and the expected trajectory can be reliably predicted by a single-species model. Indirect effects of increased abundance are a decrease in individuals in the trophic levels above and below the target species. The decrease in biomass of the neighbouring trophic levels is expected to be much smaller than the increase in the target species and to be largest in species on the trophic level above. We discuss which effects could be responsible when a rebuilding plan does not result in the expected increase and how our results could be applied in a practical management situation.

Keywords: asymptotic size, ecosystem approach to fisheries management, size-based model, size spectrum.

K. H. Andersen: National Institute of Aquatic Resources, Technical University of Denmark, Charlottenlund Slot, DK-2920 Charlottenlund, Denmark. J. C. Rice: Ecosystem Sciences Branch, Department of Fisheries and Oceans, 200 Kent Street, Ottawa, Canada K1A 0E6. Correspondence to K. H. Andersen: tel: +45 3588 3399; fax: +45 3396 3333; e-mail: kha@aqua.dtu.dk.

Introduction

An international commitment has been made to rebuild fished stocks to at least a level consistent with producing maximum sustainable yield (UNEP, 2002). Subsequent agreements embed this commitment in an overall ecosystem approach to management and sustainable use of fisheries resources (UNGA, 2006). Before a rebuilding plan for a specific target species is implemented, the necessary management measures and the associated time-scale have to be established. Furthermore, an ecosystem approach to fisheries management requires that the broader consequence of actions targeted at improving the status of the target species is assessed. Therefore, rebuilding plans should also describe indirect effects on the rest of the community, and possible ecosystem constraints on rebuilding should be considered when developing such plans.

We make a general assessment of the effects of a reduction in fishing mortality (F) on one (or a group of) species. Specifically four questions are addressed: (i) what is the expected time-scale of the recovery of an individual species when F is reduced, (ii) what is the trajectory of the expected increase in spawning-stock biomass (SSB) following a reduction in F, (iii) which indirect effects could be expected, both on smaller and on larger fish in the community, and (iv) if the expected increase in SSB of the target species fails to happen, what could then be the cause?

The assessment is based on a size- and trait-based framework of fish stocks, where population dynamics are described based on individual-level processes (Andersen and Beyer, 2006). The single-species version of the model is a size-based version of the classical Beverton–Holt framework (Beverton and Holt, 1957), where growth and mortality of an individual are fixed and prescribed

using equilibrium size-based theory (Andersen et al., 2009). The community version is based on the same equations as the single-species model, but growth is determined by the availability of food from smaller individuals or from zooplankton, whereas a substantial part of the non-fishing mortality depends on the consumption by predators. The community model is essentially a dynamic version of the simple size-based model of Pope et al. (2006), and distinguishes itself from other size-based models (Benoît and Rochet, 2004; Hall et al., 2006; Pope et al., 2006; Maury et al., 2007; Blanchard et al., 2009) by both resolving food-dependent growth and describing individuals not only their current size, but also by their asymptotic (maximum) size. Defining species by their asymptotic size makes it possible to take account of other life-history traits, such as investment in reproduction and background mortality rates through the life-history invariants (Charnov, 1993, 2008), before the explicitly modelled influences of food supply and predator abundance are accounted for dynamically.

The models are applied to simulate scenarios for rebuilding one (or a group) of stocks, from a base case of a heavily exploited system where all trait classes are exploited. Three scenarios are explored where F is reduced selectively for large, medium-sized, and small fish, respectively, as differentiated by their trait (asymptotic size). Results from the single-species and the community models are compared, and the indirect effects are quantified.

The simulations focus on stock rebuilding driven by management changes in F and resultant effects on trophic interactions, leading to changes in growth and mortality. They do not consider changes in habitat, evolutionary changes, or Allee effects (Hutchings and Reynolds, 2004). If a population has been depleted

to a point where recovery rather than just rebuilding is necessary, then model results are informative of recovery trajectories only to the extent that depensation is not included. The potential influences of these effects for the models applied are discussed.

Models

Both the single-species and the community model are size- and trait-based, with size being individual weight w and the trait being asymptotic weight W. All basic processes are related directly or, in the case of the stock–recruitment relationship, indirectly to individual-level processes. The model and associated parameters are described in Andersen and Pedersen (2009) and summarized in the Appendix. The resulting dynamics of the size spectrum $N_i(w, t)$ describe the density of individuals (measured in numbers per volume per weight) with size w and asymptotic size W_i as a function of time t. Scaling from individual-level processes of growth g_i and mortality μ_i to the population-level size spectrum is achieved by a numerical solution of the classical McKendrick–von Foerster equation, which is just a mathematical formalization of the conservation of numbers of individuals (McKendrick, 1926; von Foerster, 1959):

$$\frac{\partial N_i}{\partial t} + \frac{\partial g_i N_i}{\partial w} = -\mu_i N_i. \quad (1)$$

Somatic growth is described by a bioenergetic budget accounting for losses attributable to assimilation (specific dynamic action), standard metabolism, and allocation to reproduction

$$g_i(w) = (\alpha f(w) h w^n - k w^p)(1 - \psi_i(w)), \quad (2)$$

where α is the assimilation efficiency, $f(w)$ the feeding level, hw^n the maximum consumption rate, and kw^p are losses attributable to standard metabolism and activity. The term in the first set of brackets is the energy available after standard metabolism has been subtracted, and $\psi_i(w)$ then determines the fraction of the available energy allocated to reproduction.

In the single-species model, growth and predation mortality rates are fixed, whereas these parameters in the community model are determined by changes in the abundance of prey and predators, such that there is balance between growth and mortality. In other words, for every predator consuming a prey, there is a corresponding mortality on that prey.

Recruitment is assumed constant in time and independent of the SSB, which implies that the stocks are not experiencing recruitment failure (i.e. SSB is above the limit reference point B_{lim}). The level of recruitment is determined from the theoretically expected abundance of larvae of that trait class in an unfished community, which is a decreasing function of asymptotic size (Andersen and Beyer, 2006). This assumption imposes increasing density-dependence as a function of asymptotic size in accordance with the experience from other community models (Pope *et al.*, 2006) and theoretical expectations (Andersen *et al.*, 2008; Gislason *et al.*, 2008).

Single-species model

In single-species calculations, growth and mortality are determined from a community size spectrum using the equilibrium size-spectrum theory (Andersen and Beyer, 2006). Growth is given by Equation (2), using a constant feeding level f_0. Consumption rate

of prey by an individual with size w is then $f_0 h w^n$. For the community to be in mass balance, this feeding rate implies a corresponding predation mortality rate of $\mu_p \approx f_0 h \beta^{1+n-\lambda} w^{n-1}$ (Andersen *et al.*, 2009), where β is the preferred predator–prey mass ratio, $\lambda = 2 + q - n$ is the slope of the size spectrum, and q is the exponent of the volumetric search rate. Using the fixed growth and mortality, Equation (1) can be readily solved numerically for the size spectrum of the species $N_i(w)$.

Community model

In contrast to the single-species model, the community model does not resolve specific species, but solves for groups of species within a specified range of asymptotic sizes. Each asymptotic size class i represents all species with asymptotic sizes in the range W_i to W_{i+1}. This trait-based approach combined with size-based scaling of parameter values results in a parsimonious model that describes generic properties of marine communities. A given community is described essentially by two parameters: h represents the maximum consumption rate and κ is the carrying capacity of the resource spectrum (Andersen and Pedersen, 2009). The value of h determines the growth rate corresponding to the productivity (e.g. temperature) of the fish community. Therefore, h determines the time-scale of the dynamics in the community: higher h (higher productivity) results in faster biomass increase. The value can be derived from its relation to the von Bertalanffy growth constant K as $h \propto K L_\infty$ (Andersen *et al.*, 2009).

Expected rebuilding

Rebuilding is simulated by reducing F on either a specific species (in the single-species model) or a group of species falling within a range of asymptotic sizes (in the community model). The simplest way to describe the expected increase in biomass of a population is to assume an exponential relaxation from the state before some measure was taken (denoted by subscript "0") to the final state (subscript "f"). In the following, SSB is used to characterize the population as

$$\text{SSB}(t) = \text{SSB}_f - (\text{SSB}_f - \text{SSB}_0)e^{-t/\tau}, \quad (3)$$

where τ is the time-scale of relaxation. The expected time-scale of relaxation to a new steady state following a perturbation is the age of maturation. If the exponent of standard metabolism is assumed to be the same as the exponent of maximum consumption, i.e. $p = n$, then the growth rate until maturation is $\alpha f_0(h - k)w^n$. Because size-at-maturation is a fraction $\eta \approx 0.25$ of the asymptotic weight (Beverton, 1992), the age-at-maturation T_{mat} can be found by integrating the growth equation up to the weight-at-maturation:

$$T_{mat} = \frac{3(\eta W)^{1-n}}{\alpha f_0(h - k)}.$$

We use T_{mat} to normalize the time-scale of stock rebuilding.

Simulations

Simulations of stock rebuilding are done from a base case of a heavily exploited community (Figure 1a). All trait classes are fished with a fishing mortality described by a logistic function of individual size with a knee point at $0.05\,W$ (Figure 1b; see M11 in Appendix Table 1 or Equations (4) and (5) in Pope *et al.*, 2006). The average fishing mortality in the community is $F_{0,i} =$
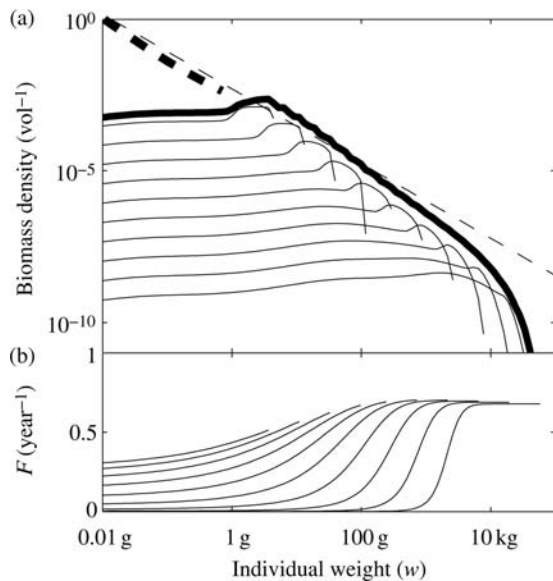
Figure 1. Simulations of the base case with the community model: (a) resulting biomass spectra for ten asymptotic size classes (thin lines), their sum (thick line), the spectrum of the resource (thick dashed line), and the theoretically expected spectrum of an unfished system (thin dashed line); and (b) input fishing mortalities for the ten asymptotic size classes.

0.7 year^{-1} (roughly corresponding to the state of the North Sea today; Pope *et al.*, 2006). From the base case, F is suddenly reduced to 0.25 year^{-1} either for a specific asymptotic size class or for a range of asymptotic size classes, corresponding to either large predatory species (cod-like: $W > 15$ kg), smaller consumer species (herring-like: $0.5 < W < 4$ kg), or forage fish (25 g $< W < 200$ g). For each biomass trajectory, the exponential relaxation in Equation (3) is fitted to the time-series of SSB to determine the time-scale τ and the relative increase in SSB: $R = \text{SSB}_f/\text{SSB}_0$.

Results

Simulations of both models demonstrate a reasonable fit to the exponential relaxation of the SSB (Figure 2). As expected, τ increases as a function of asymptotic size and varies between $\sim 0.5\ T_{\text{mat}}$ for large species and $2\ T_{\text{mat}}$ for small species (Figure 3a). The greater the reduction in F, the faster the increase in SSB, the faster it reaches any specific biomass along the trajectory to its new steady state, and also the longer complete rebuilding takes, if rebuilding is taken as reaching the equilibrium biomass implied by a particular F (such as F_{MSY}). However, the difference in rebuilding time is modest compared with the differences in the steady-state biomasses consistent with the different Fs. The relative increase in SSB is an exponentially increasing function of the reduction in fishing mortality ΔF (Figure 3b). F is a larger contributor to the total mortality for large species than it is for small species; therefore, the former are hit harder by a given F. Consequently, they are also expected to achieve a greater increase in SSB for a given relaxation of F. The differences in the final SSB between the single-species and the community models are due to differences in predation mortality; predation mortality in the former is fixed as a power law function, whereas in the community model, it is a result of the simulation and varies in an oscillatory
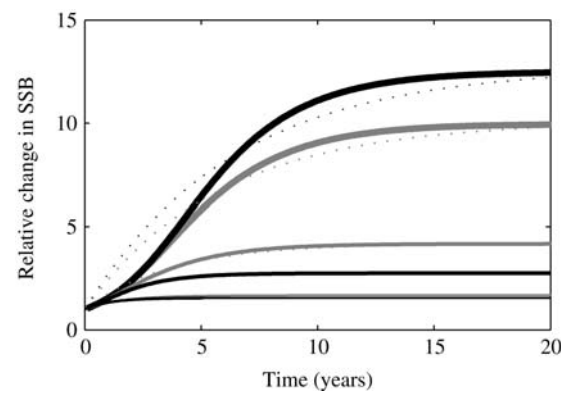
Figure 2. Rebuilding of SSB of large (thick lines, $W = 12$ kg), medium (medium lines, $W = 0.5$ kg) and small (thin lines, $W = 20$ g) asymptotic size classes after suddenly reducing the maximum fishing mortality from 0.7 to 0.25 year^{-1} for each specific group of asymptotic size classes (but corresponding to the logistic function given in Figure 1b) according to the community model (black) and the single-species model (grey). Dotted lines represent fitted exponential relaxations.
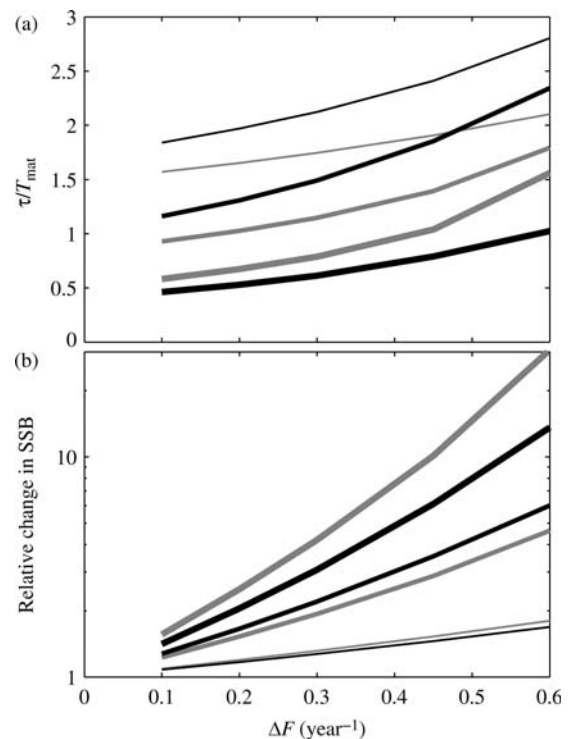

Figure 3. Rebuilding patterns as a function of change in the maximum fishing mortality ΔF (cf. Figure 1b) simulated by the single-species model (grey lines) and the community model (black lines) for three target asymptotic sizes (12 g, thin lines; 360 g, medium lines; and 11 kg, thick lines): (a) time-scale of the increase in biomass τ divided by the generation time T_{mat}; and (b) relative change in SSB following a complete rebuilding (log scale).

manner around the expected power law (Andersen and Pedersen, 2009). Nevertheless, simulations with the simple single-species model predict the results from the community model remarkably well. The time-scale of the increase in biomass is typically a little longer in the latter, and the recovery a little greater.

Indirect effects of the rebuilding of a range of trait classes propagate in the community model to trait classes with both smaller and larger asymptotic sizes via a trophic cascade (Figure 4). The decrease in SSB of trait classes with smaller asymptotic size is ~30% of the increase in SSB of the species in the target range. Surprisingly, the influence on larger asymptotic sizes is more severe than on smaller ones, with an expected decrease in SSB by ~50% of the expected increase in the target species.

A closer examination of the community spectrum reveals that the biomass of individuals within a given size range is dominated by individuals with asymptotic sizes in the same range (Figure 5a). The cascading effect observed on the asymptotic size classes
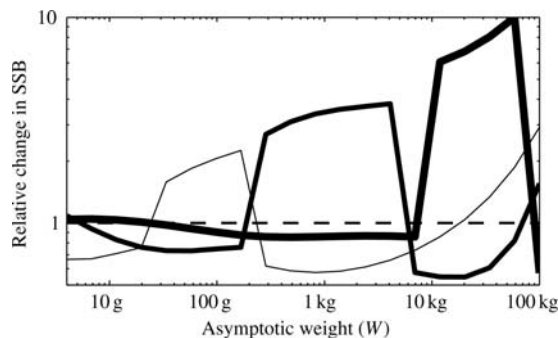

Figure 4. Indirect effects expressed as the relative change (log scale) in SSB of all asymptotic size classes caused by the rebuilding of small (33–200 g, thin lines), medium (200 g–4.5 kg, medium lines), and large (4.5–70 kg, thick lines) trait classes.
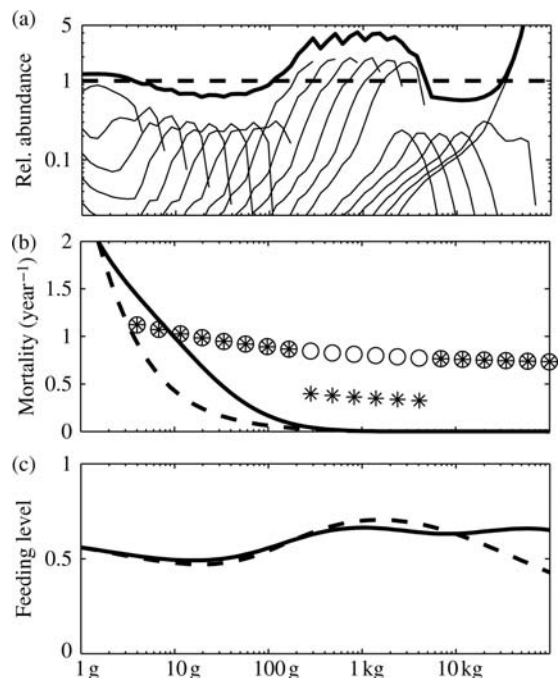
Figure 5. Indirect effects of rebuilding trait classes with intermediate asymptotic size (0.5 < W < 4 kg, solid lines) as a function of individual size compared with the baseline situation (dashed lines): (a) relative abundance of individuals of 20 trait classes (thin lines) compared with the total spectrum; (b) predation mortality (lines) and background plus fishing mortality of each trait class (circles: baseline; stars: rebuilt situation); and (c) feeding level.

therefore corresponds to a cascading effect on individual (absolute) sizes. The reduced abundance of smaller asymptotic size classes is due to increased predation pressure from the adults of the target species (Figure 5b), whereas the larger asymptotic size classes are also affected by increased predation pressure during their juvenile stages. Furthermore, when the individuals of the larger asymptotic size classes are in the same size range as the fully grown individuals of the target groups, they experience increased competition with the latter, which lowers their growth rate somewhat (Figure 5c). Taken together, the increased predation pressure on juveniles and increased competition for food of individuals in mid-range result in an even greater reduction of the SSB of the large asymptotic size classes. Individuals of asymptotic size classes that are very much larger than the target groups could benefit from the increased food availability resulting from the increase in the target groups. This increase in food availability for the adults could be so large that it outweighs the effects of increased predation on their juveniles and increased competition in their mid-range.

In the single-species model, growth and mortality are fixed and the biomass will therefore always increase if F is reduced. However, could intraspecific competition in the community model impede rebuilding? In other words, what happens if a trait class comprises more than one species and only one is subjected to a reduction in F? To examine this question, simulations were done with the community model where one asymptotic size class contains two species with the same asymptotic size and equal abundance. Because these two species were identical, the simulation gave exactly the same results as when the biomasses of the two species were summed to give the total biomass in their asymptotic size class. Three cases were considered: (i) F on one species remains unchanged at 0.7 year^{-1}, whereas it was lowered from 0.7 to 0.25 year^{-1} on the other; (ii) F on both species was lowered to 0.475 year^{-1} (corresponding to dividing the reduction in F evenly between the two species); and (iii) F on both species was lowered to 0.25 year^{-1} (Figure 6). In case 1, the total increase in biomass was larger than when the ΔF was halved for both species (case 2). Furthermore, the increase in SSB of the target
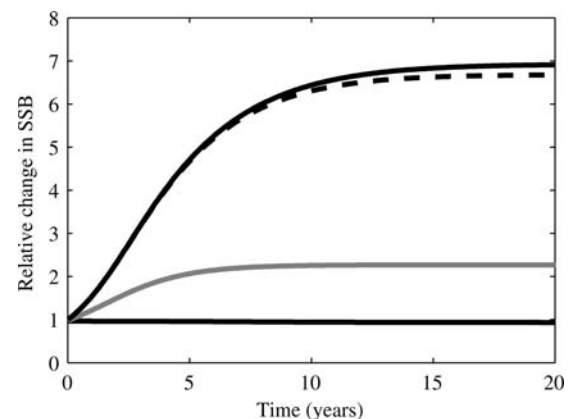
Figure 6. Relative change in biomass of two species with the same trait value (W = 12 kg), but subjected to different fishing mortality regimes (base case: F = 0.7 year^{-1}): (i) F reduced to 0.25 year^{-1} on one species and kept at 0.7 year^{-1} on the other (solid black lines; top and bottom, respectively); (ii) F reduced to 0.475 year^{-1} on both species (grey; overlapping); and (iii) F reduced to 0.25 year^{-1} on both species (dashed; also overlapping).

species in case 1 was slightly higher than in case 3, but its higher final biomass was compensated for by a small reduction in the biomass of the other species. Case 3 in fact gave exactly the same result as the original formulation when species in the same trait class were just treated as a single trait.

Discussion

The simulations illustrate the power and flexibility of combining principles from life-history theory with scaling of individual-level rates of somatic growth and mortality with size. Within the size-spectrum framework, it is possible to construct a general single-species model that can be used for a specific population simply by relating the model parameters to the observed von Bertalanffy growth parameters (K and asymptotic size) and natural mortality, M—perhaps using an M/K relation (Andersen *et al.*, 2009). The same general relations can be used to parametrize a model for a typical fish community. This community model may be tuned towards a specific system by adjusting the free parameters in the model to make it reproduce observable quantities, such as the slope of the community size spectrum or yield of specific asymptotic size groups (Pope *et al.*, 2006). It could be adapted to different environmental conditions by adjusting key metabolic processes to the characteristic temperature of the ecosystem (Pope *et al.*, 2009); here, we assumed a temperature of 10°C, typical of the North Sea. This flexibility allows investigations of many different management questions, such as potential community effects of the rebuilding of depleted fish populations.

Simulations of rebuilding following a reduction in F with the two models demonstrated three general effects:

(i) The expected increase in SSB of a species is reasonably described by an exponential relaxation towards the new steady state with a time-scale in the range of 0.5 to 2 times the age of maturation. Rebuilding smaller species takes proportionately more time (in terms of generations) than larger species, but because larger species have longer generation times, larger species take longer to rebuild, measured in absolute time.

(ii) The single-species model gave results comparable with those of the community model. Single species models are therefore sufficient to get an approximate estimate of the expected time-scale and extent of biomass increase for a given reduction in F. Greater reductions in F will lead faster to any specific target population size being reached, but it would also take longer for a population to reach the equilibrium population size consistent with the new mortality and growth rate. These are straightforward results, but highlight the importance of clearly identifying what is meant by "rebuilding" a population.

(iii) Rebuilding a target species is expected to result in a decrease in SSB of fish with both larger and smaller asymptotic sizes. These indirect effects appear to be substantially smaller than the increase in SSB of the target species. The decrease is more pronounced for the larger fish than for the smaller fish. This appears to be due to the larger species experiencing indirect effects of the target species twice during life, first through an increased mortality as juveniles and later through increased competition with the rebuilt species. Although the reductions in biomass caused by indirect effects are relatively

small, they might be important if the affected populations are currently exploited close to biologically safe limits.

The model can therefore deliver predictions of how a population might respond to a rebuilding plan, taking account of a species' life history and how a community might experience indirect effects of the rebuilding of one or more species.

A subtle issue concerning the use of trait-based community models is the relation between specific species and the asymptotic size classes. An examination of the difference between the rebuilding of two identical species within one trait class demonstrated that it is legitimate to interpret the rebuilding of an asymptotic size class as comparable with the rebuilding of a single species, if the trait class in practice contains more than one species and rebuilding measures are implemented in ways that benefit all members of the trait class. This suggests that fleet-based rebuilding measures might provide benefits to the full suite of species harvested by the fishing methods of the fleet (whether as targeted catch, bycatch, or discards), if those measures actually reduce fishing effort rather than just redirect it at other species.

In practice, populations often fail to respond as expected to a reduction in F (Hutchings and Reynolds, 2004). This might be due to effects not covered by the models applied:

(i) If the population has several stable states, the fishery might have reduced the population to a low-biomass state (or even to extinction). The existence of two stable states has been attributed either to an emergent Allee effect (de Roos *et al.*, 2003) or to cannibalism (Ricker, 1954; Claessen and de Roos, 2003). The existence of multiple stable states has been demonstrated experimentally in whole-lake manipulation experiments (Persson *et al.*, 2007) and is made plausible in a model of the Baltic fish community (van Leeuwen *et al.*, 2008). To represent the possible effects of multiple stable states, a model should be physiologically structured (de Roos *et al.*, 1992), i.e. account for food-dependent growth, maturation, and reproduction. The community model used does account for food-dependent growth (and consequently food-dependent maturation), but reproduction is fixed. The model therefore cannot resolve the potential effect of a population impeding rebuilding, because it is caught in a low-biomass state, owing to depressed recruits-per-spawner. A direct analysis of time-trends in recruits-per-spawner should be part of any science initiative to inform a rebuilding plan; therefore, such impediments should be identified independently.

(ii) Evolutionary responses to fishing result in changes in growth, size- and age-at-maturation, and allocation of energy to reproduction (Jørgensen *et al.*, 2007). Rapid evolutionary responses have been demonstrated for collapsing stocks (Olsen *et al.*, 2004), but, in general, evolutionary responses are expected to be small compared with the direct effects of overfishing and the direction of change in affected traits depends on details in the imposed selection pattern by the fishery (Andersen and Brander, 2009). Evolutionary changes are therefore not expected to be generally responsible for failures of stocks to rebuild, although they are expected to slow down rates of increase in biomass (Enberg *et al.*, 2009).

(iii) Other species with similar ecological function might have taken over the niche of the focal species. This process is

actually consistent with size-based and trait-based approaches to modelling ecosystem dynamics, which implicitly assume that species with similar life-history traits necessarily have similar ecological niches (Shin *et al.*, 2005; Pope *et al.*, 2006). However, for this process to be a major impediment to stock rebuilding, a single species out of a suite of species with similar traits would have been overfished, whereas others would have to have increased well above historical levels in order to play—in addition to their own historical ecological roles—also the roles once played by the now-depleted species. Such patterns should also be examined as part of the science to inform development of rebuilding plans. However, in heavily fished ecosystems, community studies indicate that many populations in a trait group seem to be depleted together and species in other (generally smaller) trait groups are the ones increasing in abundance (Choi *et al.*, 2005; Daan *et al.*, 2005).

(iv) Collapse to near-extinction (with SSB $\ll B_{\text{lim}}$). Many high-profiled recovery efforts have been made for species that have collapsed to near-extinction (Hutchings and Reynolds, 2004), which are much more susceptible to exhibiting Allee effects, either as intrinsic population responses or caused by the establishment of species with complementary life-histories in the marine ecosystem, or simply exhibit loss of memory of spawning migrations, etc., within their populations. A recovery from a near-extinction collapse is expected to be harder to achieve than a rebuilding trajectory from just a depleted state. It is in this context where distinguishing between recovery/collapse and rebuilding/depletion becomes important, because the difficulty of recovery from a state of near-extinction collapse might not be representative of the potential for rebuilding of stocks that have been depleted by overexploitation. So far, clupeids seem to be able to recover from near-extinctions (Hutchings and Reynolds, 2004) and Allee effects have not been directly demonstrated for commercially exploited marine fish (Vergnon *et al.*, 2008).

(v) Where overexploitation of a species has been associated with loss of essential habitat, impaired productivity by contaminants, or through other causes (Powers *et al.*, 2005; Lotze, 2007), merely reducing F might not be sufficient to ensure rebuilding. Other mitigation measures might also be necessary for rebuilding populations.

Because these effects are not covered in our models, rebuilding might not proceed as predicted. Nevertheless, our models do provide a baseline prediction of the expected outcome of a rebuilding plan involving a reduction in F. Under no circumstances is rebuilding expected to proceed faster than predicted by the life-history characteristics of the species. Moreover, major effects of a species-specific rebuilding plan on species higher up and lower down the food chain can be expected, which would argue for a gradual reduction of all fleets, if a system as a whole is considered overexploited. On top of the baseline prediction, a full impact assessment of a rebuilding plan should nevertheless include considerations of the processes not described by the model, but which could affect the planned rebuilding.

Acknowledgements

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Appendix: model description

The community model and the set of parameters are almost identical with the one used by Andersen and Pedersen (2009), where the results of the base case are also described in more detail. The model equations are listed in Appendix Table 1 and the parameters in Appendix Table 2.

The model produces the size spectrum $N_i(w)$ of each asymptotic size class i, where w is the weight of an individual. This spectrum can be used to determine the number of individuals per volume in the size range $[w: w + dw]$ as $N_i(w)dw$, and is similar to a probability distribution, except that its integral $\int N_i(w)dw$ is not one, but the total number of individuals from larvae to adults. The size spectrum is found from a numerical solution of the conservation equation (1) supplemented by a boundary condition specifying how recruits with size w_0 enter the population:

$$\frac{\partial g_i(w_0)N_i}{\partial w} = R_i,$$

where R_i is the recruitment. The core of the model comprises the specifications of growth, mortality, and recruitment, which largely follow the principles of "the North Sea model" (Andersen and Ursin, 1977).

Food is either fish from the size spectra of trait classes $N_i(w)$ or from a resource spectrum $N_r(w)$. Selection of prey size is based on the ratio between predator and prey size w/w_{prey} and described by the classical lognormal size-selection model (Ursin, 1973; M1). Consumption of encountered food (M2–3) is described by a functional response type II to represent satiation (M4–5). The feeding level $f(w)$ (M5) is the amount of consumed food relative to maximum consumption hw^n.

Consumed food $f(w)hw^n$ is assimilated with an efficiency α. Ingested food is first used for standard metabolism and activity kw^p. A fraction $\psi(w)$ of the remaining energy is used for reproduction and the remainder $1 - \psi(w)$ for somatic growth. The function $\psi(w)$ therefore plays the role of a maturation function (M6). For a constant feeding level f, this description of growth (M7) results in a von Bertalanffy-like growth curve with asymptotic size W and a von Bertalanffy growth constant $K \approx \alpha h f W_i^{n-1}/(1 - n)$.

Recruitment is constant at a level given by the theoretical abundance at small sizes calculated from equilibrium size-spectrum theory (M8; Andersen and Beyer, 2006). The free parameter κ_0 scales the abundance of all asymptotic size classes, and it is

adjusted such that the spectra of the fish populations form a continuation of the resource spectrum.

Mortality is composed of a constant background mortality (M9) and predation mortality (M10). The formulation of the predation mortality ensures that the model maintains a mass balance, i.e. all consumption by predators results in a corresponding mortality on its prey (Andersen and Ursin, 1977).

The smallest individuals in the model do not eat fish from the N_i spectra, but zooplankton and/or benthic production. This production is described by a resource spectrum, where each size class has semi-chemostatic growth (M12) with a fixed carrying capacity (M13).

The model is solved numerically using standard finite-difference techniques for partial differential equations (Press *et al.*, 1992). The size axis is discretized with 100 logarithmically spaced grid points, 20 trait classes are evenly distributed in $\log(W)$, and the time-step is 0.02 year. The results do not depend on the discretization (e.g. the number of size and trait classes) as long as it is not made coarser than what is used here.

Appendix Table 1. Model equations.

Process	Equation	Number
Encounter and consumption		
Prey size selection	$\phi\left(\dfrac{w}{w_{\text{prey}}}\right) = \exp\left[-\dfrac{(\ln(\beta w_{\text{prey}}/w))^2}{2\sigma^2}\right]$	M1
Volumetric search rate	$V(w) = \gamma w^q$	M2
Encountered food	$E(w) = V(w)\sum_i \int_0^w \phi\left(\dfrac{w}{w_{\text{prey}}}\right) N_i(w_{\text{prey}}) w_{\text{prey}} dw_{\text{prey}}$	M3
Maximum consumption rate	$I_{\max} = hw^n$	M4
Feeding level	$f(w) = \dfrac{E(w)}{E(w) + I_{\max}}$	M5
Growth and reproduction		
Maturation function	$\psi_i(w) = \left[1 + \left(\dfrac{w}{\eta W_i}\right)^{-10}\right]^{-1} \left(\dfrac{w}{W_i}\right)^{1-n}$	M6
Somatic growth	$g_i(w) = (\alpha f(w)hw^n - kw^p)(1 - \psi_i(w))$	M7
Recruitment		
Recruitment	$R_i = \kappa_0 W_i^{2n-q-3+a}$	M8
Mortality		
Background mortality	$\mu_{0,i} = Z_0 W_i^z$	M9
Predation mortality	$\mu_p(w_{\text{prey}}) = \sum_i \int_{w_0}^{\infty} \phi\left(\dfrac{w}{w_{\text{prey}}}\right)(1 - f(w))V(w)N_i(w)dw$	M10
Fishing mortality	$F_i(w) = F_{0,i}\dfrac{1 - c(AW_i^{1-n} - L_0)}{1 + \exp[(A/3)W_i^{1-n} - Aw^{1-n}]}$	M11
Resource spectrum		
Growth rate	$\dfrac{\partial N_r(w)}{\partial t} = r_0 w^{n-1}(\kappa(w) - N_r(w)) - \mu_p(w)N_r(w)$	M12
Carrying capacity	$\kappa(w) = \kappa_r^{-2-q+n}$ for $w < w_{\text{cut}}$	M13

Appendix Table 2. Parameters (units of time are in years and weight in g).

Symbol	Parameter	Value
Encounter and growth		
α	Assimilation efficiency[a]	0.6
n	Exponent of maximum consumption[b]	2/3
h	Factor of maximum consumption[c]	40
q	Exponent of search volume[d]	0.9
p	Exponent of standard metabolism[e]	3/4
k	Factor of standard metabolism[f]	4
γ	Volumetric search rate[g]	2 552
β	Preferred predator–prey mass ratio[h]	100
σ	Width of size-selection function[i]	1.3
η	Size-at-maturation relative to asymptotic size[j]	0.25
Mortality		
Z_0	Factor for background mortality[k]	3
z	Exponent of background mortality[l]	−0.25
Resource spectrum		
r_0	Productivity[l]	4
κ_r	Carrying capacity	0.005
w_{cut}	Cut-off size	10
Recruitment		
a	Physiological mortality[m]	0.18
κ_0	Level of recruitment[n]	1.1
Fishing mortality		
A	Factor in length-weight relation[o]	0.01
L_0	Centre length of slope parameter[o]	70
c	Constant[o]	0.01

[a]Kitchell *et al.* (1977).
[b]Jobling (1994) states that $2/3 < n < 3/4$. We have used $n = 2/3$ to be consistent with the von Bertalanffy growth curves.
[c]Adjusted such that emergent growth rates are in the range of those observed in the North Sea.
[d]Considerations on the bioenergetic budget of swimming predict a value of q between $2/3$ and 1 (Andersen and Beyer, 2006).
[e]West *et al.* (1997).
[f]Data of Winberg (1956) indicate a standard (resting) metabolism factor for fish of $\sim 4\ g^{0.25}\ year^{-1}$ at 10°C.
[g]Calculated from the other parameters as specified in Andersen and Pedersen (2009).
[h]Ursin (1973) and Jennings *et al.* (2001).
[i]Ursin (1973) finds $\sigma \approx 1$ for a single species. To account for species diversity within trait classes, a higher value is used.
[j]Beverton (1992).
[k]Adjusted to result in a background mortality of the same order (but lower) than the predation mortality.
[l]Savage *et al.* (2004); temperature: 10°C.
[m]$a \approx \beta^{2n-q-1}/\alpha$ (Andersen and Beyer, 2006); see Andersen and Pedersen (2009) for exact expression.
[n]Free, see text.
[o]Pope *et al.* (2006).