

Post-harvest recovery dynamics depend on predator specialization in size-selective fisheries

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Supplement 1. Sensitivity of biomass recovery time to growth, predation, and harvest parameters

In order to determine whether our choice of the default predation parameters affected the relative behavior of the size-independent, generalist, and obligate predation models, we analyzed sensitivity of each model to different values for scaling of growth variance (γ), predator capture rate (size-independent c_b or gape-limited c_p), and maximum prey size ($l_{\max P}$). We used the equal-with-harvest obligate model for all sensitivity tests.

We tested the sensitivity of recovery time to the growth variance scaling factor γ which determines how growth standard deviation relates to growth mean (Eq. 5 in the main article). Recovery time for the all models decreased as γ increased (Figure S1), though the effects were most pronounced for obligate predation on cod (dotted line; Figure S1a) and generalist predation on haddock (dashed line; Figure S1b). Lower growth variance reduces the proportion of “high growth” individuals who escape predation at an earlier age, thereby increasing the effect of the obligate predator and decreasing equilibrium abundance, but the recovery trajectories are qualitatively similar (Figure S2).

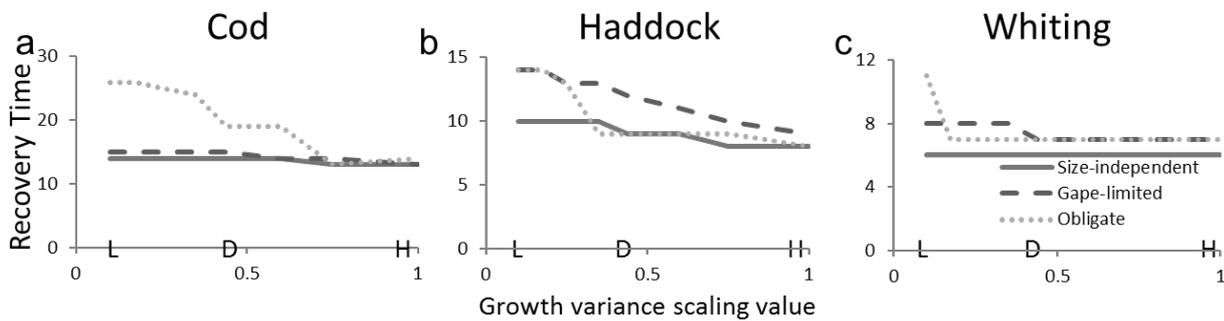


Figure S1. Sensitivity of recovery time to growth variance scaling. Recovery times for species for different values of γ , the growth variance scaling parameter. L, D, and H indicate the low variance, default, and high variance values used in Figure S2. (a) Cod. (b) Haddock. (c) Whiting.

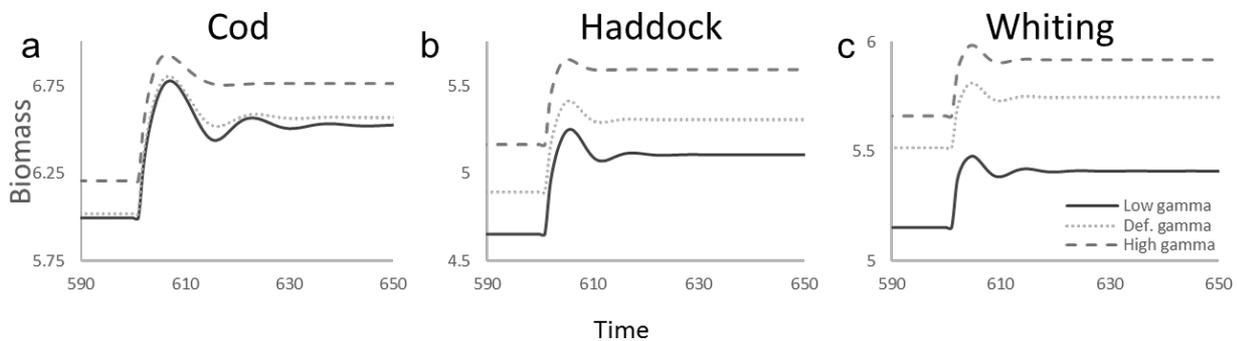


Figure S2. Sensitivity of recovery patterns to growth variance scaling. Time series for three values of γ , the growth variance scaling parameter (low=0.1, default=0.44, high=1.0). (a) Cod. (b) Haddock. (c) Whiting.

We found that although increasing predator capture rate changed population equilibria, it had only a small effect on recovery for the size-independent and generalist models (solid and dashed lines; Figures S3a,c,e). Increased capture rate for the obligate predator decreased recovery time for cod and haddock, but increased recovery for whiting due to an increased magnitude of population oscillations (dotted lines; Figures S3a,c,e). Decreasing capture rate tended to increase long-term oscillations for cod and haddock until c_p approached 0. In contrast, increasing maximum prey size dampened population oscillations for cod but increased their magnitude for haddock and whiting (dotted lines; Figures S3b,d,f). As maximum prey size increases, the relatively constant pressure from the generalist predator is only slightly increased while for the obligate predator an increasing portion of the population is exposed to the strong numerical response. This suggests that for obligate predation the primary factor affecting recovery time is total lifetime exposure to predation, though with cod there is still sufficient size refuge for adults to damp oscillations. For our default l_{maxP} of 35cm, many cod outgrow predation vulnerability within a few years and breeding adults have low non-harvest mortality. For haddock and whiting, conversely, predation pressure is heavy even into the mature size classes. As l_{maxP} increases, the size refuge narrows and cod recovery times begin to resemble those of the smaller species. Note that c_p was kept constant as l_{maxP} was changed, meaning that overall predation pressure increased or decreased as well. However, the low sensitivity to predator capture rate for cod and haddock suggests that varying c to maintain a constant lifetime predation level would only minimally affect the generalist predator and have no effect on the obligate predator.

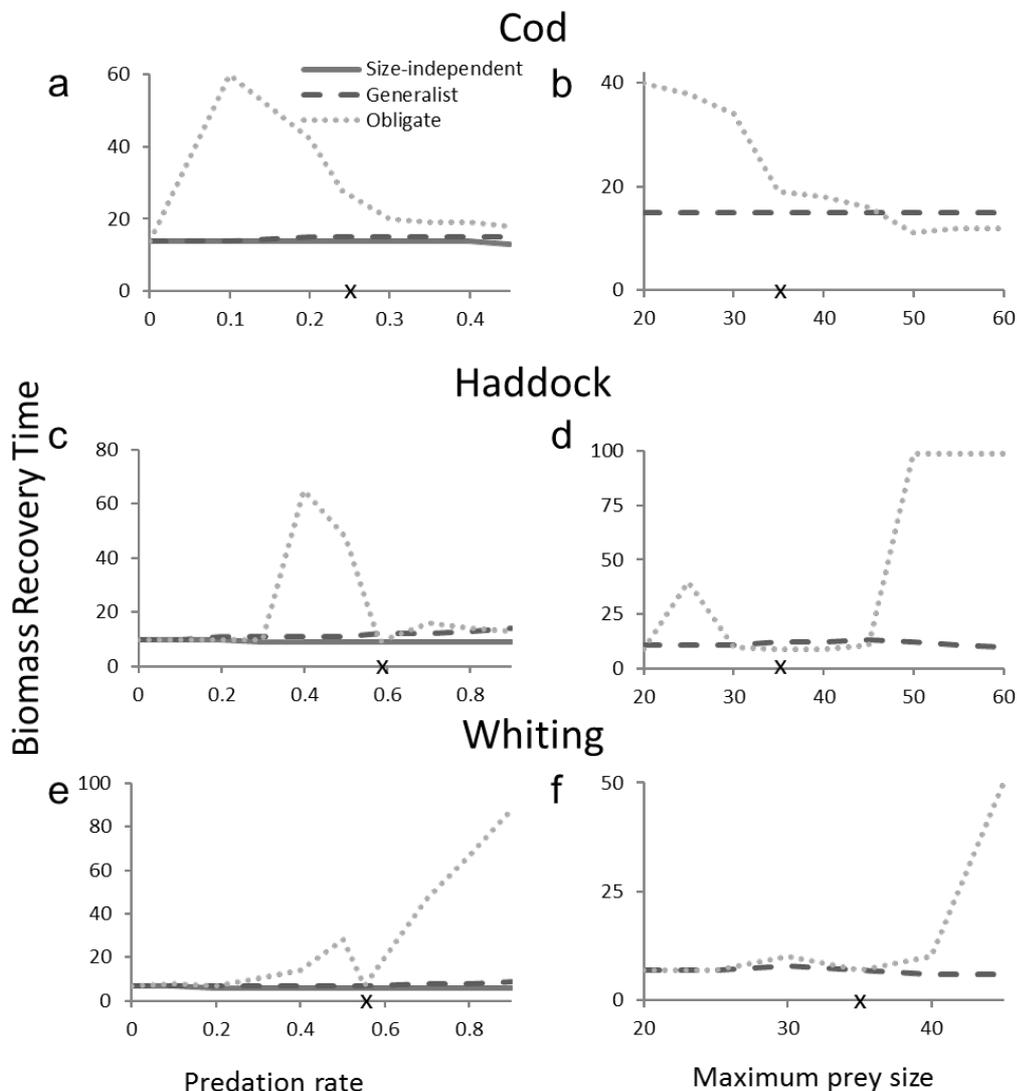


Figure S3: Biomass recovery time versus predation rate and maximum prey size. Biomass recovery time is defined as the number of time-steps before mean biomass is within 2.5% of post-harvest equilibrium. Horizontal axis for graphs on the left is gape-limited predation rate (c_p ; scaled by 10^4 for clarity) and for graphs on the right is maximum prey size (l_{maxP}). Default values are marked with 'x'. Note that recovery time in the right column is in log-scale. For clarity,

maximum recovery time was capped at 100 years even if the population had not stabilized yet at that point. (a,b) Cod. (c,d) Haddock. (e,f) Whiting.

In order to determine whether our choice of default harvest parameters affected the relative behavior of the base, generalist, and obligate predation models, we analyzed sensitivity of each model to different values for harvest rate (h) and minimum harvest size ($l_{\min H}$). As with $l_{\max P}$, we kept h constant as $l_{\min H}$ varied and lifetime harvest increased or decreased accordingly.

We found that increasing harvest rate caused a small increase in recovery time for all models, though this leveled off with higher harvest rates (Figures S4a,c,e). Recovery time for all species and models decreased with increasing minimum harvest size (Figures S4b,d,f) with a similar though inverse pattern to harvest rate. This analysis suggests that sensitivity to harvest parameters is low for the non-obligate models, and for obligate models sensitivity to harvest depends on the strength of predation control of the species. Only for cod, with a relatively large proportion of size classes safe from predation, did a change in intermediate-to-high values of harvest produce a large change in recovery time.

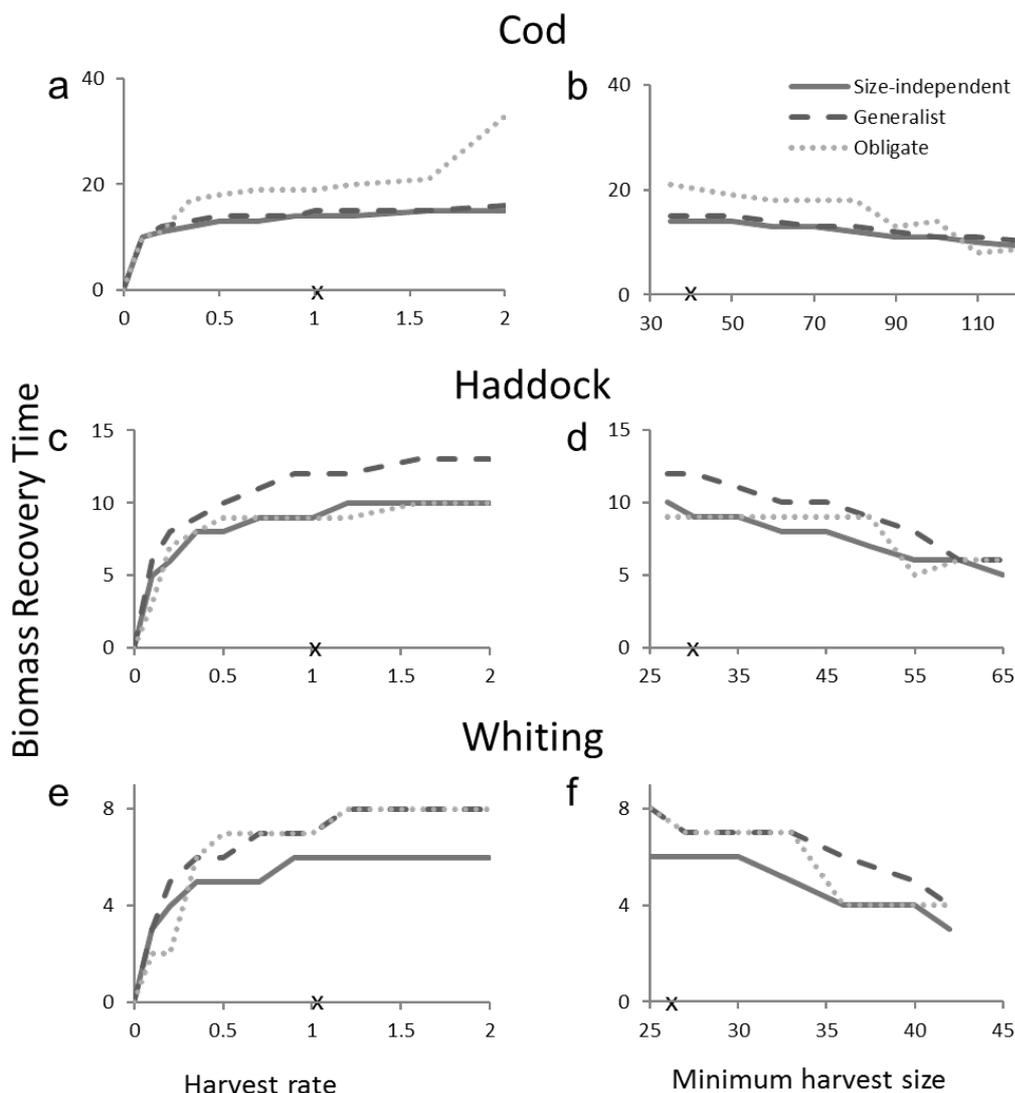


Figure S4: Biomass recovery time versus harvest rate and minimum harvest size. Biomass recovery time is defined as the number of time-steps before mean biomass is with 2.5% of post-harvest equilibrium. Horizontal axis for graphs on the left is harvest rate (h) and for graphs on the right is minimum harvest size ($l_{\min H}$). Default values marked with 'x'. Note differing x-axis scales for minimum harvest size. a,b) Cod. c,d) Haddock. e,f) Whiting.

Supplement 2: Derivation of discrete growth function and comparison with Euler approximation

To determine the discrete growth function, we start with the continuous growth form of the 2-stage model with linear growth before maturity and von Bertalanffy growth afterwards (see Table 1 in the main article for parameter and variable definitions):

$$dl/da_l = \begin{cases} l_\infty \left(\frac{1}{1-k_a} - 1 \right) & \text{if } l < l_{mat} \\ k_a (l_\infty - l) & \text{if } l \geq l_{mat} \end{cases}. \quad (\text{S.1})$$

We set $k_j = \frac{1}{1-k_a} - 1$, $a_{mat} = \frac{l_{mat}-l_0}{l_\infty k_j}$, and $l_{diff} = l_\infty - l_{mat}$ so that the length-at-age function is smooth. We integrate Equation B.1 to arrive at length as a function of time within lifespan, or effective age (a_l):

$$l(a_l) = \begin{cases} l_\infty k_j a_l + l_0 & \text{if } a_l < a_{mat} \\ l_\infty - l_{diff} e^{-k_a(a_l - a_{mat})} & \text{if } a_l \geq a_{mat} \end{cases}. \quad (\text{S.2})$$

To determine growth based on current length, not absolute time, we reformulate Eq. S.2 to determine equivalent age a_l from current length, then calculate $l(a_l+1)$:

$$a_l(l) = \begin{cases} \frac{l-l_0}{l_\infty k_j} & \text{if } l < l_{mat} \\ -\frac{\ln\left(\frac{l_\infty-l}{l_{diff}}\right)}{k_a} + a_{mat} & \text{if } l \geq l_{mat} \end{cases}. \quad (\text{S.3})$$

Mean growth is the difference between $l(a_l+1)$ and l , using Equation S.2:

$$G(l) = \begin{cases} l_\infty k_j (a_l(l) + 1) + l_0 - l & \text{if } a_l(l) + 1 < a_{mat} \\ l_\infty - l_{diff} e^{-k_a(a_l(l)+1-a_{mat})} - l & \text{if } a_l(l) + 1 \geq a_{mat} \end{cases}. \quad (\text{S.4})$$

We explored using different values of Δa , but found no increase in accuracy for $\Delta a < 1$. Using the first order approximation of continuous growth instead of the discrete form slightly over-estimated the abundance of longer length individuals.

Supplement 3: Addressing the search and aggregation assumptions of Nicholson-Bailey predation

Nicholson-Bailey predation is a form of rapid obligate predation based on random search for prey in a homogeneous environment (Nicholson & Bailey 1935, Beddington et al. 1978, Murdoch et al. 1985). Rapid obligate predation encompasses a number of further assumptions (such as a rapid numerical response and dependence on a single prey species) which we discuss in the main text (in Discussion: Model assumptions). Here we focus on the search and aggregation aspects of Nicholson-Bailey by comparing our model to those from a non-random search model which incorporates predator aggregation in an environment with implicit patchiness. We do not address patchiness effects on predator-prey stability, because our model includes multiple stabilizing factors in addition to classic Nicholson-Bailey predation (in particular, prey size refuge and prey density-dependence). However, introducing any form of aggregation is expected to increase system stability (Chesson & Murdoch 1986, Murdoch & Stewart-Oaten 1989).

May (1978) proposed a discrete-time predation model which assumes predator attack follows a negative binomial distribution rather than the Poisson distribution used in Nicholson-Bailey. Besides the attack rate c , the model includes a clumping parameter k which May (1978) interprets as a measure of the variance of predator distribution across patches. The predation equation, rewritten to match the format of Eq. 10 in the main article, is:

$$P(l) = \begin{cases} -\ln \left(\left(1 + \frac{c p_t}{k} \right)^{-k} \right) & \text{if } l < l_{maxP} \\ 0 & \text{if } l \geq l_{maxP} \end{cases}. \quad (\text{S.5})$$

Note that the negative logarithm is added so that $P(l)$ fits into our existing survival and predator abundance equations (Equations 8,11 in the main article).

By varying k , we can compare varying degrees of predator patchiness from highly clumped ($k < 0.5$) to relatively even distribution ($k > 1.0$), with the Nicholson-Bailey distribution approximated as $k \rightarrow \infty$. Low k lessens the strength of predation, because predator search is more varied across the environment and less

efficient overall. Search effectiveness, and hence the strength of obligate predation, increases with increasing k . Our results show that for lower values of k , obligate predation behaves more like the generalist model for all three species (Figure S5). For higher values, however, the negative-binomial model produces recovery trajectories similar to the Nicholson-Bailey model. This suggests the delayed recovery seen in our results is most applicable to a predator with relatively even distribution and search ability within the range of the prey population.

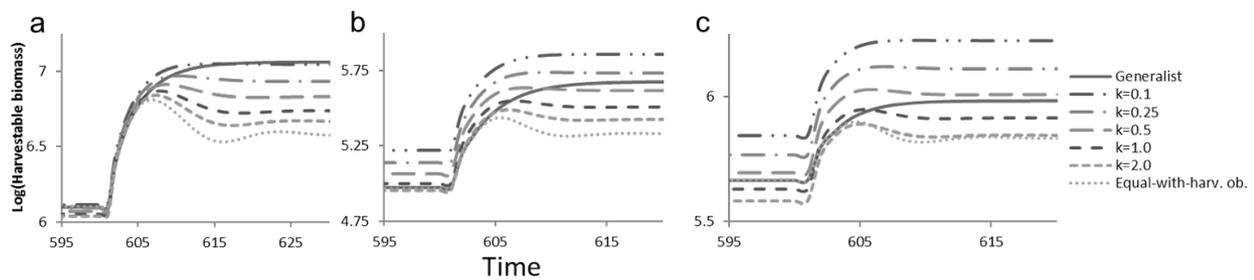


Figure S5. Recovery trajectories for predator clumping models versus Nicholson-Bailey model. Vertical axis shows harvestable biomass in \log_{10} (metric tonnes). Horizontal axis shows time in years, with harvest starting at $t=600$. Both axes vary between species. Generalist predation model and equal-with-harvest Nicholson-Bailey obligate predation model are represented by solid and dotted lines, respectively. Representation for the negative-binomial models with clumping (k) values of 0.1, 0.25, 0.5, 1.0, and 2.0 are shown in the legend. Note that the variable k models are not individually tuned to match the with-harvest biomass of the generalist model, and consequently have different equilibria. (a) Cod. (b) Haddock. (c) Whiting.