

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

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ABSTRACT: Fisheries typically truncate target species' size distributions through an increase in mortality, especially if harvest is size-selective. Such truncation can push a harvested species' size distribution into classes most vulnerable to gape-limited predation, such that predator–prey dynamics might affect the rate of recovery from fishing. Understanding this rate of recovery is crucial to adaptive management of no-take reserves and fisheries closures. We used a 2-species size-structured model to examine how gape-limited predation alters post-harvest recovery for 3 example prey species, viz. cod, haddock, and whiting. We found little difference in recovery patterns of prey abundance and size structure between systems with gape-limited generalist predation and those with no size-dependent predation. However, gape-limited obligate predation can lead to fluctuations, with transient declines, that delay recovery to the pre-harvest equilibrium for both biomass and mean size due to a time lag in predator recovery. Fluctuating recovery dynamics under obligate predation were most likely for predators that experienced greater declines due to prey loss during harvest and for slow-growing prey with an adult size refuge. We conclude that through these delays, the presence of a strong dynamically linked predator can alter the expectations of the time scale for different recovery metrics used in adaptive management.

KEY WORDS: Size-selective harvest · Species interactions · Gape-limited predation · Size structure · Multi-species fisheries models · Ecosystem-based fisheries management · Marine reserves · Monitoring

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INTRODUCTION

Overfishing has occurred in a number of fish stocks globally (Jackson et al. 2001, Myers & Worm 2003, Pitcher & Cheung 2013, Watson & Pauly 2013; though not universally—see Worm et al. 2009). Measures taken to restore depleted stocks (e.g. NMFS 2009) include the use of catch quotas, gear restrictions, the establishment of marine protected areas including no-take marine reserves, and the temporary closure of entire fisheries. Responses to recovery efforts have been mixed, however, with many species showing little of the rapid growth predicted by single-species models (Hutchings 2000, Dulvy et al. 2003, Hutchings & Reynolds 2004, Claudet et al. 2008). Although marine reserves are generally effective at increasing

fish density and biomass within their boundaries (Halpern 2003, Lester et al. 2009), variation in recovery is high and clear positive effects are likely only for older reserves (Micheli et al. 2004a, Molloy et al. 2009). Recruitment time lags due to a high age at maturity can delay population recovery for several years after management programs go into effect (Matsuda & Nishimori 2003, White et al. 2013). Identifying the key ecological factors which affect recovery, such as altered food webs, dispersal out of no-take regions, and diminished spawning success (e.g. Myers et al. 1996, Rowe & Hutchings 2003, Brander 2005, Shelton et al. 2006), is a critical task for effective management.

One factor potentially important to recovery is population size structure, because body size governs

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much of an individual's ecology (Wilson 1975, Werner & Gilliam 1984, Ebenman & Persson 1988). Fisheries can truncate size structure through increased mortality, which lowers the probability of survival to older age classes, and selective targeting of large individuals (e.g. as arises from minimum size limits) can increase such truncation (Shin et al. 2005, Berkeley 2006). The change in size distribution affects recruitment, species interactions, and fishery sustainability, amongst other factors (Goñi 1998, Berkeley et al. 2004, Anderson et al. 2008, Fenberg & Roy 2008). After fishing ceases, we expect a restoration of size structure as older size classes become relatively more abundant, along with an increase in overall abundance (White et al. 2013), and thus changes in size structure are often an essential element of monitoring to determine the effectiveness of temporary and permanent fisheries closures (e.g. Halpern 2003, Lester et al. 2009). In addition, any model used in adaptive management on a short time scale, i.e. a model designed to predict short-term post-harvest transient responses that set expectations for effective management and determine if adjustments are necessary (White et al. 2011), will need to account for any ecological dynamics which further affect size structure.

One ecological dynamic with the potential to substantially affect size structure is size-specific predation. Prey selection for many predators is constrained by relative body size due to factors such as gape limitation or relative speed (e.g. Paine 1976, Hambright 1991, Christensen 1996a, Persson et al. 1996, Rodd & Reznick 1997, Urban 2007). Consequently, predation levels are usually highest on juveniles and often diminish rapidly as an individual grows (Zaret 1980, Brose et al. 2006). Size-dependent predation, particularly on eggs and young recruits, has been shown to regulate the populations of even large piscivores such as cod or tuna (Essington 2004, Speirs et al. 2010, Hunsicker et al. 2012). Reserves can protect predators as well as prey, causing a decrease in abundance of prey species through trophic cascades (e.g. Babcock et al. 1999, Pinnegar et al. 2000, Russ & Alcala 2003, Shears & Babcock 2003, Guidetti 2006, Stockwell et al. 2009), depending on the relative pre-reserve harvest rates and size-dependent interactions (Baskett 2006, Mumby et al. 2006, Kellner et al. 2010). Incorporating predation in general into marine reserve design can increase the reserve size necessary for target species recovery (Micheli et al. 2004b, Baskett et al. 2007). Because of the size-dependence of predation, a truncation of size structure due to harvest can increase the proportion of the

population that experiences heightened predation and might delay recovery.

Accounting for species interactions such as predation is a key component of ecosystem-based fisheries management, which incorporates a more holistic ecological approach (Larkin 1996, Zabel et al. 2003, Pickett et al. 2004, Francis et al. 2007). By changing relative abundance, behavior, and size structure, strong interactors such as predators can alter the optimal management strategy and delay post-harvest recovery (e.g. Christensen 1996b, Tsou & Collie 2001, Matsuda & Abrams 2004, Baskett et al. 2006, Irigoien & de Roos 2011, Hunsicker et al. 2012), and incorporating these effects is essential to effective management (Bax 1998, Hollowed et al. 2000, Hunsicker et al. 2011, Tyrrell et al. 2011). Multi-species size-structured models have found that harvest can change community diversity and size distribution very rapidly (Hall et al. 2006), while maximum sustainable yield can depend strongly on egg and juvenile predation by smaller species (Speirs et al. 2010).

The effect of size-dependent predation, in combination with harvest-induced truncation of size structure, suggests the potential for predation to play a role in recovery after marine reserve establishment or a temporary fishery closure. A further question is which types of predators might have the largest role in prey recovery and which types of prey might be the most affected by predators during recovery. Considering the degree of predator specialization, a generalist predator would likely have a greater abundance during a given prey's initial recovery period, and therefore exert a greater predation pressure, than an obligate predator that would have declined with prey decline; however, an obligate predator that is dynamically linked to the prey would exert an increasing predation pressure just as recovery is occurring. Considering the type of prey in terms of life history, smaller-bodied, faster-growing species have a faster turnover and recovery potential that might increase their response rate, but they will also have the greatest susceptibility to gape-limited predators that might disproportionately decrease their response rate.

To quantify the potential for size-dependent predation to affect expectations for post-harvest recovery, we developed a dynamical, continuous size-structured model of a harvested prey species. We used this model to explore how the biomass and size distribution trajectories for a recovering species within the immediate post-harvest period depend on the degree of predator specialization and the prey life history. Our approach differs from existing multi-species harvest recovery models (e.g. Micheli et al. 2004b, Bas-

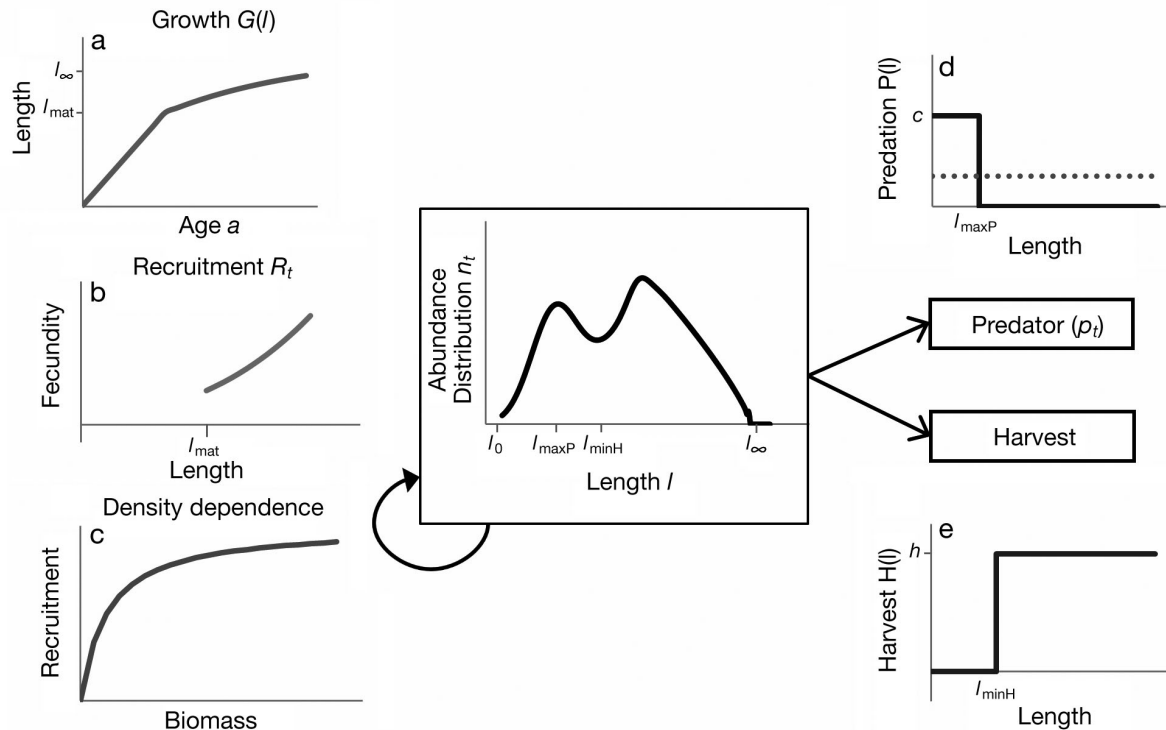


Fig. 1. Model dynamics. Functions are defined in 'Methods' and parameters are defined in Table 1. The model follows the size-structured population density distribution (n_t) of the target species as it depends on growth, recruitment, harvest, and predation (Eq. 1), excluding new recruits ($l = l_0$). (a) Mean growth is linear until length-at-maturity l_{mat} is reached, after which it becomes asymptotic with maximum length l_∞ via a van Bertalanffy equation (Eq. 7). Growth within the population is distributed normally around the mean (Eqs. 4 & 5). (b) Reproduction occurs for individuals with $l > l_{mat}$ and increases exponentially with size (Eqs. 2 & 3); (c) recruits then undergo Beverton-Holt density dependence (Eq. 2). (d) Predation mortality is either size-independent (dashed line) or gape-limited (solid line; only below a maximum length l_{maxP} ; Eq. 10). Predator abundance (p_t) is either constant (generalist predator) or follows Nicholson-Bailey dynamics (obligate predator; Eq. 11). (e) Harvest is a constant mortality h for the target species above a minimum harvest length l_{minH} (Eq. 9)

kett et al. 2006, Kellner et al. 2010) in 2 key ways. First, we focused our analysis on demographic transients (i.e. short-term population responses; Hastings 2001, 2004) during the management-critical monitoring period following the change in policy, rather than on long-term equilibrium outcome. Second, we tracked recovery of the complete size distribution, rather than only biomass density or mean size, to better match the metrics (such as size spectra or legal and sublegal size classes) used empirically in monitoring programs (e.g. Babcock et al. 1999, Fisher & Frank 2002, Denny & Babcock 2004, McClanahan & Graham 2005).

METHODS

Model overview

The target species in our model follows the prey population density distribution over a continuous size

structure in discrete time with overlapping generations. Given a specified size at maturity, growth is slower after maturity while fecundity increases with adult size. Recruitment is deterministic and negatively density-dependent. There are 2 size-dependent sources of mortality for the target species: a constant harvest proportion above a minimum size limit and size-dependent predation below a gape size limit. We modeled size-dependent predation as a generalist (constant abundance) or obligate (dynamic abundance) gape-limited predator targeting individuals smaller than a designated size (Fig. 1). Additionally, we used a model with a constant non-size-selective predation as a baseline. We analyzed speed of recovery of abundance and mean size, focusing firstly on size-dependent versus size-independent mortality and secondly on generalist versus obligate predation. We then compared post-harvest size distribution trajectories between the 3 models to determine whether predation type affects the speed and pattern of the return to the unfished size distribution.

Note that our goal is to construct a strategic (as opposed to tactical) model sensu May (2001), i.e. that we mean the model to provide general insight as a ‘way of thinking clearly’ (May 2004, p. 791) through a logical expectation as opposed to providing a quantitatively precise forecast. As such, we form the simplest possible model to address our central question (where all models involve at least some simplification of reality), which allows us to understand the drivers of our outcome (May 2004), much like experiments control for a variety of potentially important factors in order to be able to isolate causality for the factor of interest (Caswell 1988). Specifically, here our goal was to determine how the size-dependency and type of predation (obligate versus generalist) affect post-harvest recovery. In our focus on size-dependent dynamics and comparing 2 extreme categories of predation types, we ignored many additional dynamics (e.g. stochasticity in recruitment, intermediate predation types between the extremes of obligate and generalist, greater realism in predation curves) that will inevitably be important to precisely forecasting recovery dynamics in a given system (see the ‘Discussion’ for more on these assumptions). The primary utility of this modelling approach to management is to provide general insight into (1) whether and when a manager might need to include predation into a tactical model applied to quantifying expectations for and monitoring recovery in their system, and (2) whether predation might be a possible explanation considered for dynamics observed in a given system based on the predation type most relevant to that system.

Target species demography

We modeled the target species in discrete time with continuous size structure, in the form of an integral projection model (Coulson 2012). We used a 1 yr time step to match the annual recruitment cycle of the target species. We use length (l) as a proxy for body size (Table 1) and model a continuous population density distribution ($n_t(l)$) between length at settlement (l_0) and maximum adult length (l_∞). Abundance of new recruits ($n_{t+1}(l_0)$) is equal to total recruitment after density dependence (R_t). After recruitment, individuals grow from l' to l according to the density distribution $G^*(ll')$ and survive each year with probability $S(l')$. The iteration for the population density across lengths is then:

$$n_{t+1}(l) = \begin{cases} R_t & \text{if } l = l_0 \\ \int (G^*(ll') S(l')) n_t(l') dl' & \text{if } l > l_0. \end{cases} \quad (1)$$

Recruitment

We determined total recruits (R_t) by applying Beverton-Holt density dependence (with saturation parameter β) to total fecundity pre-density-dependence. Total fecundity is the integral of individual, size-dependent fecundity multiplied by abundance ($n_t(l)$) across all mature lengths ($l > l_{mat}$). To calculate individual fecundity, we multiplied recruits-per-gram (A) by body mass ($M(l)$), calculated by converting length to volume (exponent B) and then to mass ($g\ cm^{-B}$; M_g) which yields:

$$R_t = \frac{\int_{l_{mat}}^{l_\infty} A \cdot M(l') n_t(l') dl'}{1 + \beta \int_{l_{mat}}^{l_\infty} A \cdot M(l') n_t(l') dl'} \quad (2)$$

$$M(l) = M_g l^B. \quad (3)$$

Growth

The probability of growing ($G^*(ll')$) from size l' to l is normally distributed, with mean growth ($G(l)$) dependent on length and standard deviation ($\sigma_{l'}$) scaled to the mean according to γ :

$$G^*(ll') = \begin{cases} \frac{1}{\sqrt{2\pi\sigma_{l'}^2}} e^{-\frac{(l-l'+G(l'))^2}{2\sigma_{l'}^2}} & \text{if } G(l') > 0, l' < l \leq l_\infty \\ 0 & \text{otherwise} \end{cases} \quad (4)$$

$$\sigma_{l'} = \begin{cases} \gamma G(l') & \text{if } G(l') > 0 \\ 0 & \text{otherwise.} \end{cases} \quad (5)$$

Note that we assume that both $G(l') < 0$ (shrinkage) and $l > l_\infty$ (growth beyond the maximum size l_∞ , which does not vary) are impossible, and we re-normalize after setting that portion of the growth distribution to 0 so that the integral of the growth distribution, $\int_{l'}^{l_\infty} G^*(ll') dl = 1$. The assumption that growth follows a normal distribution has little effect on age-length conversions and the shape of length-frequency distributions over time in size-structured models with size-selective mortality (Ricker 1969, Gascuel 1994). We test sensitivity to γ in Supplement 1 at www.int-res.com/articles/suppl/m564p127_supp.pdf.

Mean growth $G(l)$ follows a 2-stage von Bertalanffy growth model (Beverton & Holt 1957). Juveniles grow at a linear rate until length-at-maturity (l_{mat}) is reached, after which growth slows due to reproductive expenditure and becomes asymptotic with maximum length l_∞ (Roff 1983). Mean juvenile

Table 1. Model symbol definitions and values

Symbol	Definition	Unit	Cod	Haddock	Whiting	Source
State variables						
$n_t(l)$	Total abundance of target species at time t for length l					
p_t	Predator abundance at time t					
l	Length	cm				
Parameters						
l_0	Length at settlement	cm	7	5	5	Speirs et al. (2010) ^a
l_{mat}	Length at maturity	cm	60	25	20	Speirs et al. (2010) ^a
l_{∞}	Maximum adult length	cm	123	65	43	Speirs et al. (2010) ^a
m	Background mortality	yr ⁻¹	0.30	0.53	0.72	Cury & Pauly (2000), Charnov et al. (2013) ^b
h	Harvest rate for targetable sizes	yr ⁻¹	1.0	1.0	1.0	Pope & Macer (1996) ^c
l_{minH}	Minimum harvest size	cm	45	30	27	Speirs et al. (2010) ^a
k_a	Adult growth parameter	yr ⁻¹	0.164	0.292	0.402	Speirs et al. (2010) ^a
γ	Scaling of growth standard deviation from mean growth		0.44	0.44	0.44	Shackell et al. (1997)
M_g	Linear scaling of length-to-mass	g cm ^{-B}	5.06×10^{-3}	5.2×10^{-3}	6.2×10^{-3}	Speirs et al. (2010) ^a
B	Exponential scaling of length-to-mass		3.192	3.155	3.103	Speirs et al. (2010) ^a
A	Scaling of successful recruits to mass	g ⁻¹	7.11×10^{-2}	8.19×10^{-2}	2.98×10^{-1}	Daan et al. (1990), Baskett et al. (2005) ^d
β	Density-dependence parameter for fecundity		2×10^{-10}	2×10^{-10}	2×10^{-11}	Daan et al. (1990) ^e
\bar{p}	Predator abundance for non-dynamical predation	ind.	10 000	10 000	10 000	This study ^f
c_b	Predation rate for size-independent predation	yr ⁻¹	0.015×10^{-4}	0.068×10^{-4}	0.183×10^{-4}	This study ^g
c_p	Predation rate for gape-limited models ($l < l_{\text{maxP}}$)	yr ⁻¹	0.24×10^{-4}	0.58×10^{-4}	0.55×10^{-4}	Speirs et al. (2010) ^h
l_{maxP}	Maximum prey size for gape-limited models	cm	35	35	35	Savenkoff et al. (2006) ⁱ
v_p	Prey biomass conversion rate for obligate predator, equal-without-harvest	g ⁻¹	3.25×10^{-10}	1.14×10^{-9}	1.72×10^{-10}	This study ^j
v_h	Prey biomass conversion rate for obligate predator, equal-with-harvest	g ⁻¹	1.35×10^{-9}	2.54×10^{-9}	2.36×10^{-10}	As for footnote j, but for harvest (v_h)
^a Minimum harvest size based on pre-1989 legal minimums						
^b Calculated using $m = 1.8 \times k_a$ estimation						
^c Estimated multi-year average						
^d Estimated using a combination of spawning values from the 2 studies						
^e Adjusted using standing stock estimates						
^f A scaling constant for capture rate, chosen as a moderate abundance, close enough to 0 to allow the obligate version to potentially go temporarily extinct						
^g Calculated by averaging c_p rate over life expectancy of individual						
^h Sum of non-egg predation, scaled by the default non-dynamical abundance						
ⁱ Chosen as the dividing line for cod between juvenile and adult and, in particular, represents a transition from high to low predation mortality						
^j Chosen to produce obligate mortality at equilibrium equivalent to generalist mortality given no harvest (v_p) at the value for h specified here						

growth is calculated from adult asymptotic growth rate (k_a) and l_{∞} (Roff 1983, Baskett et al. 2005). We use a piecewise form of the von Bertalanffy model which determines estimated age from current length ($a_l(l)$):

$$a_l(l) = \begin{cases} \frac{l - l_0}{l_{\infty} k_j} & \text{if } l < l_{\text{mat}} \\ -\frac{\ln\left(\frac{l_{\infty} - l}{l_{\text{diff}}}\right)}{k_a} + a_{\text{mat}} & \text{if } l \geq l_{\text{mat}} \end{cases} \quad (6)$$

where $k_j = \frac{1}{1 - k_a} - 1$, $a_{\text{mat}} = \frac{I_{\text{mat}} - I_0}{I_{\infty} k_j}$, and $I_{\text{diff}} = I_{\infty} - I_{\text{mat}}$

to ensure a smooth function for mean size versus age. Mean growth is the difference between length at the next age $a_i(I) + 1$ and length at the previous age $a_i(I)$ (see Supplement 2 for the derivation and comparison with the first-order approximation):

$$G(I) = \begin{cases} I_{\infty} k_j (a_i(I) + 1) + I_0 - I & \text{if } a_i(I) + 1 < a_{\text{mat}} \\ I_{\infty} - I_{\text{diff}} e^{-k_a(a_i(I) + 1 - a_{\text{mat}})} - I & \text{if } a_i(I) + 1 \geq a_{\text{mat}} \end{cases} \quad (7)$$

Background mortality and harvest

We determine annual survival $S(I)$ from background mortality, predation ($P(I)$), and harvest ($H(I)$). Background mortality is independent of size and occurs at constant rate m . Individuals longer than a minimum length (I_{minH}) are harvested at a constant rate (h). This harvest model is commonly used in the literature (e.g. Yodzis 1994, Gardmark et al. 2003, Potts & Vincent 2008), and we use it for simplicity and to focus our analysis on the effects of predation dynamics. We describe size-dependent predation in the next section below. Size-dependent survivorship and harvest are then:

$$S(I) = e^{-m - H(I) - P(I)} \quad (8)$$

$$H(I) = \begin{cases} 0 & \text{if } I < I_{\text{minH}} \\ h & \text{if } I \geq I_{\text{minH}} \end{cases} \quad (9)$$

Predation

We compare size-independent non-dynamical predation with 2 gape-limited forms of predation, a constant generalist and a dynamical obligate. We simulate gape-limited predation using a size-specific predator with abundance p_t , capture rate c , and maximum prey length I_{maxP} :

$$P(I) = \begin{cases} c p_t & \text{if } I < I_{\text{maxP}} \\ 0 & \text{if } I \geq I_{\text{maxP}} \end{cases} \quad (10)$$

For the non-dynamical predation models, predator abundance $p_t = \bar{p}$ independent of time t , i.e. the species under consideration represents a small enough fraction of the predator's diet such that the predator has a constant abundance independent of the prey population. For the base size-independent model, we set $I_{\text{maxP}} = I_{\infty}$ and calculated capture rate $c = c_b$ to produce the same lifetime survivorship as the gape-limited generalist model given capture rate $c = c_p$. This holds overall mortality constant when compar-

ing the base and generalist models and allows us to determine the effect of the size-dependent versus size-independent predation.

For the specialist predator, we modeled the obligate predator dynamics as gape-limited predation and mass-based Nicholson-Bailey dynamics (Nicholson & Bailey 1935). Obligate predator abundance (p_t) is equal to total biomass consumed across all prey sizes ($I < I_{\text{maxP}}$), converted to mass using $M(I)$ in Eq. (3), and adjusted by a conversion factor (v):

$$p_{t+1} = v \int_{I_0}^{I_{\text{maxP}}} M(I) n_t(I) (1 - e^{-P(I)}) dI. \quad (11)$$

Note that the obligate predator is dynamical but has no size structure.

To determine the effects of predator dynamics alone on recovery, we parameterized the obligate predator such that predation pressure at equilibrium would be equal to that of the generalist predator. Because there are 2 potential equilibria, unharvested and harvested, we used 2 approaches based on the value of v : we assumed equivalency in predator abundance and therefore predation pressure either in the unharvested state ('equal-without-harvest obligate'; $v = v_p$) or in the harvested state ('equal-with-harvest obligate'; $v = v_h$). We set minimum predator abundance to a very low non-0 value to prevent extinction during harvest under some parameterizations.

Example species

To parameterize the model for numerical simulation, we chose 3 example species from the North Sea fishery (Table 1). These species cover a range of possible growth, fecundity, and mortality values and are all sufficiently large to have size-specific effects from a gape-limited predator. The largest species, Atlantic cod *Gadus morhua*, has a large adult body size, moderate fecundity, and experiences low predation rate and background mortality. The second example species, haddock *Melanogrammus aeglefinus*, has a medium body size and slightly higher fecundity than cod. It experiences the highest predation rate of the 3 species and the second highest background mortality. The final species, whiting *Merlangius merlangus*, has a small body size, the highest fecundity and background mortality, and experiences a predation rate almost as high as haddock. We set the default value of $h = 1.0 \text{ yr}^{-1}$ as representative of the intensive fishing rate seen in all 3 example fisheries (Pope & Macer 1996), and because the question of how pre-

ation affects recovery is only of interest if fishing was intensive enough to trigger recovery-oriented management actions. This value of h is approximately on par with total non-harvest mortality.

As none of the example species is reported to have a single tightly coupled obligate predator, we used the same hypothetical obligate across all 3 prey species to explore the potential effects of a strong dynamical predator. To compare the effects of different growth rates on predation escape, we kept maximum prey size and average predator mass constant across prey species but used the species-specific predation rates. We chose the maximum prey size for our simulated predator to match observed heightened predation rates on juvenile cod (Savenkoff et al. 2006). With the given parameters and assuming mean growth, cod outgrows the predator within 2 yr and reaches maturity within 3 yr. Haddock reaches maturity after 1 yr but outgrows the predator after 2 yr, and has higher predation and background mortality. Whiting reaches maturity after 1 yr but is vulnerable to the model predator for 3 yr. We used the 3 species to explore a range of biologically relevant scenarios rather than simulations of specific populations.

Analysis

Our primary goal was to determine how the form of predation (size-independent vs. gape limited, generalist vs. specialist) alters post-harvest recovery. We first ran the simulations without harvest ($h = 0$) until equilibrium, then implemented harvest ($h > 0$) and ran until the harvested equilibrium, and finally we stopped harvest ($h = 0$) and compared demographic transients in the recovery period as well as at equilibrium (analogous to White et al. 2013). We defined recovery time as the number of time-steps before a particular metric was within pre-harvest equilibrium $\pm 2.5\%$; in preliminary runs, we found that the relative trends that are the focus here are analogous for a recovery threshold of 1%. Our 2 metrics for population recovery are harvestable biomass (biomass of $l > l_{\min H}$ individuals) and mean post-recruit length (mean length for all $l > l_0$ individuals). Additionally, we compared pre-harvest equilibrium size distributions (excluding l_0 individuals) with 5 yr, 10 yr, 20 yr, and equilibrium post-harvest distributions for each species and predation type. By comparing size-independent mortality with the generalist predator, we explored the importance of size dependence when assuming constant mortality. Comparison between the generalist and obligate predators indicates

the effect of the dynamical nature of the predator on prey recovery. To make a clear distinction with the generalist predator, we assumed a strong obligate predator with a fast numerical response. Because our focus is on the form of predation, we excluded other sources of size structure variability such as stochastic recruitment, environmental drivers, and spatial dynamics. We used Python 2.7.2 (van Rossum 2012) for all simulations and analysis. For length integrations (Eqs. 1, 2, & 11), we used Simpson's integration with a 1 mm length step.

RESULTS

There was little difference in recovery patterns between the size-independent mortality model and the size-dependent generalist predation model (Fig. 2). However, recovery under obligate predation differed in the potential for fluctuations, at first overshooting the no-harvest equilibrium biomass as predatory recovery lagged, then declining to return to that biomass as the obligate predator recovered (Fig. 2). Therefore, the total time to reach the no-harvest equilibrium was greater in the obligate predator scenarios: for example, cod biomass took longer to reach post-harvest equilibrium under the equal-with-harvest obligate predator (35%, Table 2, Fig. 2b) and substantially longer under the equal-without-harvest obligate predator (300%, Table 2, Fig. 2b). The difference in the 2 obligate types' recovery is due to a difference in the level of predator depletion: for the equal-without-harvest obligate model, predator abundance during harvest was at near-extinction levels (Fig. 2c). Due to the lower impact of harvest on haddock and whiting populations, the predator maintained a higher abundance in both scenarios and the difference in recovery time between the size-independent model and the equal-with-harvest and equal-without-harvest obligate predation models was smaller (0%/78% for haddock and 17%/33% for whiting, respectively; Fig. 2e,f, Table 2).

The recovery for mean size was also similar for the generalist predation and base size-independent models (0–17%; Table 2), although the equilibrium mean size is slightly higher post-harvest in the generalist model due to a decrease in abundance of $l < l_{\max P}$ individuals (Fig. 3a). Under equal-with-harvest obligate predation for cod, mean size during recovery increased above equilibrium as the recovering predators overshoot their equilibrium and lowered abundance of smaller prey individuals, then stabilized in a damped oscillation (peak of 23% above

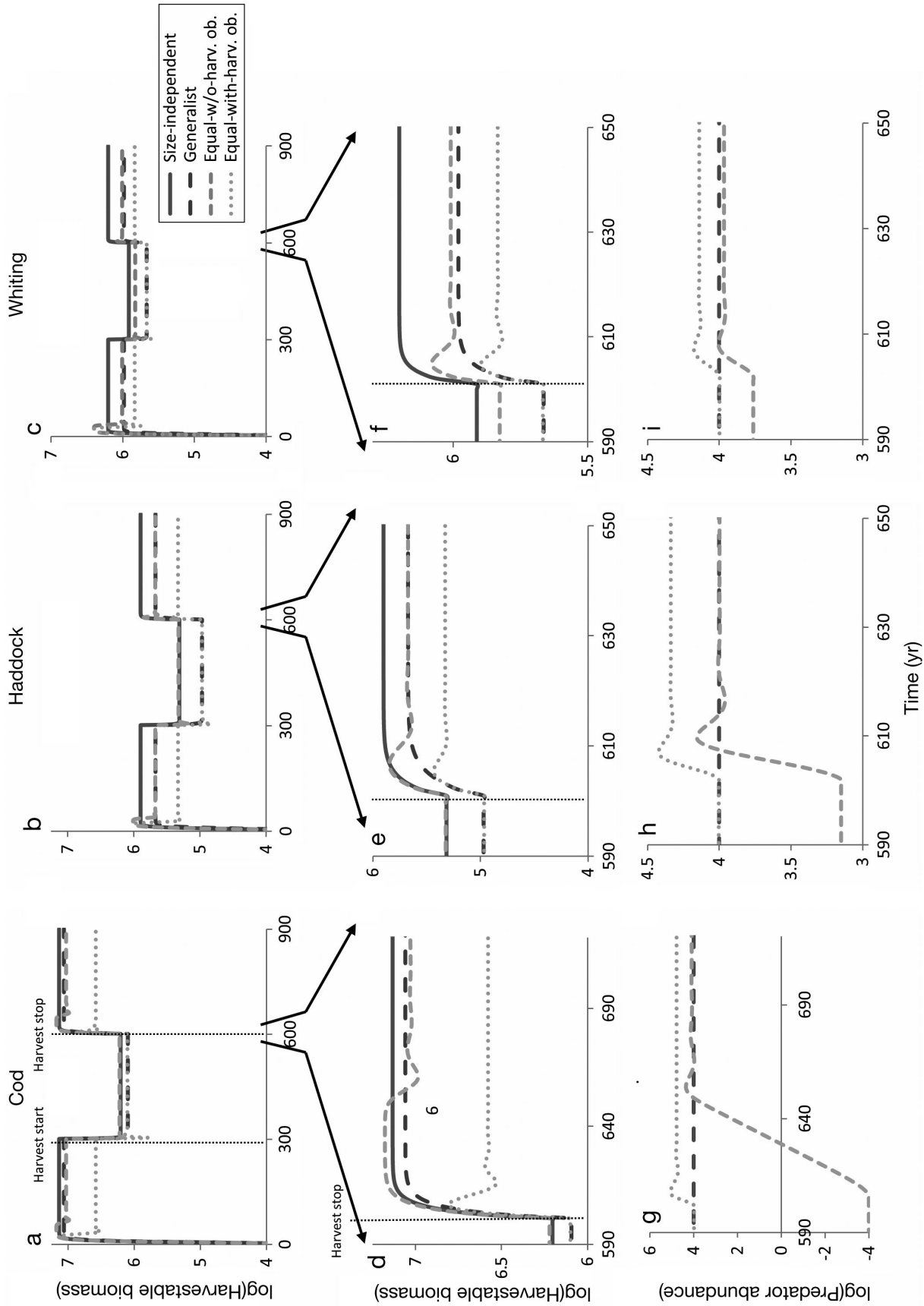


Fig. 2. Harvestable biomass trajectories and predator abundance for cod, haddock, and whiting models. Horizontal axis indicates time in years, with harvest commencing at $t = 300$ and ceasing at $t = 600$. (a–c) Vertical axis shows harvestable biomass in $\log_{10}(t)$. Solid lines indicate size-independent predation, dashed lines the gape-limited generalist predator, short-dashed lines the equal-without-harvest (gape-limited) obligate (ob.) predator, and dotted lines the equal-with-harvest obligate predator. (d–f) Biomass recovery in the post-harvest period. Note shift in x-axis scale. (g–i) Log-abundance of predator. Predator abundance under size-independent predation is identical to that under the generalist predator, and is omitted for clarity

Table 2. Recovery times (yr). Recovery is defined as years to a return to within post-harvest equilibrium $\pm 2.5\%$. For the obligate model, population oscillations must remain within this range for all subsequent years. Numbers in parentheses indicate years when oscillations first begin

Species	Metric	Size-independent	Generalist	Obligate	
				Equal without harvest	Equal with harvest
Cod	Biomass	14	15	56 (37)	19 (8)
	Mean length	11	12	65 (55)	21 (11)
Haddock	Biomass	9	12	16 (8)	9 (6)
	Mean length	6	8	13 (11)	10 (9)
Whiting	Biomass	6	7	8 (6)	7 (6)
	Mean length	3	3	3	3

equilibrium; Fig. 3a). The dynamics for the equal-without-harvest obligate predator were similar but with lower magnitude oscillations (up to 7%) that began after a 50 yr delay caused by the slower recovery of the predator (Fig. 3a). Recovery under equal-with-harvest obligate predation took almost twice as long as recovery under the generalist predator (91% longer; Table 2), and full recovery under the equal-without-harvest obligate predator was even

more delayed for cod (491% longer; Table 2). Similar to biomass and mean size recovery, recovery of size structure for cod under the equal-with-harvest obligate predation took twice as long as that under generalist predation (Fig. 3b,d). The decrease in smaller individuals from the rapidly increasing predator temporarily inverted the size distribution over the first 20 yr (Fig. 3a,d). Recovery under equal-without-harvest obligate predation was initially as fast as under generalist predation, but the eventual

recovery of the predator caused a delayed fluctuation (after 55 yr; Fig. 3c). As with biomass, mean size recovery in haddock was slower under obligate predation, but the difference was less than that for cod (~25–65% slower; Table 2, Fig. 4). There was no difference in size structure recovery times for whiting (Table 2, Fig. 5).

The slowest-growing species (cod) experienced the highest depletion and slowest recovery; followed by

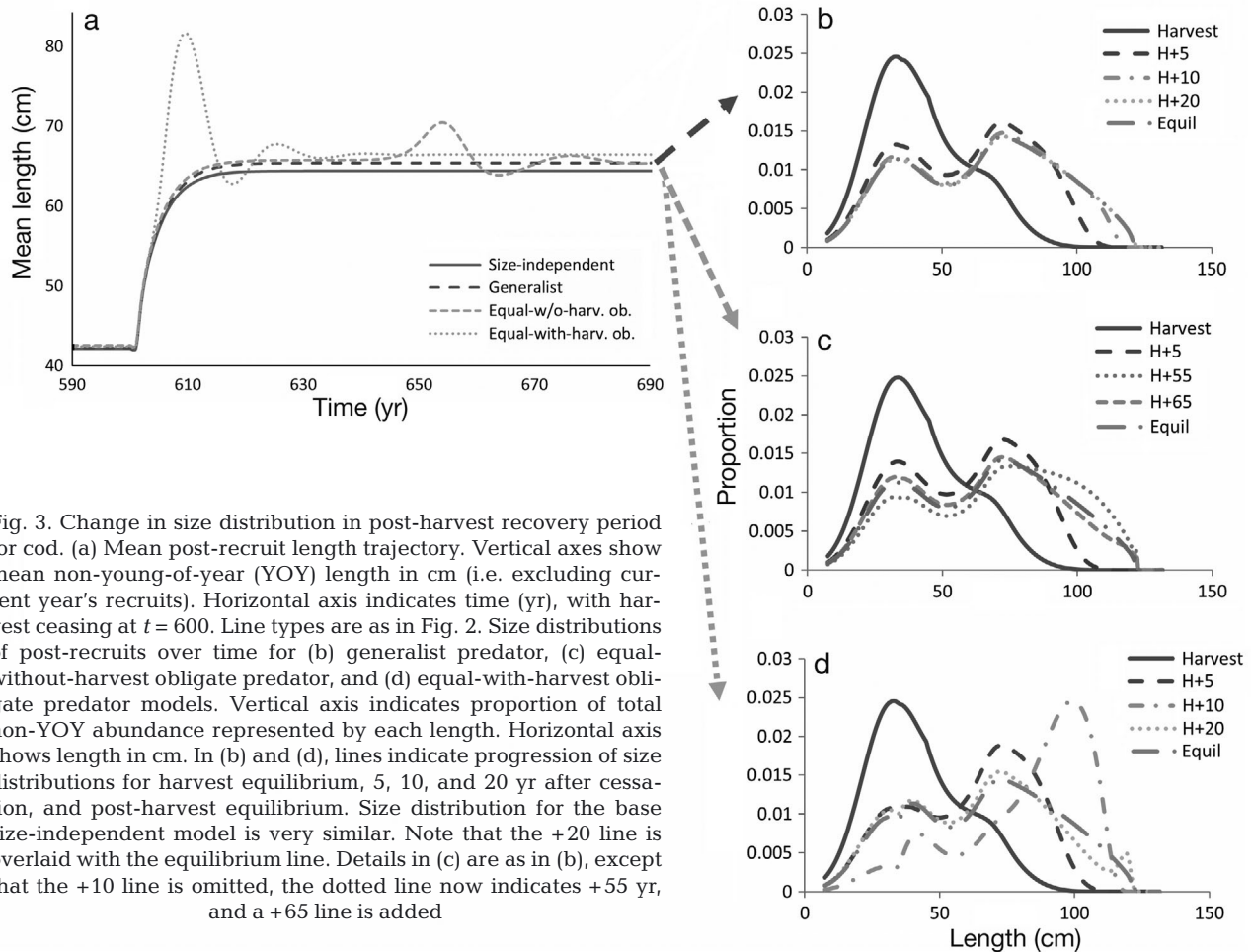


Fig. 3. Change in size distribution in post-harvest recovery period for cod. (a) Mean post-recruit length trajectory. Vertical axes show mean non-young-of-year (YOY) length in cm (i.e. excluding current year's recruits). Horizontal axis indicates time (yr), with harvest ceasing at $t = 600$. Line types are as in Fig. 2. Size distributions of post-recruits over time for (b) generalist predator, (c) equal-without-harvest obligate predator, and (d) equal-with-harvest obligate predator models. Vertical axis indicates proportion of total non-YOY abundance represented by each length. Horizontal axis shows length in cm. In (b) and (d), lines indicate progression of size distributions for harvest equilibrium, 5, 10, and 20 yr after cessation, and post-harvest equilibrium. Size distribution for the base size-independent model is very similar. Note that the +20 line is overlaid with the equilibrium line. Details in (c) are as in (b), except that the +10 line is omitted, the dotted line now indicates +55 yr, and a +65 line is added

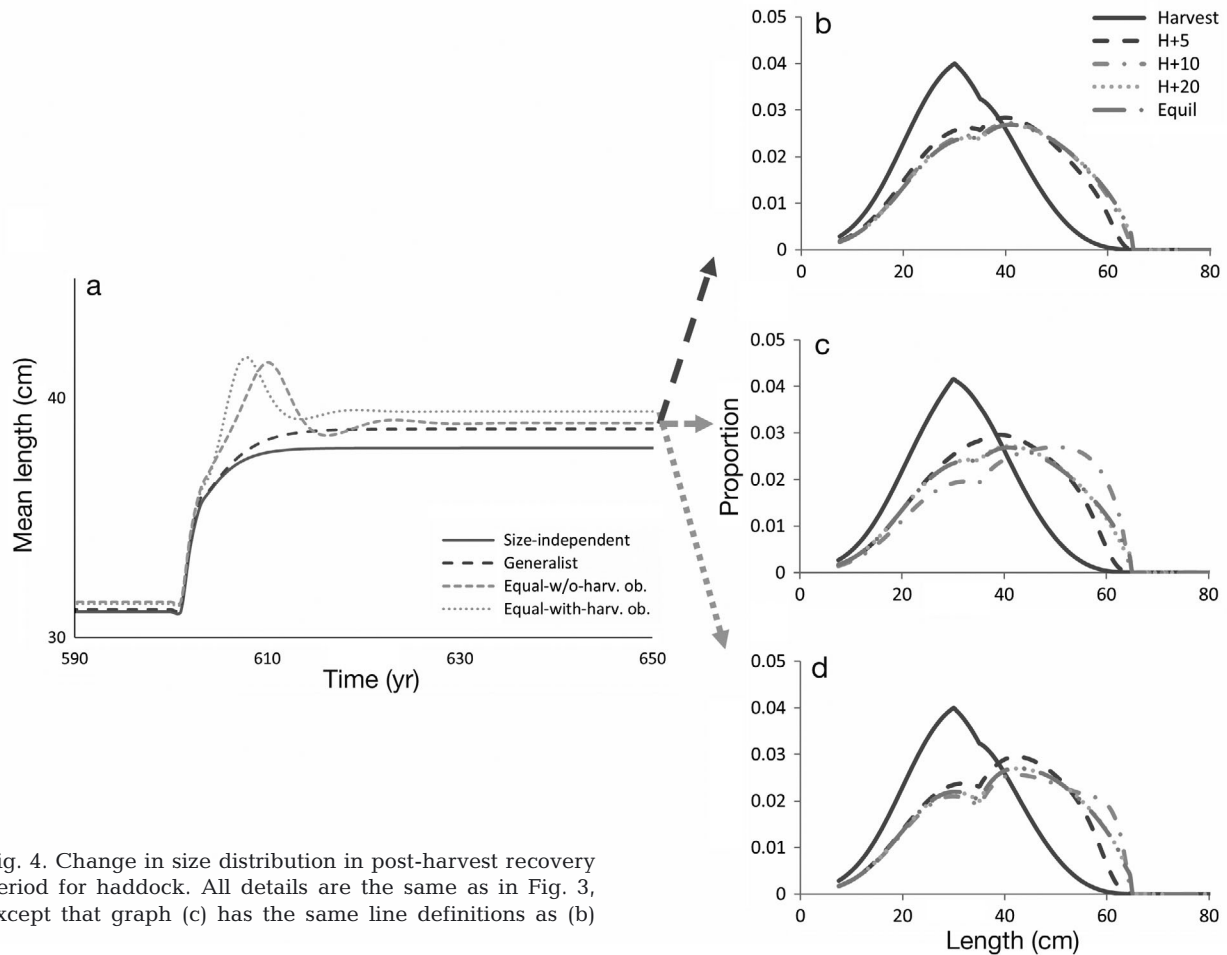


Fig. 4. Change in size distribution in post-harvest recovery period for haddock. All details are the same as in Fig. 3, except that graph (c) has the same line definitions as (b)

haddock and then the fastest-growing species, whiting, with a diminishing difference between recovery time for generalist and obligate predation as recovery rate increased. This pattern held for both harvestable biomass (Fig. 2a–c) and mean size (Figs. 4a & 5a), and was reflected in size distribution recovery as well (Figs. 4b–d & 5b–d). For haddock and whiting, there was little difference in recovery times between the equal-before- and equal-with-harvest obligate models (Fig. 2a–c). Qualitative trends were consistent across key predation and harvest parameter values, with obligate model recovery time most strongly affected by maximum prey size and predation rate (Supplement 1).

DISCUSSION

In our model, the dynamical linkage between a predator and prey mattered more to delayed recovery in a marine reserve or fishery closure than gape size limitation: a dynamically linked, obligate predator can drive fluctuations that increase time to equi-

librium by 50% or more compared to a generalist, non-dynamical predator (where we measure recovery in terms of biomass, mean size, and size distribution; Fig. 2b). In contrast, the effect of excluding versus including gape limitation in a generalist predator had a negligible effect on recovery time (Fig. 2b, Table 2). Because of this secondary role of gape limitation, the faster population growth rates of the smaller-bodied species modeled here outweighed the effect of greater susceptibility to gape-limited predation to drive faster recovery rates and produce less of an impact of predation type (Table 2). However, the high sensitivity of recovery under the obligate predator to gape size (Supplement 1, Fig. S3) suggests the potential for an interaction between gape limitation and predator specialization. These findings build on the results from prior non-size-structured species interaction models which found that increases in a dynamically linked predator could delay post-harvest increase in a fully vulnerable prey species (e.g. Micheli et al. 2004b, Baskett 2007, Kellner et al. 2010) by quantifying the relative roles of the dynamical link to and gape limitation of the predator.

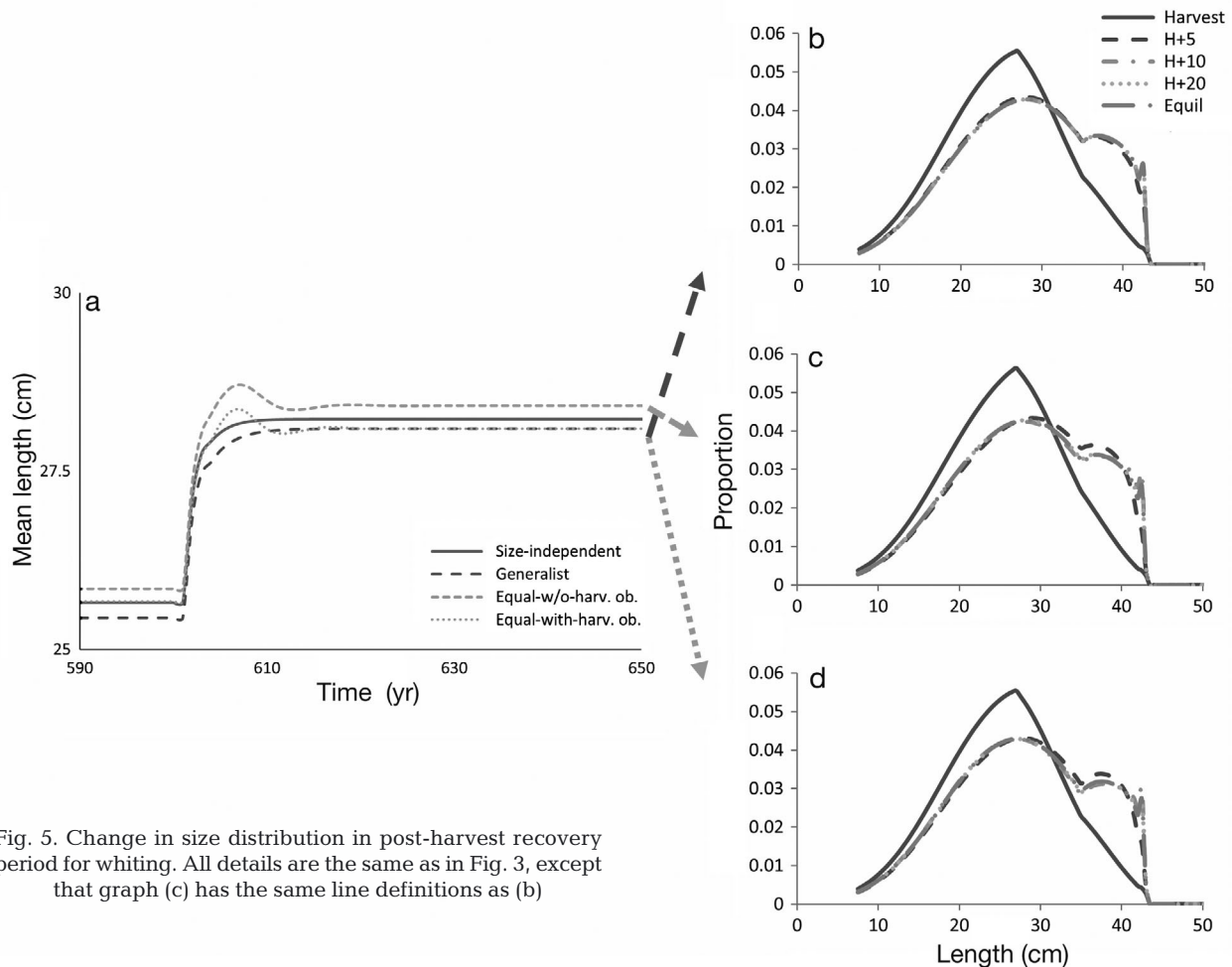


Fig. 5. Change in size distribution in post-harvest recovery period for whiting. All details are the same as in Fig. 3, except that graph (c) has the same line definitions as (b)

Similar dynamics governed the recovery of size structure, with the largest fluctuations seen for cod under equal-with-harvest obligate predation. The high initial predator population allowed predators and prey to increase in concert during the initial recovery period, causing the predator population to overshoot its equilibrium and severely deplete smaller cod. Because the large prey size refuge maintained a high abundance of large adults, production of new recruits stayed high even as predator abundance spiked, leading to a greater overshoot than any other scenario (Fig. 3a,d). In contrast, under equal-without-harvest obligate predation, the delay in predator recovery was long enough that the cod population had already stabilized and predator overshoot produced smaller fluctuations (Fig. 3a,c). This suggests that predator-induced fluctuations will be strongest when (1) a numerically responsive predator is present in high enough abundance to immediately respond to increased prey recruitment, and (2) larger prey individuals can temporarily maintain high recruitment despite heavy predation on juveniles, allow-

ing the population to overshoot its long-term equilibrium. Because haddock and whiting have shorter lifespans and less of a size refuge from predation, the fluctuations in mean size were of lower magnitude and produced a less pronounced shift in size distribution or almost none at all (Figs. 4 & 5). Because both the fluctuations in mean size and the temporary pulse of large individuals are created by the overshoot of predator abundance in response to the recovering prey, they do not occur for the non-dynamical predator scenarios for any of the example species. However, recovery of mean size was slightly faster for the size-independent model than for the generalist gape-limited predator for cod and haddock (1–2 yr; Table 2), suggesting that size-dependent predation may partially hinder recovery.

The fluctuations in the obligate-predator cases due to the delayed predator recovery indicate the potential for transient declines to be a natural component of post-harvest recovery. Declines after fishery closure, transient or otherwise, might arise from a variety of dynamics, include age-structure-dependent

processes given a delay to maturity (White et al. 2013), stochastic recruitment (White & Rogers-Bennett 2010, White et al. 2013), and diseases with density-dependent spread (McCallum et al. 2005, Wootton et al. 2012) as well as predation (Micheli et al. 2004b) and short-term trophic cascades (Frank et al. 2011). Our results suggest that predation-driven transient declines are most likely for specialist predators due to the tight dynamic coupling with prey, predators with collapsed populations due to the greater lag in predation effect, and prey with slower life histories due to the resulting lag time in population dynamics.

Empirical context and model assumptions

Delayed prey recovery and fluctuations in size structure due to predator recovery have occurred in cases of marine reserve establishment (Russ & Alcala 2003, Guidetti 2006, Babcock et al. 2010) and fisheries closures (Pinnegar et al. 2000, McClanahan & Humphries 2012). Babcock et al. (2010) found that indirect effects on lower trophic levels following reserve establishment typically took 36% longer to manifest than direct effects on the exploited species, a delay similar to those seen for the equal-with-harvest obligate predator in our results (Table 2). They further found that predator recovery often decreased prey abundance within reserves and, in the case of the Maria Island reserve (Tasmania), recovery of an exploited species (abalone) was prevented by the recovery of another exploited species (lobster). The decadal-scale recovery under strong predator-prey interactions observed here has also occurred in limpet-urchin communities (Shears & Babcock 2003, Babcock et al. 2010). Mean body size continued to increase after 42 yr of fishery closure in Kenya, primarily linearly with some leveling after 30 yr, suggesting that recovery of a community-level metric may be slower than that of an individual species (McClanahan & Humphries 2012). An unexpected decrease in mean trophic level suggests that predatory fish were not heavily impacted by the fishery, although there is no indication of fluctuations in mean size. Russ & Alcala (2003) found a brief decrease in modal length after 12 yr of no fishing in the Apo reserve in the Philippines, similar to our results for cod and haddock, but as the fish involved were large predatory reef fish, it is unclear if the decrease was due to species interactions or environmental variation.

As with any model, our model includes a number of simplifying assumptions. Most importantly, our re-

sults for the obligate predator are based on the assumption of a strong numerical response between the predator and prey. Completely obligate predators are rare in nature, particularly in marine systems with diffuse interactions and complex food webs (Polis & Strong 1996), and predators in reality are likely to fall in between the obligate/generalist extremes. Predators with multiple prey species or slow population dynamics would be expected to affect the prey species more like generalists, with less predation delay and less pronounced recovery fluctuations (see Supplement 3, www.int-res.com/articles/suppl/m564p127_supp.pdf for an example of the effects of diminished predation strength). Although prey regulation in our model depends on numerical response, a similar effect can occur through changes in predator behavior (Bax 1998, Hunsicker et al. 2011). Specifically, positive prey switching (Murdoch 1969, Murdoch et al. 1975, Chesson 1984) and predator aggregation (Anderson 2001, White et al. 2010) in response to increased prey abundance can regulate prey by mimicking a numerical response. Strong predation pressure can also be exerted by smaller, faster-growing species via egg or juvenile predation (Essington 2004, Speirs et al. 2010), and such species could more realistically change abundance on the same time scale as the larger prey. Although we chose the classical obligate predation model to explore the effects of predator dynamics in the scenario with the strongest numerical response, the results are relevant to any system in which predator recovery is at least partially dependent on that of the target prey species. A predator recovering concurrently from harvest or by-catch mortality with no dependence on the prey population would produce a similar delayed drop in prey abundance, but without the fluctuations caused by predator overshoot and decline.

Our model focuses on pairwise interactions that, in reality, occur within complex food webs with multiple species at each trophic level and multi-level interactions. More realistic models of such complex food web simulations indicate how post-harvest recovery depends on a network of direct and indirect interactions. Blanchard et al. (2014), for example, found that recovery of cod in their multi-species size-spectrum model was associated with a decrease in haddock and whiting (though not all smaller species). In their model, cod recovered in approximately 20 yr, similar to the timing in our single-species model, with the same overshoot-then-decline fluctuation. This pattern is mirrored in the large fish indicator metric and, to a lesser extent, the maximum individual weight for the community. Although Blan-

chard et al. (2014) did not give species-specific size results, the change in community species composition and size structure suggests recovering predator 'overshoot' dynamics similar to those seen in our results. Collie et al. (2013) simulated recovery in 2 similar communities, Georges Bank and the North Sea, using a 21-species length-based food web model and found that Georges Bank recovered (in 10–15 yr) and the North Sea did not, despite similar initial structure. For Georges Bank, metrics for biomass, mean mass, and size diversity show slight fluctuations, overshooting at 5 yr then decreasing to equilibrium, but it is unclear if the cause is increased predation. Collie et al. (2013) predicted that smaller species recovered quickly in both systems due to predation release, but the recovery of large, slow-growing predators such as cod took place on a longer time-scale due to heavy depletion, particularly in the North Sea. We do not consider direct harvest of the predator in our model, which would further delay predator recovery similarly to that of our equal-without-harvest obligate predator (Fig. 2c) and increase the possibility of prey declines (Micheli et al. 2004b). Finally, Fung et al. (2013) found that in a 1000-species model, recovery time to 90% equilibrium for large species ranged from 25 to 62 yr, depending on prior harvest intensity, with an initial overshoot and fluctuations across 50 to 150 yr. Two key mechanisms delaying recovery of large species in their model involved size-dependent species interactions. The first was increased competition between juvenile predators and the abundant prey species which had benefited from predation release during the harvest period. The second was that, as predatory species recovered, the smaller, faster-growing species consumed juveniles of larger species, adding further fluctuations to community size structure recovery. An analogous effect can occur when prey can consume juvenile predators, as has been demonstrated for herring and cod (Walters & Kitchell 2001, Fauchald 2010, Minto & Worm 2012). In these cases, recovery of a prey species could delay recovery of its own predator, potentially enhancing the 'delayed predation' found here.

The Nicholson-Bailey predation model used here also assumes random search by a homogeneously distributed predator. We tested this assumption in Supplement 3 using a negative binomial model with variable search effectiveness, and found that, as the variance in predator search rate increases, the prey recovery trajectory shifts from that of the Nicholson-Bailey specialist predator to that of the generalist predator. An alternative approach to better under-

stand the dependence of the recovery delay on a pure numerical response worth future investigation is a pseudo-obligate model of predation that combines dynamical and generalist aspects, such as that used by Kellner et al. (2010). Incorporating size structure into the predator as well would create more realistic time-lagged predator dynamics, allowing us to explore the potential for transient population declines as seen by Micheli et al. (2004b) and White et al. (2013) in species with slower life history patterns. We chose to use the simplest possible predator-selectivity model because of a lack of specific predator-selectivity data and preliminary results suggesting little effect on recovery transients. However, increasing the realism of the model by adding more complex predator selectivity, such as a dome-shaped size-preference function, would allow us to better explore alternate impacts on size structure. For example, in a model by Harvey et al. (2008), closing a hake fishery increased rockfish recovery time, despite eliminating rockfish bycatch, but the delay depended on the degree of prey selectivity. For canary rockfish, a late-maturing species with high predation from hake, predicted recovery time doubled from 35 to 70 yr, whereas for darkblotched rockfish, a species with low predation mortality and highly stochastic recruitment, predicted recovery time only increased from 22 to 25 yr.

We did not include bottom-up forcing through environmental drivers, another factor which Collie et al. (2013) suggested may accelerate prey recovery and decouple their dynamics from those of higher trophic-level species. Incorporating a variable environment is likely to increase recruitment variability and slow growth for severely depleted stocks (e.g. McGarvey 1994, Brander 2005), though a well-timed series of consecutive years with favorable conditions could speed recovery. If it occurs on a time scale that resonates with natural population dynamics, environmental forcing can cause cycling across age groups or chaotic behavior and can destabilize a recovering population (Higgins et al. 1997, Botsford et al. 2011). Whether such resonance and amplified population variability with environmental variability occurs depends critically on the age-dependent life history (growth, survival, reproduction) of the population, where changes in survival can have a particularly strong effect on the variability in population size (Worden et al. 2010). The specialist predator modeled here represents a case of changing age-dependent survival such that both a specialist predator and its gape size limitation are likely to have a significant effect on a population's relative sensitivity to different time scales of environmental variability.

We assumed no spatial dynamics and a static environment with the entire population experiencing the same harvest scenario. Marine reserves, by their nature, are spatial, and optimal implementation must account for connectivity between protected and harvested regions (Tuck & Possingham 2000, Botsford et al. 2001, 2009). Micheli et al. (2004b) considered predator–prey systems in newly established marine reserves spatially linked to harvested regions and found potential for initial, transient population declines in both predator and prey abundance after local harvest stops. These initial declines arose from recruitment time-lags due to separate predator life stages as well as differences in predator and prey dispersal ability, and cannot develop from our non-spatial unstructured predator dynamics. On one hand, including spatial dynamics could incur a reproductive loss that would further slow recovery within the protected area, although strong outside recruitment could smooth out transients and increase recovery (White et al. 2013). On the other hand, including spatial dynamics could accelerate recovery if external harvest or top-down control of the predator (e.g. as in Micheli et al. 2004b and Kellner et al. 2010) dampens the ability of the obligate predator to respond numerically to increasing prey abundance. Therefore, determining the overall effect of connectivity between protected and harvested areas would require quantifying the balance of the effect on reproductive dynamics and on the strength of the predator–prey dynamical linkage. In particular, the fluctuations in our model occur as the population nears carrying capacity. Such high abundance levels might be reached after establishment of a no-take marine reserve, but if the closure is a temporary measure to allow stock recovery, the fishery would likely be reopened well before 100% recovery. We would thus expect these predator-driven fluctuations to be less evident in, for example, a fishery shifting from heavy exploitation to moderate but sustainable catch levels.

Size-selective fisheries can cause rapid evolutionary change as well as alter species interactions (Heino & Godø 2002). Fisheries exert strong selective effects on many life history traits, including growth rate and size at maturity (Jennings et al. 1999, Stokes & Law 2000, Ernande et al. 2004, Sharpe & Hendry 2009), and evolutionary effects can influence management decisions (Hutchings 2009), including marine reserve design (Baskett et al. 2005). Rapid evolution affects species interactions as well (Jørgensen et al. 2007), and can combine with the selective effects of predation for higher age-at-maturity (Abrams &

Rowe 1996) to increase target species depletion (e.g. Gardmark et al. 2003). By holding both fecundity parameters and size-at-maturity constant, we did not account for trait change which can hinder recovery in the post-harvest period. Walsh et al. (2006) found that the high selection pressure from size-selective harvest favored traits (i.e. small size, slow growth) which were maladaptive in the post-harvest period, and this diminished genetic variation hindered recovery.

Management implications

Overall, our results suggest that incorporating predation into predictions for adaptive management is more important for tightly linked, specialist predator–prey interactions than for prey with generalist predators, regardless of gape limitation. When managing a reserve with a strong predator–prey interaction, particular consideration to monitoring both predator abundance and prey size distribution would help detect whether a dynamical predator is affecting prey recovery. An obligate predator will increase concurrently with its prey, causing prey biomass and size distribution to fluctuate (Fig. 3d). Incorporating the effects of changes in predation and size distribution into monitoring predictions alters the trajectory and time scale of recovery for other commonly used metrics such as population-level biomass, and may consequently be an important aspect of adaptive management.

Acknowledgements. We thank Marcel Holyoak, Alan Hastings, and 3 anonymous reviewers for valuable suggestions and comments on previous versions of this manuscript. Funding for this project was provided by a Sea Grant Population and Ecosystem Dynamics Fellowship from the National Oceanic and Atmospheric Administration, the California Sea Grant College Program grant no. R/FISH-211, and the UC Davis Hellman Fellowship Program.

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