

A length-based multispecies model for evaluating community responses to fishing

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Abstract: Quantitative ecosystem indicators are needed to fulfill the mandate for ecosystem-based fisheries management. A variety of community metrics could potentially be used, but before reference levels for such indices can be established the sensitivity of candidate indices to fishing and other disturbances must be determined. One approach for obtaining such information is to test candidate indicators with models that mimic real ecosystems and can be manipulated experimentally. Here we construct a size-based multispecies model of a community of fish species that interact by predation. The model was parameterized for 21 fish species to obtain a predation-regulated community. Following an analysis of the sensitivity of the model to parameter uncertainty, we tested the sensitivity of community-level indicators to increasing levels of fishing mortality (F). Abundance and biomass spectra were sensitive to fishing mortality, with the slope decreasing with increasing F . Species diversity size spectra were also very sensitive to F , with diversity in the largest size classes declining rapidly. In contrast, k -dominance curves were less sensitive to fishing pressure. Importantly, however, although most community-level metrics showed clear trends in response to fishing, single-species declines in spawning stock biomass were the most sensitive indicators of fishing effects.

Résumé : Des indicateurs écosystémiques quantitatifs sont nécessaires afin de remplir le mandat de la gestion des pêches basée sur les écosystèmes. On peut utiliser une variété de métriques de la communauté, mais avant que les niveaux de référence de ces indices puissent être établis, il faut déterminer la sensibilité des indices à la pêche et aux autres perturbations. Une façon d'obtenir cette information est de tester les indicateurs considérés avec des modèles qui reproduisent de vrais écosystèmes et qui peuvent être manipulés expérimentalement. Nous construisons ici un modèle multispécifique structuré d'après la taille d'une communauté de poissons qui interagissent par prédation. Nous avons déterminé les paramètres pour 21 espèces de poissons de manière à obtenir une communauté contrôlée par la prédation. Après une analyse de sensibilité du modèle à l'incertitudes des paramètres, nous avons évalué la sensibilité des indicateurs de type communautaire à des niveaux croissants de mortalité due à la pêche (F). Les spectres d'abondance et de biomasse sont sensibles à la mortalité due à la pêche et leur pente diminue en fonction inverse de F . Les spectres de diversité spécifique en fonction de la taille sont aussi très sensibles à F et la diversité dans les classes de tailles plus grandes décline rapidement. En revanche, les courbes de dominance k sont moins sensibles à la pression de pêche. De façon importante, cependant, alors que la plupart des métriques de type communautaire montrent des tendances claires en réaction à la pêche, les diminutions de la biomasse du stock des reproducteurs d'espèces individuelles sont les indicateurs les plus sensibles aux effets de la pêche.

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Introduction

There is increasing recognition of the need for ecosystem considerations in fisheries management (Food and Agricultural Organisation of the United Nations 2001), but progress with defining and setting management objectives has been

slow. Reference points provide measurable criteria for determining whether quantitative management objectives are met. For example, to ensure the long-term sustainability of a target stock, a short-term management goal may be to minimize the risk that it will fall below some specified biomass level (a limit reference point), while a simultaneous longer-

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term goal might be the rebuilding of the stock to a target reference point (Sissenwine and Shepherd 1987). The benefits of using reference points for managing target stocks is now widely recognized and some efforts have been made to use the same approach for some nontarget species of conservation interest (Hall and Mainprize 2004).

A potentially useful extension of the above approach would be the development of quantitative management objectives using reference point metrics, which capture valued aspects of whole communities or ecosystems. To date, however, although there have been efforts to understand the sensitivity to trophic interactions of single-species metrics for which reference points might be set (Collie and Gislason 2001), multispecies or ecosystem level metrics are still being proposed and evaluated (Rochet and Trenkel 2003).

Although the ideal properties of metrics for which reference points might be selected are well known, the development of a sound body of theory that would allow us to understand the mechanisms controlling the sensitivity and behaviour of candidate community- or ecosystem-level reference points is required (Rochet and Trenkel 2003). Such understanding is the first step towards identifying appropriate metrics because underpinning theory would allow rigorous evaluation of the alternatives. As it did with the development of single-species reference points, we expect the construction of defensible mathematical models to provide a basis for development and testing of multispecies and ecosystem metrics. Using a modelling approach we are already beginning to appreciate, for example, how trophic interactions might determine community size distributions and how fishing might modify them (Rice and Gislason 1996; Duplisea and Bravington 1999; Bianchi et al. 2000). Recent analyses with size-structured models indicate, for example, that the slope of size spectra becomes steeper if the predator-prey size ratio is smaller (predators can eat larger prey) and (or) predator growth efficiency is lower (Benoit and Rochet 2004; Shin and Cury 2004). Increased fishing mortality also results in a steeper slope and downward curvature at the largest sizes.

With the exception of biomass size distributions, however, approaches remain to a large extent phenomenological — we describe changes (or lack of them) in community attributes such as species diversity, but the underlying causes and consequences of these changes are largely unknown. At this stage, therefore, most metrics of community structure do not have practical value for assessing the significance of fisheries effects and deciding on management actions.

As a general rule, species that have larger body size, mature later, and have lower rates of potential population increase experience larger population declines in response to fishing, even when differences in fishing mortality rate are accounted for (Jennings et al. 1999). Such differences imply that different life-history characteristics may explain underlying responses to fishing at both the individual species level and the community level (Jennings et al. 1999). If we are to fully develop an ecosystem level theory of fishing, the life-history attributes of component species seem most likely to be at its core. In an effort to help further develop the necessary theory we have developed a size-structured multispecies model of a fish community with a realistic distribution of life-history attributes. The purpose of this paper is to de-

scribe that model, examine its sensitivity to key model parameters, and present some preliminary results examining the utility of various community-level metrics of fishing effects.

Model assumptions and equations

Our approach differs from that reported from most other size-based models in that it maintains both the identity of the species in the system and the size structure of the individual populations. To maintain a level of realism and to help ensure internal consistency, we have chosen to develop a model that is loosely based on a single real fish community and have selected the Georges Bank fish community for this purpose because of the large body of information available on the fish species and their dynamics in this region. Despite this specificity, however, our model should be considered as strategic in focus and is directed explicitly at understanding the dynamics of the emergent properties of fish communities rather than providing quantitative predictions for species abundances in any particular system. This approach builds on the results obtained with entirely abstract size-structured models (Benoit and Rochet 2004; Shin and Cury 2004), while ensuring that the model can be parameterized for a real fish community. Although the model has been parameterized for Georges Bank in an effort to ground our parameterization in a defensible manner, we would not necessarily expect the results to mimic either the relative abundances of species or the temporal trends that have been observed there.

A food web matrix defines the feeding relationships between the 21 species represented in the model system (Table 1). Building on previous work by Murawski and Idoine (1992) and Duplisea and Bravington (1999), the model follows length cohorts of individuals from each species throughout their life. The baseline or standard model includes fifteen 10 cm length classes, though the model is programmed to allow for variable numbers and widths of size classes. All key parameters and state variables are listed in Table 2. For convenience, we have named the model LeMANS (length-based multispecies analysis by numerical simulation). In the following sections we begin by describing how each of the key biological processes has been modelled before going on to describe the sequence in which they were implemented.

Growth

We assume that fish grow continuously throughout their lives according to the von Bertalanffy growth equation:

$$(1) \quad L_{t,i} = L_{\infty,i} (1 - e^{-k_i(t-t_0)})$$

where both $L_{\infty,i}$, the asymptotic length, and k_i , the instantaneous growth rate, are estimated empirically for each species i (Penttilä et al. 1989).

For convenience, we represent growth in the model as a deterministic process, parameterised from field data, which is not affected by the abundance of prey resources. Thus, there is no feedback between variations in predation mortality (and hence predator food intake), resulting from time-varying prey abundances, and predator growth. In addition, the formulation does not account for the increased variance

Table 1. The food web matrix for the 21 species represented in the model.

Prey species	Scientific name	Predator species																				
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1. Sand lance	<i>Ammodytes americanus</i>	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
2. Longhorn sculpin	<i>Myoxocephalus octodecemspinosus</i>	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0
3. Atlantic herring	<i>Clupea harengus</i>	0	1	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	0	1
4. Witch flounder	<i>Glyptocephalus cynoglossus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
5. Windowpane	<i>Scophthalmus aquosus</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
6. Winter flounder	<i>Pseudopleurinctes americanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
7. Atlantic mackerel	<i>Scomber scombrus</i>	0	0	0	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	0	1
8. Fourspot flounder	<i>Paralichthys oblongus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
9. Yellowtail flounder	<i>Limanda ferruginae</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
10. Little skate	<i>Leucoraja erinacea</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
11. Red hake	<i>Urophycis chuss</i>	0	0	0	0	1	0	0	0	0	1	1	0	1	1	1	0	1	1	0	1	1
12. Silver hake	<i>Merluccius bilinearis</i>	0	0	0	0	1	0	0	1	0	1	1	1	1	1	1	0	1	1	1	1	1
13. Sea raven	<i>Hemitripterus americanus</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0	0	0
14. Haddock	<i>Melanogrammus aeglefinus</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	0	0
15. Spiny dogfish	<i>Squalus acanthias</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
16. Pollock	<i>Pollachius virens</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	0	0	1
17. Winter skate	<i>Raja ocellata</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
18. Goosefish	<i>Lophius americanus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
19. White hake	<i>Urophycis tenuis</i>	0	0	0	0	1	0	0	0	0	1	1	0	1	1	1	0	1	1	1	1	1
20. Summer flounder	<i>Paralichthys dentatus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0
21. Atlantic cod	<i>Gadus morhua</i>	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	1	0	0	1
No. of prey species		0	3	1	1	5	3	1	2	1	11	6	4	7	8	19	4	11	20	5	4	8
No. of predator species		20	5	12	3	3	2	9	2	2	2	10	13	3	6	2	7	1	1	11	3	7

Note: In the matrix, which predators eat which prey is denoted by the number 1. The matrix is derived from food habits data in Link (2002).

Table 2. State variables and key model parameters.

Symbol	Description	Units	
State variables			
$N_{i,j}$	Number of individuals of species i in size class j	individuals	
S_i	Spawning stock biomass of species i	tonnes	
R_i	The number of recruits of species i in a given year	individuals	
t	Time	t	
Parameters			
a_i	*	The intercept parameter of the length–weight relationship for species i	—
b_i	*	The slope parameter of the length–weight relationship for species i	—
$L_{\infty,i}$	*	Asymptotic length parameter of the von Bertalanffy growth equation	cm
k_i	*	Growth parameter of the von Bertalanffy growth equation	t^{-1}
$\Phi_{i,j}$		The proportion of species i in size class j that move to the next size class in a single time step	—
α_i		Productivity parameter of the Ricker stock–recruitment equation for species i	—
β_i		Density dependence parameter of the Ricker stock–recruitment equation for species i	tonne ^{−1}
$S_{\max,i}$	*	The maximum observed spawning stock biomass of species i	tonnes
κ_i	*	Curvature parameter for the maturity ogive of species i	—
L_{M50}	*	The length at which 50% of species i are mature	cm
$\bar{\omega}_{i,j}$		The proportion of species i in size class j that are mature	—
$F_{i,j}$		Instantaneous rate of fishing mortality on species i in size class j	t^{-1}
ϕ_i	*	A binary variable indicating whether species i is fished	—
F_{\max}		The maximum annual fishing mortality rate for a fully recruited fish	t^{-1}
η		Steepness parameter for the fishing selectivity ogive	—
L_{F50}		The length at which 50% selection by the fishery occurs	cm
$M1_{i,j}$		Natural (nonmodelled) mortality for species i in size class j	t^{-1}
Ψ, υ		Parameters of the beta distribution for $M1$	—
$M2_{i,j}$		Predation mortality for species i in size class j	t^{-1}
$\tau_{m,i}$	*	The preference for prey species m by predator species i	—
$\zeta_{n,j}$		Size preference for prey of size n by predator of size j	—
$v_{i,j,m,n}$		The relative preference (suitability) for predator i of size j of prey m of size n	—
$I_{i,j}$		The ration (ingestion rate) that must be consumed by species i in size class j to account for modeled growth in a given time step	tonnes · t^{-1}
Ge_j		The growth efficiency (proportion of food consumed that is converted to body mass) of fish in size class j	—

Note: Asterisks denote species-specific input parameters, estimated from empirical data and input directly to the model.

in body size of a cohort as it gets older. The assumption of growth rates independent of feeding levels is consistent with the multispecies virtual population analysis (MSVPA) equations (Magnusson 1995) and with a lack of evidence for food-dependent growth rates in temperate fish communities (Collie 2001). However, this assumption may not hold for boreal communities, where there is some evidence of food-limited growth (Livingston and Tjelmeland 2000).

Because the von Bertalanffy equation provides a continuous description of growth but our model deals with discrete size classes, it is necessary to discretize the growth function. This discretization was achieved in the following way. For each species – length class combination, the time taken for an individual to grow from the lower to the upper limit of length class j was calculated from the following equation (Hilborn and Walters 1992, p. 428):

$$t_{i,j} = \frac{1}{k_i} \left[\log \left(1 - \frac{L_{\text{lower}}}{L_{\infty}} \right) - \log \left(1 - \frac{L_{\text{upper}}}{L_{\infty}} \right) \right]$$

This equation can be simplified to

$$(2) \quad t_{i,j} = \frac{1}{k_i} \log \left(\frac{L_{\infty} - L_{\text{lower}}}{L_{\infty} - L_{\text{upper}}} \right)$$

Assuming that individuals are evenly distributed across a size class, the proportion that leave the size class solely because of growth in any given time interval is then given by $\Phi_{i,j} = 1/t_{i,j}$. However, because time steps in the model are arbitrary and, for computational convenience, we wish to avoid the possibility that individuals could skip more than one size class in a given time step, we set the time step so that, in the absence of mortality, all individuals in the fastest-growing species – length class combination (t_{\min}) would always reach the next length class in a single time step by rescaling the times such that $\Phi_{i,j} = t_{\min}/t_{i,j}$.

Because growth in length is entirely deterministic with no feedback from the abundance of prey resources, this matrix of proportions had only to be calculated at the beginning of a model run. For the parameter values used here, this led to

Table 3. Species-specific parameters used in base model run, as defined in Table 2.

Species	Scientific name	<i>a</i>	<i>b</i>	<i>k</i>	<i>L</i> _∞	<i>L</i> _{M50}	κ	<i>S</i> _{max}	τ
Sand lance	<i>Ammodytes americanus</i>	0.003	3.211	0.500	24.0	12.0	0.587	13.1	0
Longhorn sculpin	<i>Myoxocephalus octdecemspinosus</i>	0.010	3.078	0.720	30.0	15.0	0.587	10.0	0
Atlantic herring	<i>Clupea harengus</i>	0.010	2.990	0.280	35.0	25.0	0.587	165.0	1
Witch flounder	<i>Glyptocephalus cynoglossus</i>	0.003	3.428	0.230	39.3	20.0	0.392	28.0	1
Windowpane	<i>Scophthalmus aquosus</i>	0.011	3.000	0.242	41.0	22.0	2.43	29.0	1
Winter flounder	<i>Pseudopleurinctes americanus</i>	0.011	3.138	0.283	45.5	25.0	0.587	21.0	1
Atlantic mackerel	<i>Scomber scombrus</i>	0.007	3.319	0.243	46.1	30.0	0.641	183.0	1
Fourspot flounder	<i>Paralichthys oblongus</i>	0.008	3.000	0.335	50.0	25.0	0.306	29.0	1
Yellowtail flounder	<i>Limanda ferruginae</i>	0.008	3.129	0.335	50.0	23.0	0.487	52.0	1
Little skate	<i>Raja erinacea</i>	0.005	3.141	0.352	53.0	50.0	0.587	15.0	1
Red hake	<i>Urophycis chuss</i>	0.005	3.222	0.190	60.2	25.0	0.507	16.0	1
Silver hake	<i>Merluccius bilinearis</i>	0.007	3.050	0.180	65.4	23.0	0.587	465.0	1
Sea raven	<i>Hemitripterus americanus</i>	0.019	3.100	0.720	68.0	25.0	0.587	10.0	0
Haddock	<i>Melanogrammus aeglefinus</i>	0.010	3.068	0.376	73.8	28.0	0.375	421.0	1
Spiny dogfish	<i>Squalus acanthias</i>	0.003	3.122	0.100	100.0	80.0	0.587	136.0	1
Pollock	<i>Pollachius virens</i>	0.010	3.028	0.100	111.0	40.0	0.154	200.0	1
Winter skate	<i>Raja ocellata</i>	0.004	3.317	0.144	114.1	85.0	0.587	30.0	1
Goosefish	<i>Lophius americanus</i>	0.020	2.897	0.108	126.0	49.0	0.587	10.0	1
White hake	<i>Urophycis tenuis</i>	0.006	3.220	0.106	136.0	34.0	0.137	16.0	1
Summer flounder	<i>Paralichthys dentatus</i>	0.007	3.278	0.173	137.0	26.0	0.306	29.0	1
Atlantic cod	<i>Gadus morhua</i>	0.009	3.052	0.120	148.0	40.0	0.149	72.1	1

Note: Species ordered by body size (*L*_∞). Data sources for direct input parameters: *a* and *b*, US National Marine Fisheries Service databases (J.S. Link, personal communication); *k* and *L*_∞, Penttilä et al. (1989); *L*_{M50}, O'Brien et al. (1993); *S*_{max}, Myers et al. (1995); κ, O'Brien et al. (1993); τ, US National Marine Fisheries Service food-habits database (J.S. Link, personal communication).

a time step in the standard model that was equivalent to approximately 80 days.

All conversions between length (cm) and weight (g) that were required by the model were calculated with species-specific values for *a* and *b*, empirically estimated parameters of the standard length–weight relationship $W = aL^b$, obtained from the US National Marine Fisheries Service (Table 3).

Recruitment

Perhaps the most difficult aspect of any model of fish population dynamics is the choice and parameterization of the stock–recruitment relationship. This difficulty is particularly acute when a relationship is required for many species. For this model, recruitment was described by the Ricker stock–recruitment equation:

$$(3) \quad R_i = \alpha_i S_i e^{-\beta_i S_i}$$

where R_i is recruitment, S_i is spawning stock biomass, and α_i and β_i are species-specific parameters. For some of the species in our model community, no direct study of stock and recruitment has been undertaken, whereas for others a variety of estimates are available. Our approach to this problem was to use estimates of the two parameters of the Ricker equation for 65 of the stocks collated by Myers et al. (1995) for which recruitment was estimated at age 1. Both parameters were scaled to common recruit and spawning stock size units (individuals $\times 10^6$ and tonnes $\times 10^3$, respectively) and the relationship between α and the parameters of the von Bertalanffy growth equation were examined to determine whether there was any empirical basis for a generalized relationship between life-history attributes describing individual growth and spawners per recruit at low population size (Myers et al. 1999). Our analysis showed that there was a

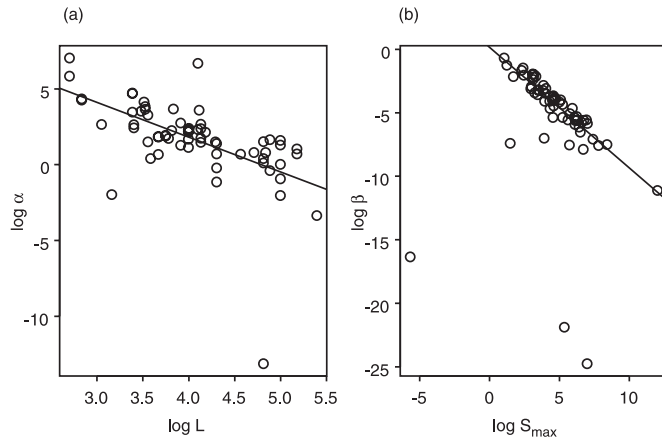
significant negative linear relationship between $\log \alpha$ and $\log L_{\infty}$ and a positive linear relationship with *k*. Of these two, the relationship with *L*_∞ fitted best ($\ln(\alpha) = 11 - 2.30 \ln(L_{\infty})$, $r^2 = 0.33$, $P < 0.001$; Fig. 1a). This regression equation was used to estimate α values from empirical estimates of *L*_∞ for all species in the model.

In contrast to Ricker's α , we found no clear relationship between Ricker's β and the von Bertalanffy growth parameters. This result is not surprising, however, because β , the term reflecting density dependence in recruitment, is highly sensitive to the existence of recruitment data for large stock sizes. Unfortunately, the presence of such data differs between stocks, depending on whether they were assessed early or late in the history of exploitation. The question arises, therefore, of how one can obtain estimates of β for modeling purposes?

The approach that we have adopted is to exploit the fact that $S_{r_max} = 1/\beta$. It follows from this equation that there should be a linear relationship between the stock size (*S*) at which recruitment is maximized (S_{r_max}) and β when plotted on logarithmic scales. Because β has units of $1/S$, this linearity with β should hold for other metrics related to stock size. To test this assumption we extracted maximum observed spawning stock size (*S*_{max}) for each of the time series data in Myers et al. (1995), where recruitment was estimated at age 1, and plotted this against the estimate of β (Fig. 1b). As one would expect, the majority of data fit our expectation extremely well. By omitting four outliers, we obtain the relationship $\ln(\beta) = 0.1513 - 0.9484 \ln(S_{max})$, $r^2 = 0.8476$, $P < 0.001$.

It is perhaps important to stress at this point that our purpose here is to obtain a reasonable spread of β values that are broadly consistent with the life-history characteristics of

Fig. 1. (a) The relationship between Ricker stock–recruitment parameter α and the von Bertalanffy growth parameter L_{∞} . (b) The relationship between maximum observed stock size S_{\max} and β . Data are for 65 stocks described in Myers et al. (1995).



the modeled species. Therefore, using the above fit, maximum observed stock size for each fish species in the Georges Bank time series was used to obtain the relative size of β for the species in our model. These estimates were then scaled upward or downward by a constant amount (for all stocks) to tune the model to obtain reasonable equilibrium population sizes in the absence of fishing. New recruits were introduced into the model into the smallest modeled size class during a single time step each year, which corresponded to an approximately 80-day period.

One difficulty of calculating S when discrete size classes are used is that not all individuals in the class will be mature, unless size at first maturity corresponds with the lower bound of a size class. To overcome this difficulty, the proportion of mature individuals ($\bar{\omega}$) for each species – size class combination was calculated with maturity ogives. The ogive can be described by a logistic model such that

$$(4) \quad \bar{\omega}_{i,j} = \frac{1}{1 + e^{-\kappa_i(L_{i,j} - L_{M50,i})}}$$

where L_{M50} is the length at which 50% of individuals are mature and κ is a steepness parameter. Estimates of κ and L_{M50} for Georges Bank species were obtained from O'Brien et al. (1993). For species for which estimates were unavailable, we used the mean κ for the species for which estimates were available ($\kappa = 0.587$) and the L_{M50} value of the most closely related species. For this analysis no distinction between males and females was made and only data on maturity schedules for females were used to parameterize the model.

Fishing mortality

The instantaneous rate of fishing mortality was modelled according to the following equation:

$$(5) \quad F_{i,j} = \frac{\phi_i F_{\max}}{1 + e^{-\eta(L - L_{F50})}}$$

where $F_{i,j}$ represents the fishing mortality on species i of size class j , ϕ_i is a binary variable indicating whether species i is fished, F_{\max} is the maximum annual fishing mortality

rate for a fully recruited fish, η is a steepness parameter, and L_{F50} is the size at 50% selection by the fishery. For all model runs described here, η was set at 0.25 and L_{F50} was set at 25 cm.

Residual natural mortality ($M1$)

Natural mortality from causes other than predation by the modeled species is known as residual natural mortality ($M1$). The instantaneous rate, $M1$, was described by a U-shaped function with rapidly decreasing mortality during the early period of life, a fairly constant mortality for middle-sized fish, and increasing mortality in very large fish, because of increasing senescence, disease, etc. Although we have no data to support such a functional form, it seems intuitively obvious that it must occur at the limit in unexploited fish populations to prevent the buildup of very large fish (Quinn and Collie 2005). A suitably shaped curve was provided by the beta function

$$(6) \quad M1_j = \frac{1}{B(\psi, \nu)} \left(\frac{L_j}{L_{\max}} \right)^{\psi-1} \left(1 - \frac{L_j}{L_{\max}} \right)^{\nu-1}$$

where $0 < \psi < 1$, $0 < \nu < 1$, L_j is the midlength of size class j , and L_{\max} is the maximum size of fish observed in the model. The shape of this function is shown for $\psi = 0.8$, $\nu = 0.4$ (Fig. 2a), which provides a suitable description of our intuition about natural mortality. Initial runs of the model suggested that the parameterization adopted was reasonable.

Predation mortality ($M2$)

Using the von Bertalanffy growth equation we can calculate the growth increment for an average-sized individual (L) in each size class during a given time step from the following equation:

$$\Delta L = (L_{\infty} - L)(1 - e^{-k\Delta t})$$

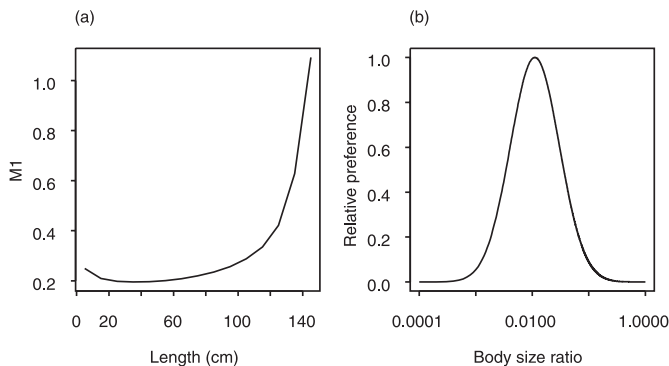
Converting this increment to weight and dividing by a conversion efficiency will provide an estimate of the ration, $I_{i,j}$, that must be consumed by that predator – size class combination to account for the growth. Growth efficiency (Ge), the efficiency with which consumed food was converted to body mass, was estimated by

$$(7) \quad Ge_{i,j} = \left(1 - \left(\frac{W_{i,j}}{W_{i,\infty}} \right)^{0.11} \right) \times 0.5$$

where $Ge_{i,j}$ is the growth efficiency of species i in size class j , $W_{i,j}$ is the weight at the midpoint of size class j , and $W_{i,\infty}$ is the weight at L_{∞} . The above relationship exploits the observed allometric relationship between production, ingestion, and energy expenditure, where production = $\pi W^{0.75}$ – $\pi' W^{0.86}$ (Jobling 1994), along with the fact that when maximum size is reached all energy is used for metabolism (i.e., there is no growth). This approach gave growth efficiencies by size ranging from 0.35 for very small individuals of a species and close to zero for the largest fish.

For prey species m in size class n , the predation mortality is then given by

Fig. 2. (a) Residual natural mortality ($M1$) as a function of body size (length). (b) Relative food preference, modeled as a function of prey–predator weight ratio, using a lognormal distribution function with $\mu = -3.5$, $\sigma = 1$.



$$(8) \quad M2_{m,n} = \sum_i \sum_j I_{i,j} N_{i,j} \frac{v_{i,j,m,n}}{\sum_k \sum_l v_{i,j,k,l} W_{k,l} N_{k,l} + \text{other}}$$

where W , N , and I are weight, abundance, and ration, respectively, for a given species – size class combination, “other” is food available from prey (other food) that is not explicitly represented in the model, and $v_{i,j,m,n}$ is the relative preference (suitability) for predator i of size j of prey m of size n . Equation 8 corresponds to a Holling type-II functional response, as implemented in MSVPA (Magnusson 1995). Although total feeding rate is constant in the model, predator feeding rate on a particular prey saturates at high prey abundance such that $M2$ is a decreasing function of prey abundance. The suitability parameter, v , allows the total predator ration to be apportioned among prey species. Suitability is defined as

$$v_{i,j,m,n} = \zeta_{n,j} \tau_{m,i}$$

where the parameter $\zeta_{n,j}$ is the preference for a prey of size n by predator of size j , and $\tau_{m,i}$ is the vulnerability of prey species m to predator species i .

The size-preference parameter, ζ , was calculated as a function of the ratio of prey-to-predator body weight at the midpoint in a length class (or at the midpoint between the lower bound of the largest length class for a species and L_∞). This preference function was modelled with a lognormal distribution using initial parameter values of $\mu = -3.5$, $\sigma = 1$ (Fig. 2b). This parameterization gives a maximal preference for prey that is approximately 1/33rd of the weight of the predator (Hahn and Langton 1984) and is broadly consistent with recent observations (Scharf et al. 2000).

Values for τ were set at either 0 or 1, indicating whether a particular species was known to eat a given prey. By varying the matrix of τ values, the food web topology can be altered. The suitability values (v) for all prey size-class combinations were normalized for each predator size-class combination such that they summed to 1 (Magnusson 1995).

Other food

With the above formulation, it is the contribution by other (nonmodelled) food that scales $M2$ values to sensible levels. In the future, it may be possible to back-calculate to deter-

mine what amount of other food would be required to satisfy the system, but for now, other food was used as a tuning parameter to produce a stable system with all species persisting and $M2$ levels broadly comparable with the annual average predation mortalities estimated by Tsou and Collie (2001) for selected Georges Bank species. Annual average $M2$ values ranged from a maximum of 1.63 for silver hake (*Merluccius bilinearis*) to a minimum of 0.03 for spiny dogfish (*Squalus acanthias*).

Implementation sequence

Using the formulations described above, the following implementation sequence was used within each time step. First, if it was the correct time step within the year, recruits were added to the smallest size class. Mortality was then imposed on all size classes, after which the growth function was applied to move the appropriate proportion of individuals to the next size class.

The general sequence and form for the model's governing equations to update abundance N for each species i in size class j at time t can be written as follows:

- (i) introduce recruits: $N'_{i,1,t} = N_{i,1,t-1} + R_{i,t}$
- (ii) impose mortality: $N''_{i,j,t} = N'_{i,j,t} e^{-(F_{i,j,t} + M1_{i,j,t} + M2_{i,j,t})}$
- (iii) impose growth: $N_{i,j,t} = N''_{i,j,t} (1 - \phi_{i,j}) + N'_{i,j-1,t} (\phi_{i,j-1})$

Model runs

As noted above, the model was tuned by adjusting the “other food” parameter to obtain reasonable $M2$ values. We then ran the model until it reached equilibrium and used the equilibrium abundances as the initial values for all subsequent model runs. Runs of the standard model with 10 cm size class intervals were for 114 time steps, the equivalent of approximately 25 years. To test for discretization error, we also constructed a second version of the model with thirty 5 cm length intervals, which we ran for 228 time steps, again corresponding to an approximately 25-year period. As with the standard model, this second model was tuned by altering the other food parameter to obtain quantitatively similar equilibrium behaviour under a no-fishing scenario. The behaviour of this second model in response to changes in fishing mortality was then compared with that of the standard model.

As a further test of sensitivity, we also examined the effects of uncertainty in the standard model to five of the key input parameters: the stock–recruitment parameters α and β , the size-preference parameters μ and σ , and growth efficiency, Ge . Each of these five parameters was either increased or decreased by 10% of the base level for all species at the same time. With two levels of five parameters, the full factorial design had 32 sensitivity runs. Each sensitivity trial was run for 114 time steps to reach equilibrium. The response variables were the numbers and predation mortality for each species and a set of community indices proposed by Rochet and Trenkel (2003). We then fit linear models to estimate the first-order effect of each parameter on each response variable. The sensitivities were plotted, relative to the mean of the response variable, with the S-PLUS function plot.design (Insightful 2001).

To examine the response of alternative descriptors of community structure to fishing pressure, we undertook 10 runs

Table 4. Summary of the effects of size-class width on a range of univariate community metrics.

Community metric	$F = 0$	$F = 0.4$	$F = 0.8$
Total number of individuals	-1.2	3.2	6.6
Total community biomass	-5.1	-8.0	-14.3
Mean weight of an individual	-3.9	-10.9	-19.7
Mean length of an individual	-1.2	-0.1	-0.3
Mean L_{∞} of an individual	2.7	2.3	1.9
Mean L_{M50} of an individual	0.3	1.7	0.5
Community diversity (Hill's N1)	0.5	-8.9	-2.8
Proportion of piscivores ^a	3.5	-0.6	0.3
Proportion of noncommercial species	12.1	40.6	51.1

Note: The table entries show the percentage change resulting from the use of 30 cm \times 5 cm size classes rather than the 15 cm \times 10 cm size classes used in the model key runs. Community metrics were chosen from the list proposed by Rochet and Trenkel (2003).

^aPiscivores have been arbitrarily defined as species with more than six prey species.

of the standard model using the parameter set shown (Table 3). All direct input parameters were held constant with the exception of fishing mortality, which ranged from 0 to 1 at 0.1 intervals.

Results

Sensitivity analysis

Comparison of the output from our standard model (10 cm) with that from the 5 cm interval model revealed very similar behaviour. For example, the correlation coefficients for the logarithm of total abundances and annualized $M2$ values for each species at year 25 were both 0.99 in the absence of fishing. When a fishing mortality of 0.8 was imposed, similarly high correlations were also obtained ($r^2 = 0.98$ and 0.99 for $\log N$ and $\log M2$, respectively). These data indicate that the numbers and mortality calculations in our model are quite insensitive to the choice of size interval. A comparison of the relative change in a variety of other univariate community metrics for the two different models also showed a relative insensitivity to size-class interval in the absence of fishing (Table 4). The only difference between the two models that was greater than 10% at $F = 0$ was the proportion of noncommercial species. However, because this proportion was low (~ 0.1) in the community, normalizing by this small fraction amplified the differences between models.

With increased fishing mortality, the community structure shifted to the smaller size classes where growth is more rapid through the size-class boundaries, which lead to some divergence between the outputs of the two models for mean weights and other weight-based indices (Table 4). Numbers at length were quite insensitive to the choice of size interval, but at low abundance, small differences were amplified by the power relationship between weight and length. Although the choice of size interval can impact the absolute values of weight-based community metrics, our primary concern here is the impact of these choices on our conclusions about the effects of fishing. In this respect, we are confident of our findings because the trends in community metrics with respect to fishing remained the same as those shown later, regardless of the choice of size interval.

To illustrate the results of the sensitivity analyses for the key model parameters, percentage deviations from the mean

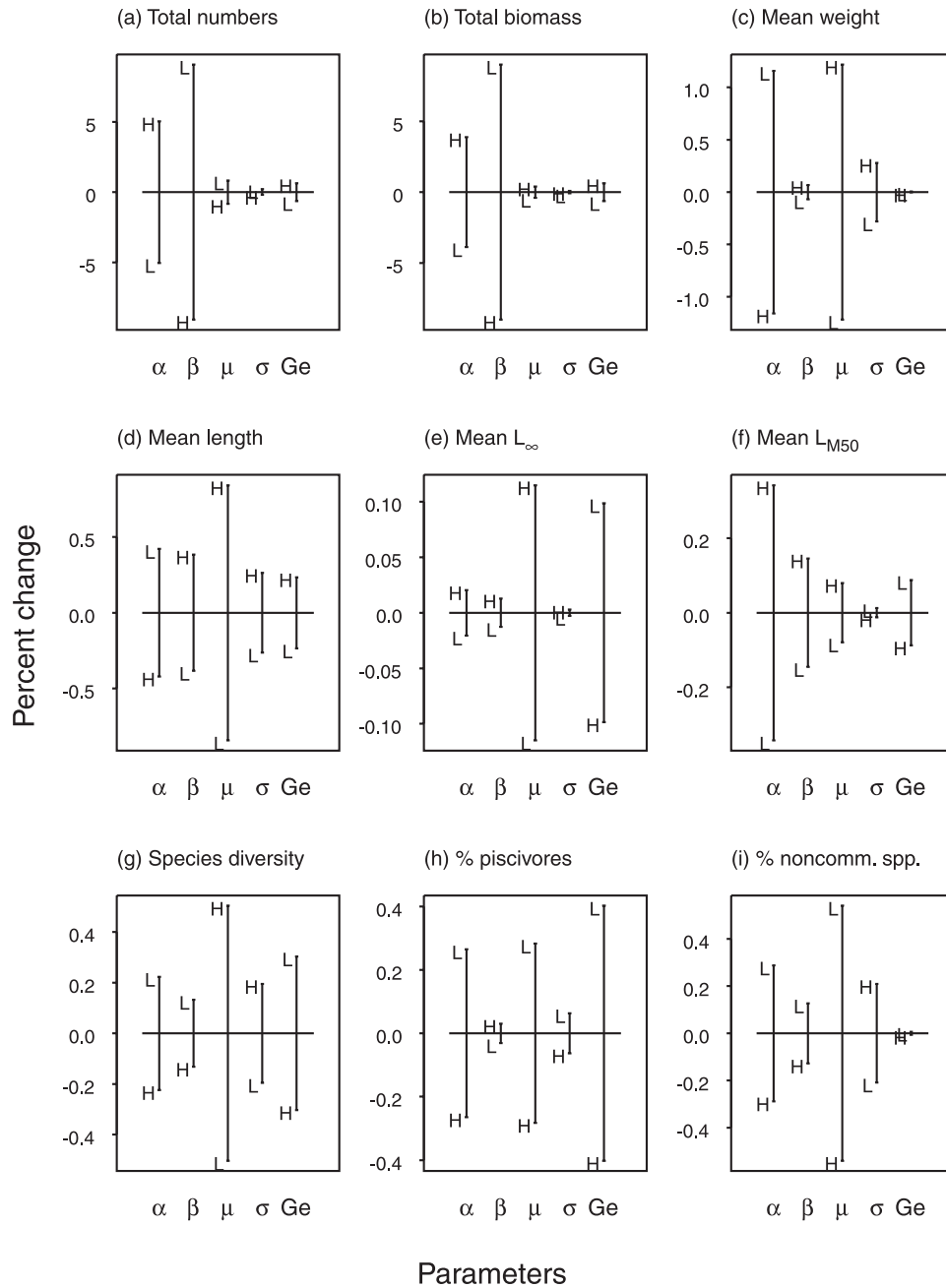
for a series of community response variables were plotted (Fig. 3). The largest deviations, of the order of $\pm 5\%$ – 8% , were for total numbers and total biomass and were in response to variations in β , the density-dependence parameter of the stock–recruitment relationship. Variations of $\pm 5\%$ were also observed in these same two variables in response to changes in the stock–recruitment parameter α . As one would expect, a low level of β results in an increase in numbers and biomass, whereas a lower level of α results in a decrease. For the remaining variables, deviations from the mean response were less than 1% with a varying pattern of relative sensitivity to the different parameters. In general, sensitivity was greatest to μ , the logarithmic ratio of prey weight to predator weight, and G_e , the growth efficiency. Taken overall, the results indicate that our model was not unduly sensitive to uncertainty in model parameters.

Species population trajectories

As one might expect, the spawning stock biomass of all species subject to fishing mortality declined under fishing (Fig. 4). After 25 years of fishing at $F = 0.8$, seven of the modeled populations had become extinct, although six of these persisted and were approaching positive equilibrium abundances with $F = 0.4$ over the same time period. In contrast, sand lance (*Ammodytes americanus*), longhorn sculpin (*Myoxocephalus octdecemspinosus*), and sea raven (*Hemirhamphus intermedius*) increased in biomass, owing to the release from predation caused by the declines in predators resulting from fishing. Of these latter species, the largest response was shown by sand lance, a feature that is to be expected because this species serves as prey for 20 of the 21 modelled species compared with 5 and 3 for the other two species.

In contrast to the pattern for spawning stock biomass, trends in numerical abundance showed a more variable pattern with fishing, leading to an increase in numerical abundance for some of the exploited species (Figs. 5 and 6). At intermediate levels of fishing, small increases occurred for four relatively small-bodied species with only two or three predators (witch flounder, *Glyptocephalus cynoglossus*; windowpane, *Scophthalmus aquosus*; winter flounder, *Pseudopleurinctes americanus*; and yellowtail flounder, *Limanda ferruginea*) (Fig. 5). Increases were also observed in mackerel (*Scomber scombrus*, which had nine predators) and the

Fig. 3. Sensitivity of community indices to 10% increases and decreases in the value of key model parameters (stock–recruitment parameters, α and β ; size-preference parameters, μ and σ ; growth efficiency, Ge). In each subplot, the vertical lines indicate the sensitivity to each parameter, relative to the overall mean level, indicated by the horizontal line. H indicates a 10% increase and L indicates a 10% decrease in each parameter. Noncommercial species, noncomm. spp.



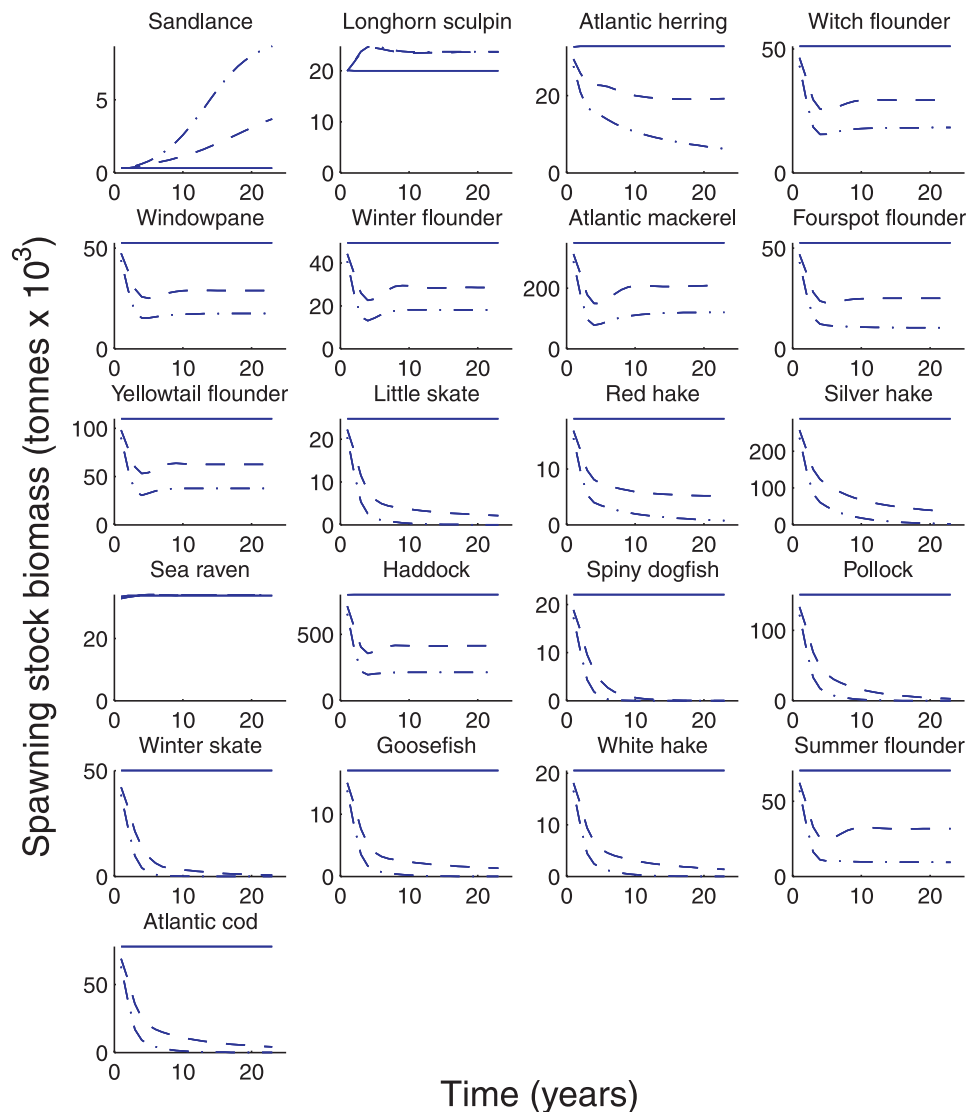
larger-bodied summer flounder (*Paralichthys dentatus*) and haddock (*Melanogrammus aeglefinus*). At high levels of fishing mortality, notable increases in abundance were only sustained for mackerel and winter flounder, as well as sand lance, which was unfished.

With no fishing mortality ($F = 0$), the community was numerically dominated by herring, mackerel, silver hake, and haddock (Fig. 6). These relative abundances are qualitatively similar to the abundance levels observed on George Bank, with the exception of Atlantic cod (*Gadus morhua*), which has historically been more abundant (Fogarty and Murawski

1998). With increasing fishing mortality, numerical dominance shifted towards sand lance, mackerel, and haddock and away from silver hake, which was very sensitive to fishing. These levels of fishing mortality are comparable with those experienced during the period of overfishing on Georges Bank (Fogarty and Murawski 1998).

Logically these increases in abundance combined with a decrease in spawning stock biomass must have arisen because the affected populations comprised a larger proportion of smaller individuals when these species were fished. This counterintuitive result must be a consequence of indirect

Fig. 4. Time series of spawning stock biomass for each modeled species under different fishing mortalities. Species are ordered from top left to bottom right according to size (L_{∞}). $F = 0$, solid line; $F = 0.4$, broken line; $F = 0.8$, dashed–dotted line.



predation effects propagated through the food web, which allowed small individuals of some species to escape predation and persist in the system, despite being subject to fishing pressure.

Community structure

The effects of fishing at the community level can be represented in a variety of ways, each emphasizing a particular aspect of structure. Here we explore the behaviour of some of the size and rank abundance based approaches that have been suggested in the literature (Rice and Gislason 1996; Bianchi et al. 2000; Rochet and Trenkel 2003).

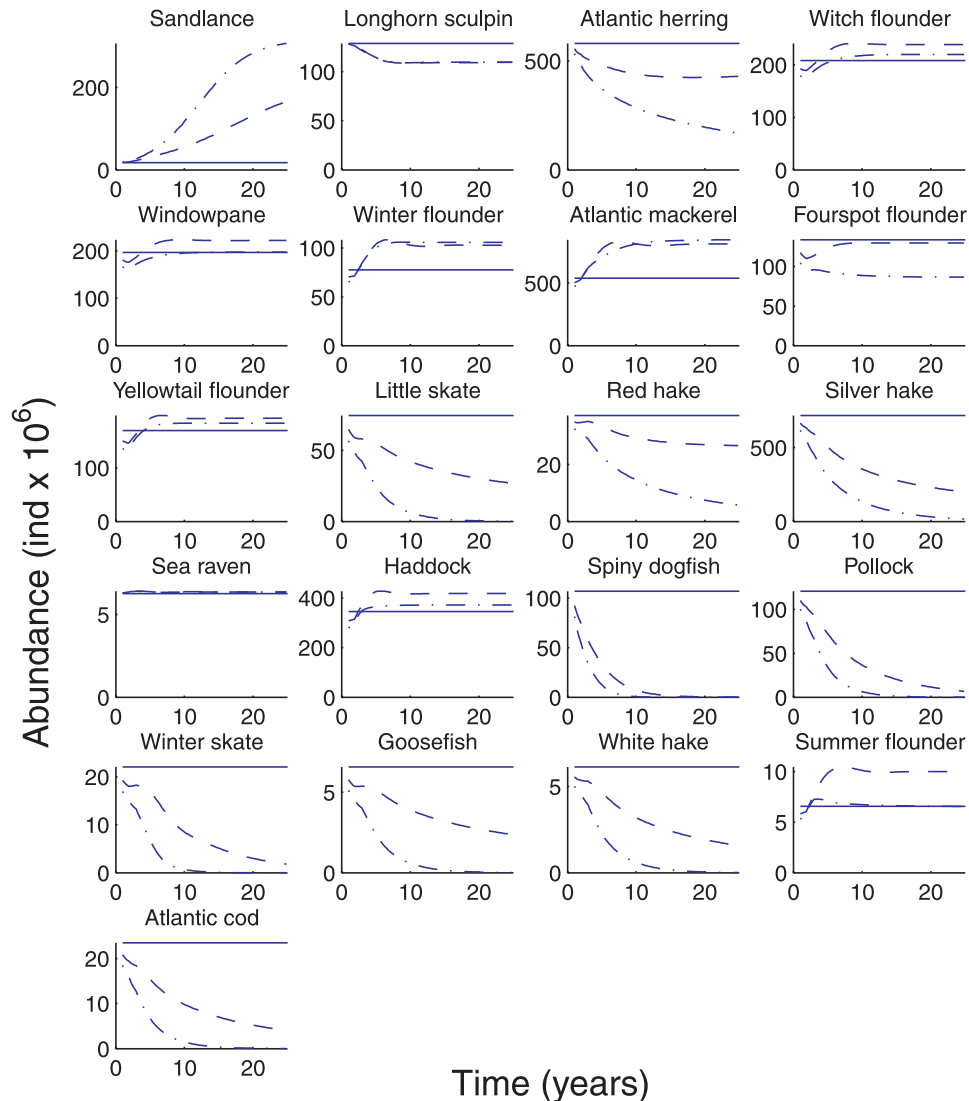
The biomass and abundance size spectra in our model are consistent in pattern with those found in natural communities and show a steady pattern of decrease after 25 years of fishing history (Figs. 7a and 7b). As one would expect, effects are most marked in the largest size classes, with both abundance and biomass falling to very low levels under high fishing pressure for the largest individuals. These results are consistent with both a priori expectations and previous em-

pirical findings (Rice and Gislason 1996; Greenstreet and Hall 1996).

In contrast to the size spectra, rank abundance plots expressed using the k -dominance approach (Clarke 1990) show relatively little separation between fishing regimes (Figs. 7c and 7d). However, some patterns are discernable, most notably that there is an increase in the numerical dominance of the most abundant species with increasing fishing, whereas the pattern for biomass shows an increase at intermediate levels of fishing and a decline when fishing increases further. This result would appear to be related to the effects on the biomass and abundance trajectories of individual species described earlier.

When species diversity within size classes is plotted against body size, a clear bimodality is apparent with a trough at about 75 cm. This feature of diversity size spectra has not previously been identified in field data and is a result of the gap in the distribution of L_{∞} values for species in our model between 74 cm and 100 cm. In a model system where a more even distribution of body sizes was represented, this

Fig. 5. Time series of abundances for each modeled species under different fishing mortalities. Data have been smoothed with a 1-year running mean to dampen within-year dynamics. Species are ordered from top left to bottom right according to size (L_{∞}). $F = 0$, solid line; $F = 0.4$, broken line; $F = 0.8$, dashed–dotted line.



feature would not occur and, as far as we are aware, has not been examined for Georges Bank.

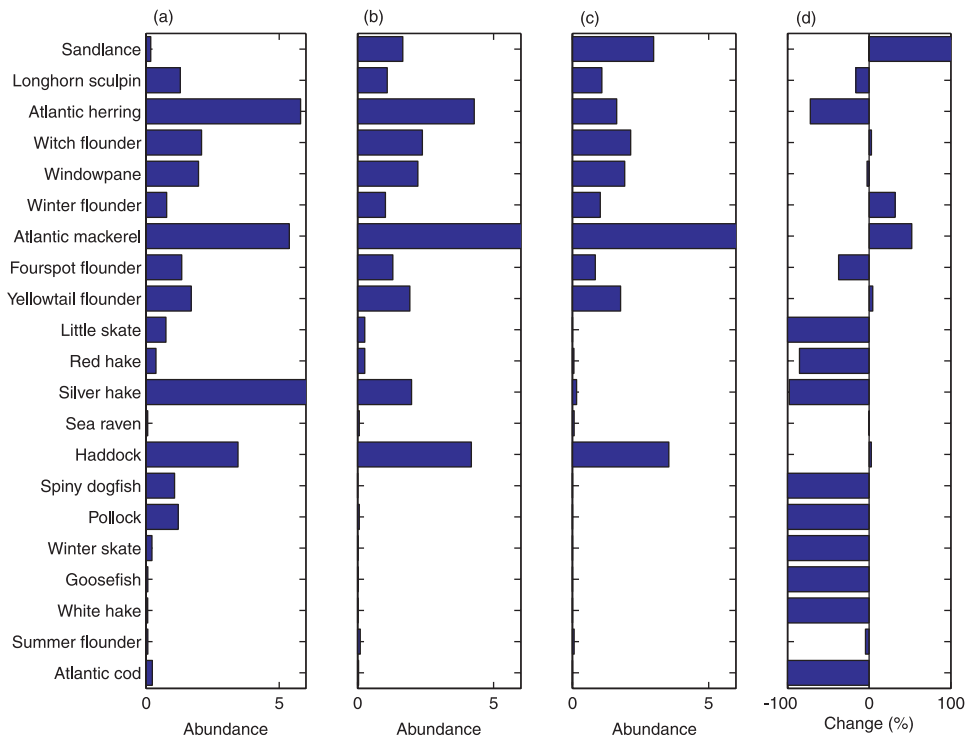
For sensitivity of the diversity size spectrum to fishing, it would appear that the diversity of individuals in larger size classes is much more affected by fishing. Indeed, the contrast between predictions for the biomass size spectrum (Fig. 7b) and the diversity size spectrum (Fig. 7f) suggests that the latter may show the effects of fishing more clearly.

In considering these results (Fig. 7), it should be borne in mind that these represent predicted changes resulting from 25 years of fishing. Clearly, for a metric to be useful for management purposes, it needs to respond over a much shorter time scale. An appreciation of temporal responsiveness can be obtained by examining the evolution of these patterns over time (Fig. 8). These data suggest that abundance and biomass size spectrum and k -dominance curves diverge rapidly from the zero fishing condition and that these features are broadly similar after 6 years. In contrast, a greater separation between time periods can be seen for the

larger part of the diversity size spectrum, suggesting that changes in this attribute of community structure as the result of fishing should be observable over a longer time frame.

We also tested the sensitivity of a number of aggregate metrics to fishing mortality (Fig. 9). Total biomass declined more steeply with F than total numbers because fishing targeted the larger fish while allowing the numbers of some small fish species to increase (Fig. 9a). Total catch was maximized at $F = 0.6$, which can be interpreted as the community-level maximum sustainable yield (Fig. 9b). All the measures of mean length declined with F as expected (Figs. 9b, 9c). Of these, mean length was the most sensitive to F (~30% decline between $F = 0$ and 1), and mean length at maturity was the least sensitive (~15% decline). Mean length at maturity was not a sensitive metric because there is less variation among species in L_{M50} than L_{∞} (Table 3). Mean weight decreased more steeply with F than mean length because of the power relationship between weight and length and because fishing increased the numbers of some small fish species. Even so,

Fig. 6. Bar plots indicating changes in abundance (number of individuals $\times 10^8$) for each species after 25 years under different levels of fishing mortality: (a) $F = 0$; (b) $F = 0.4$; (c) $F = 0.8$; (d) percent change in species abundance between $F = 0$ and $F = 0.8$ simulations.



the decrease in mean weight of $\sim 44\%$ over the F range of 0 to 1 did not match the decrease in total biomass of $\sim 80\%$.

Species diversity decreased most steeply between the range of $F = 0.2$ to 0.7 (Fig. 9d). In addition to declines in the evenness of abundances, this was also the range over which individual species were being lost from the community. The biomass of piscivorous species as a proportion of the total biomass declined only slightly with fishing mortality. This lack of sensitivity occurred because F was applied equally to all fished species and some of the species that we classified as nonpiscivorous are quite large (e.g., red hake (*Urophycis chuss*), white hake (*Urophycis tenuis*); Table 2). The biomass of noncommercial species (sand lance, longhorn sculpin, and sea raven) increased with F because of their release from predation (Fig. 9d). In summary, these aggregate metrics responded to fishing mortality in the expected directions (Rochet and Trenkel 2003). Metrics based on mass were more sensitive to F than those based on numbers or length. All metrics varied monotonically with F except total catch and species diversity, which had a threshold or inflection point at intermediate levels of fishing.

Discussion

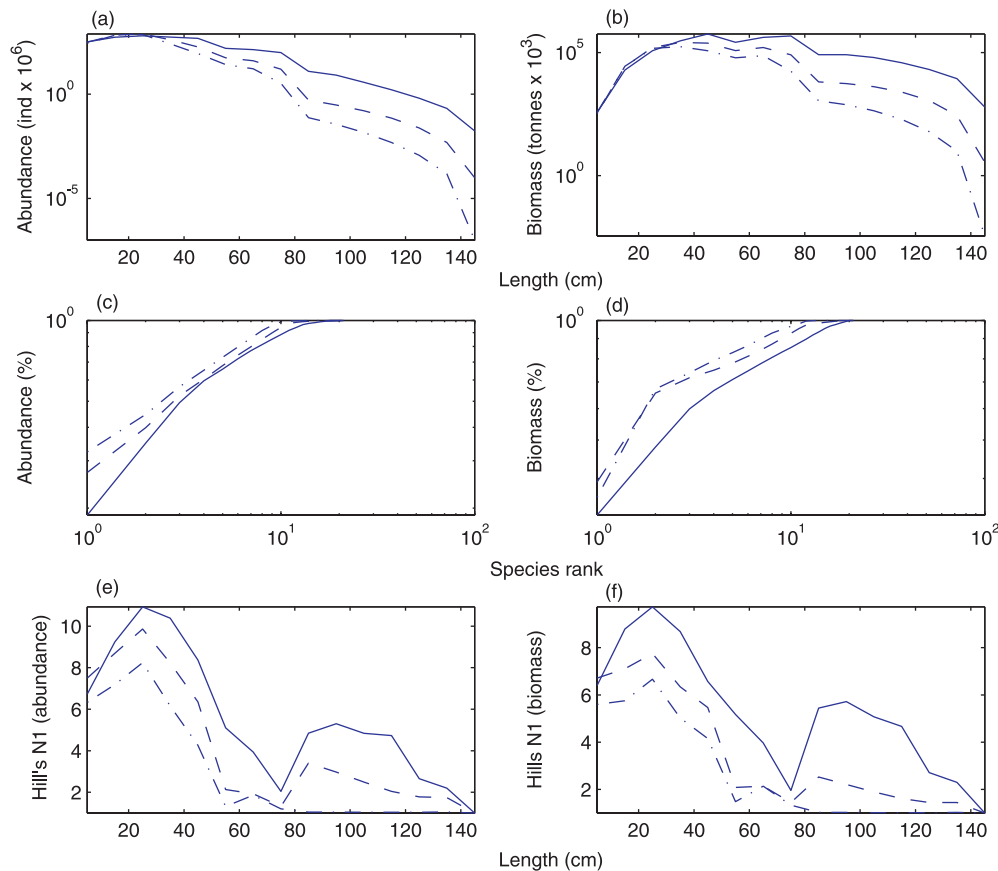
The purpose of this paper was to describe a size-based model of a fish community, examine its sensitivity to key model parameters, and present some preliminary results examining the utility of various community-level metrics of fishing effects. As noted earlier, this model should be considered as strategic in focus and is directed explicitly at understanding the dynamics of the emergent properties of fish communities rather than providing quantitative predictions for species abundances in any particular system. Thus, al-

though the model has been parameterized for Georges Bank in an effort to ground our parameterization in a defensible manner, we would not necessarily expect the results to mimic either the relative abundances of species or the temporal trends that have been observed.

Of the community-level indices we calculated, only total numbers and biomass in the community were somewhat sensitive to changes in the stock-recruitment parameters. This lack of sensitivity to possible parameter misspecification suggests that the responses of the community-level indices to fishing mortality are general to size-structured communities. The modeled community was more sensitive to the choice of size interval, especially at high levels of fishing mortality. With no fishing, numbers changed more gradually over the entire size range and were insensitive to the position of size-class boundaries relative to the size-specific demographic processes (growth, maturity, fishing, and predation). In contrast, with high fishing mortality, numbers were compressed in the lower size classes, where the positions of the size intervals affected the distribution of mean weights. Even so, the community-level indices had the same qualitative responses to fishing and most had the same quantitative patterns when comparing runs with different size-class intervals. The choice of size class is application dependent and depends partly on the size resolution of the data. For consistency, comparisons to assess the effects of fishing should be made within the same model parameterization.

The functional form of LeMANS is largely consistent with other recent size-based models (Benoit and Rochet 2004; Shin and Cury 2004); growth is described by the von Bertalanffy model, growth efficiency is on the order of 20% and nonpredation and fishing mortality both increase with size. However, unlike other models in which predation is de-

Fig. 7. The response of various community-level attributes to differing fishing mortalities imposed for 25 years: (a–b) abundance and biomass size spectra, total abundance of individuals (ind.) or total biomass in each size class; (c–d) *k*-dominance curves, log species rank versus cumulative proportional abundance or biomass; (e–f) diversity–size spectrum, species diversity, calculated as Hill's N1 (exp Shannon's H), of individuals in each size class. $F = 0$, solid line; $F = 0.4$, broken line; $F = 0.8$, dashed–dotted line.



terminated by encounter probabilities, LeMANS incorporates a type-II predator functional response. Density dependence is necessary at some point in the life cycle to stabilize the model dynamics. In LeMANS, density dependence occurs in the stock–recruitment functions, which is consistent with fisheries theory. The results obtained with LeMANS and the metrics calculated from them are also consistent with previous studies. Similarities with other work also extend to model sensitivity; as with MSVPA, our model was more sensitive to parameters related to recruitment (α and β) than to predation (μ , σ , and G_e) (Gislason 1991; Collie et al. 2003).

While individual population trajectories might not reflect those observed in the real world, we would expect our model to represent the emergent features of a natural community. In this respect, it is comforting that the patterns in community structure observed are largely consistent with those observed elsewhere (Rice and Gislason 1996; Duplisea and Bravington 1999; Bianchi et al. 2000). This degree of consistency increases our confidence that predictions made about fishing effects are robust. The trends in the various community attributes with increases in fishing pressure are also consistent with a priori expectations and previous work, which shows a loss of larger-bodied species, although until now we had relatively little feel for how quickly changes might be observed or of the scale of change to be expected (Gislason and Rice 1998; Duplisea and Bravington 1999).

Using a forward-projecting version of MSVPA, previous work by Rice and Gislason (1996) suggested that biomass size spectra may be a more useful approach than diversity size spectra for examining community-level effects. Their analysis, however, was based on a model with only 11 species and analysis of diversity effects with such a model may have been constrained. Although very preliminary, our results suggest that abundance or biomass size spectra may be very responsive to fishing effects as we observed changes after 6 years that did not change further for the next 18 years. In contrast, *k*-dominance representations show relatively little sensitivity to fishing effects and would appear to be of limited utility. This result contrasts markedly with findings for benthic communities, where *k*-dominance curves have become one of the “industry standards” for examining the effects of anthropogenic disturbance (Clarke and Warwick 1994). Contrary to Rice and Gislason (1996), we also found the diversity size spectra to show a marked effect from fishing that evolved steadily over the 25-year period.

It is encouraging that most of the community-level indices are sensitive to fishing mortality and respond in the directions predicted by theory (Rochet and Trenkel 2003). In data-limited situations, where not all metrics are calculable, simple metrics, such as mean length in the catch, can serve as proxies for the community-level effects. However, most of these metrics change monotonically with fishing and,

Fig. 8. Evolution of community-level attributes over time for $F = 0.4$: (a–b) abundance and biomass size spectra, total abundance of individuals (ind) or total biomass in each size class; (c–d) k -dominance curves, log species rank versus cumulative proportional abundance or biomass; (e–f) diversity–size spectrum, species diversity, calculated as Hill's N1 (exp Shannon's H), of individuals in each size class. $t = 0$ years, solid line; $t = 6$ years, broken line; $t = 12$ years, dotted line; $t = 25$ years, dashed–dotted line.

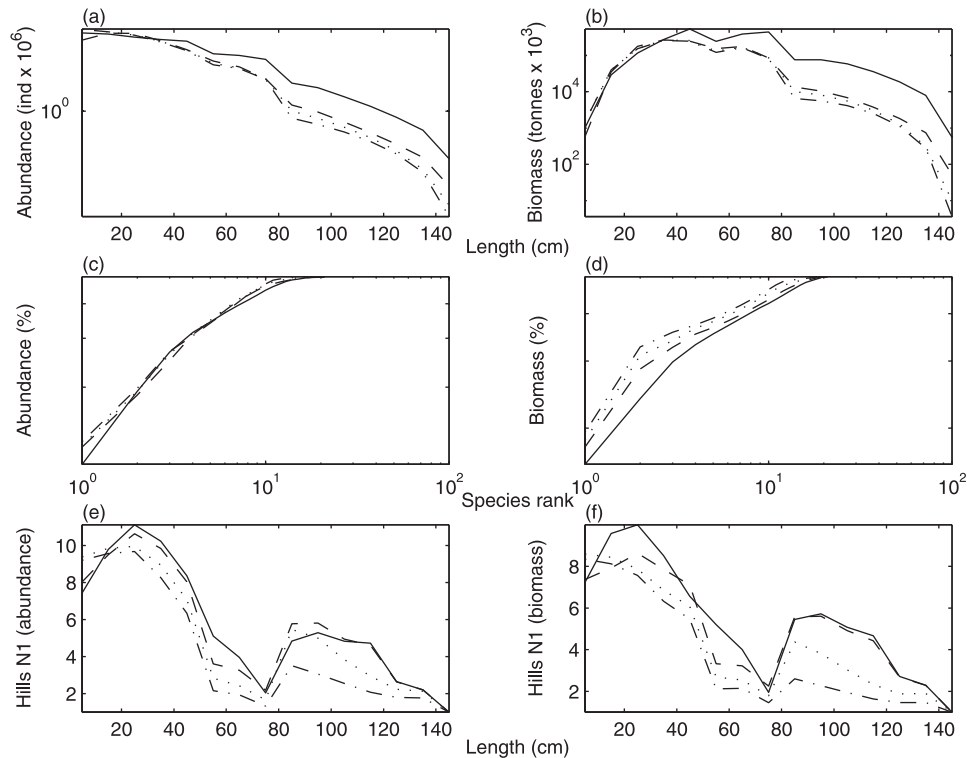
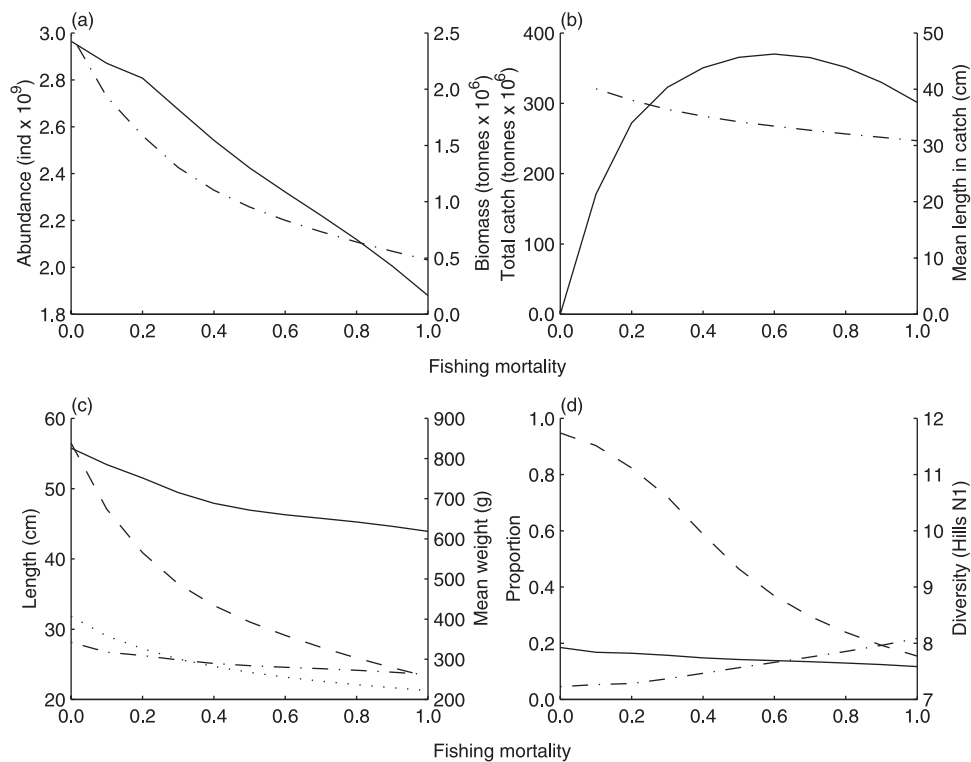


Fig. 9. Sensitivity of community-level metrics to fishing mortality: (a) total abundance, solid line; total biomass, dashed–dotted line; (b) total catch, solid line; mean length in catch, dashed–dotted line; (c) mean L_{∞} , solid line; mean length, dotted line; mean L_{M50} , dashed–dotted line; mean weight, broken line; (d) proportion of piscivores, solid line; proportion of noncommercial species, dashed–dotted line; species diversity (Hill's N1), broken line. Individuals, ind.



therefore, lack obvious points at which one might set reference levels. If the aggregate fish community is considered a “super species”, then the aggregate fishing mortality for maximum sustainable yield (MSY) could be a reference level. However, community-level metrics do not guarantee the persistence of all species in the community; at the community-level MSY of $F = 0.6$ in our model, for example, six species had been eliminated. Thus, the adoption of community- or ecosystem-level reference points alone may be insufficient to protect all the species that are considered threatened. Instead, it may be necessary to adapt single-species reference points to nontarget species and to incorporate these additional reference levels into fishery management plans. In this regard it should be noted that, in our simulations, the single-species declines in spawning stock biomass were the most sensitive indicators of fishing effects. Although single-species fisheries management has been roundly criticized for ignoring ecosystem considerations (Pikitch et al. 2004), there may be no simple alternative to species-by-species monitoring and assessment (Quinn and Collie 2005).

The primary purpose of this paper was to describe a new length-based multispecies model and to provide an illustration of its potential utility for understanding how community-level attributes change under fishing. Further work will be required to fully explore the behaviour of the model and what it can tell us about the dynamics of exploited fish communities. In particular, we need to ask how the topology of the food web alters behaviour, what the effects of differential fishing pressure (selectivity by fishing fleets) might be, and how a wider range of community-level indices responds to fishing. We also need to more fully confront the model's predictions with data and explore its behaviour when parameterized with data from other communities.

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