

Modelling an exploited marine fish community with 15 parameters — results from a simple size-based model

John G. Pope, Jake C. Rice, Niels Daan, Simon Jennings,
and Henrik Gislason

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To measure and predict the response of fish communities to exploitation, it is necessary to understand how the direct and indirect effects of fishing interact. Because fishing and predation are size-selective processes, the potential response can be explored with size-based models. We use a simulation approach to describe the relationship between size spectrum slope and overall fishing mortality and to try to understand how a linear spectrum might be maintained. The model uses 15 parameters to describe a 13-“species” fish community, where species are defined by their maximum body size and the general relationship between size and life-history characteristics. The simulations allow us to assess the role of changes in the strength and type of density dependence in controlling the response to fishing, and to investigate the trade-off between catches and stock status of the different species. The outputs showed that the linear slope of the size spectrum was a function of community exploitation rate. Density-dependent controls, specifically predation mortality and the extent of compensation in the stock-recruit relationship, were key mechanisms in maintaining a linear spectrum. A linear spectrum emerged independent of the rate of compensation in the stock-recruit relationship. When this rate was low, the effects of changes in fishing mortality on predator abundance dominated those on spawning-stock biomass, whereas the dominance was reversed when the compensation rate in the stock-recruit relationship was high. The approach allows us to explore the effects of different fishing mortality schedules on properties of the fish community, to assess how fishing affects species with different life histories in mixed fisheries, and to assess the effects of selectively fishing different size classes. The simulations indicate that the size classes to be included when developing and interpreting size-based metrics must be carefully considered in relation to the trophic structure and likely strength of predatory interactions in the community. Runs with different fishing mortality by size suggest that the dynamics of predation cannot compensate fully for changing rates and patterns of exploitation, implying that the effects of selectively fishing different size classes should be assessed on a case-by-case basis.

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J. G. Pope: Norwegian College of Fishery Science, University of Tromsø, N-9000 Tromsø, Norway. J. C. Rice: DFO Science Advisory Secretariat, Department of Fisheries and Oceans, 200 Kent Street, Ottawa, Ontario, Canada, K1A 0E6. N. Daan: Netherlands Institute for Fishery Research, PO Box 68, 1970 AB IJmuiden, The Netherlands. S. Jennings: Centre for Environment, Fisheries, and Aquaculture Science, Pakefield Road, Lowestoft, Suffolk NR33 0HT, England, UK. H. Gislason: Danish Institute for Fishery Research, Charlottenlund Slot, DK-2920 Charlottenlund, Denmark. Correspondence to J. G. Pope: The Old Rectory, Staithe Road, Burgh St. Peter, Beccles, Suffolk NR34 0BT, England, UK; tel/fax: +44 1502 677377; e-mail: PopeJG@aol.com.

Introduction

Fisheries management must ensure that the effects of fishing are sustainable at the scale of the whole ecosystem as well as for individual stocks (FAO, 2003; Pikitch *et al.*, 2004). For management to meet this requirement, it is necessary to understand how fishing affects the wider ecosystem, how

3rd fisherman: I marvel how the fishes live in the sea.

1st fisherman: Why, as men do a-land; the great ones eat up the little ones.

William Shakespeare, Pericles

these effects might be measured, and what management actions might be taken to mitigate them.

Fishing has direct effects on the biotic components of ecosystems through mortality inflicted as catch or injury. A long-standing goal of fisheries management has been to keep the direct mortality caused by fishing sustainable, although in practice this goal has been elusive for both target (FAO, 2004) and bycatch species (Kock and Benke, 1996; Casey and Myers, 1998; Vinther, 1999).

Fishing also has indirect effects on these components through modification of the foodweb, altering habitat quality or availability, productivity, and changing the life histories of species through directional genetic selection. The goals of reducing fishing mortality on target and bycatch species are consistent with an ecosystem approach to management, but have emerged from a single-species view. The metrics used to quantify direct mortality at the single-species scale are relatively well understood (catch – Hilborn and Walters, 1992; bycatch – Alverson *et al.*, 1994; non-catch – ICES, 2005), even if accurate quantification is often problematic because of weak surveillance and poor data quality. In contrast, the properties of indicators proposed to measure community-scale mortality are not well understood and have not been tested rigorously in management contexts (Fulton *et al.*, 2005). Here we attempt to address some of these issues by exploring a method of partitioning and quantifying fishing and predation mortality effects at the scale of the fish community, as a necessary step towards providing a scientific basis for managing fisheries in an ecosystem context.

One of the few tools for measuring the effects of fishing on the entire fish community is the slope of the size spectrum, as measured by surveys. Such slopes become steeper when fishing pressure increases. This general relationship between slope and fishing pressure has been observed empirically (Pope and Knights, 1982; Pope *et al.*, 1988; Rice and Gislason, 1996; Bianchi *et al.*, 2000), and is supported by simulation studies (Gislason and Rice, 1998; Benoit and Rochet, 2004; Shin and Cury, 2004). We extend the simulation approach to address two main questions: (i) is the slope of the size spectrum approximately linear, and how is this linearity maintained? and (ii) is the relationship between size spectrum slope and overall fishing pressure a simple one?

Each of those two questions, if answered even in a preliminary way, allows us to address two important management questions: (i) what value of the slope might be considered indicative of sustainable fishing at a community scale? and (ii) which exploitation strategies are likely to produce such a slope, and which are likely to produce communities that deviate severely from it?

For two reasons, we are particularly interested in how much the stock-recruit relationship in size-structured communities allows recruits-per-spawner to increase as spawning-stock biomass (SSB) decreases. The first is a typical single-species consideration: such compensation

should condition the response of each species to exploitation, by varying how productivity is affected by reduced SSB. The second is a community-scale consideration: reducing SSB by exploitation also reduces predation exerted by large fish on smaller ones. Hence, predation mortality is a second potential compensatory process functioning at the community scale, as aggregate predator biomass feeding back on aggregate prey biomass. We seek insight into if, and how, the internal predation dynamics could provide stability at the community level, by posing two additional questions: (i) does the community integrate the effects of predation and fishing on the biomasses of various sizes of fish, with resultant compensatory responses at the community scale? and (ii) if so, how does this community-scale compensation interact with the species-scale stock-recruit compensation, and do such interactions play a role in maintaining the linear relationship between the slope of the size spectrum and fishing?

The model and choice of parameters

The model describes an imaginary “fish community”, one grounded on our necessarily incomplete knowledge of the North Sea fish community, as emerging from the work of the former ICES Multispecies Assessment Working Group (ICES, 1988; Pope, 1991). The approach recognizes the fundamental role of body size in determining population dynamics and predator–prey interactions (Sheldon *et al.*, 1982; Dickie *et al.*, 1987a, b; Brown *et al.*, 2004). The fish community consists of 13 imaginary species whose key life-history parameters are inter-related in ways that are consistent with core principles and observed relationships in life-history theory (Roff, 1992; Stearns, 1992; Charnov, 1993; Gillooly *et al.*, 2001). Growth follows the von Bertalanffy growth model with asymptotic length L_∞ and growth parameter K . Species are defined by their L_∞ values ranging from 10 to 130 cm at 10-cm intervals (i.e. 13 “species”). “Recruits” of all species enter in the smallest size class (5 cm), then “grow” at their species-specific K until they reach the terminal size class defined by their species-specific L_∞ . Species-specific K is given by

$$K = \alpha L_\infty^{-\beta}. \quad (1)$$

To choose suitable values for α and β , a representative range of L_∞ and K -values for North Sea species was taken from FISHBASE. Using these data, the α and β may be simply fitted as the regression $\ln(K) = \ln(\alpha) - \beta \ln(L_\infty)$. This approach gives $\alpha = 2.30$ and $\beta = 0.52$ (95% confidence intervals: 1.01–5.27 and 0.31–0.73, respectively). However, Charnov (1993, in his Figure 4.17) derives a theoretical value of 0.65 for the slope of the $\ln(L_\infty)$ on $\ln(K)$ relationship for gadids, which suggests that $\beta > 1$. Therefore, a higher value of β seems justified, and we adopted

a value of 0.67 (i.e. a two-thirds rule). For this value of β , values of α estimated for each of the North Sea data points showed little trend with L_∞ (average $\alpha = 4.50$). These values are within the 95% confidence range of the initial estimates.

The numbers-at-length for each species are calculated for each 1-cm group using an approach similar to the length cohort analysis of Jones (1974). Thus, for species S , the number at length L_1 ($N_{L_1,S}$) that survives to length L_2 ($N_{L_2,S}$) is given as

$$N_{L_2,S} = N_{L_1,S} \left\{ \frac{L_\infty(S) - L_2}{L_\infty(S) - L_1} \right\}^{Z(L_1,S)/K(S)}, \quad (2)$$

where $Z(L_1,S)$ is the total mortality rate (y^{-1}) at length L_1 for the species in the size interval L_1 to L_2 .

The average number of fish per year $\{\bar{N}_{L_1,S}\}$ in the L_1 length group by species is given by

$$\bar{N}_{L_1,S} = (N_{L_1,S} - N_{L_2,S}) / Z(L_1,S). \quad (3)$$

The $\bar{N}_{L_1,S}$ may then be summed across species at each 1-cm group L from 5 to 130 cm to give the overall size spectrum $\bar{N}_{L,\#}$.

Following the MSVPA tradition (ICES, 1988), components of Z considered are fishing mortality rate (F), "non-predation" natural mortality rate (M_1), and predation mortality rate (M_2), where M_2 refers specifically to the predation by species within the modelled community. External predation is included in M_1 . An overall fishing mortality F acts on all species. However, this value is modified by species/size selectivity. Size selectivity is assumed to have a logistic exploitation pattern (with species-specific parameters γ_s and δ_s), and may have an additional species-specific multiplier λ_s :

$$F_{L,S} = F \times \lambda_s / (1 + \exp(\gamma_s(\delta_s L_\infty - L))). \quad (4)$$

We adopted a common δ_s of 0.33. Hence, the 50% selected length for each species is taken to be at 33% of its L_∞ . A slope parameter (γ_s) of 0.2 was chosen. Similarly, λ_s is taken to be a simple linear function of L_∞ centred on the species with $L_\infty = 70$ cm. In the simulations we used

$$\lambda_s = 1 + \kappa(L_{\infty,s} - 70), \quad (5)$$

where κ is a constant, -0.035 . The species effort multiplier λ_s was, therefore, 1.21 for the smallest species ($L_\infty = 10$ cm) and 0.79 for the largest species ($L_\infty = 130$ cm).

Functionally, this allocation of F by species and size ($F_{L,S}$) can be thought of as having fisheries on small "fodder" species (sandeel-like), on medium-sized fish (whiting-like), and large fish (cod-like), with the fishery in each case commencing exploitation when the targeted species has reached one-third of its potential maximum size. However, the effects are modelled solely through the exploitation

patterns as a function of L_∞ with a single overall F , and not by separate fleets. Different combinations of fisheries could be explored through different parameterizations of Equations (4) and (5), however, and the results of a few explorations are reported here also.

Non-predation natural mortality rate by species ($M_{1,S}$) is assumed constant and taken as a multiple of K ($M_{1,S} = \tau K_S$). Predation mortality rate ($M_{2,L,S}$) of prey species S of length L is assumed to be proportional to the sum of numbers of predators at each length (L_p) greater than L . These numbers are multiplied by a power (ω) of L_p and by a log-weight ratio size-preference function (Ursin, 1973):

$$M_{2,L,S} = \nu \sum_{\text{all } L_p} \bar{N}_{L_p,\#} L_p^\omega \times \exp\{-0.5((3 \ln(L_p) - 3 \ln(L) - \mu)/\sigma)^2\}, \quad (6)$$

where μ and σ are the mean and standard deviation of the predators' \log_e size-preference ratio, respectively. Values of μ and σ were taken as 5.0 and 1.69, respectively, broadly based upon MSVPA values (ICES, 1988, Table 6.6.2).

The choice of the power (ω) acting on the length term in Equation (6) is important if the model is to achieve a sensible M_2 -at-size. Outputs from the model resulted in a plot of $\ln(M_2)$ on $\ln(\text{length})$ that had a form that was close to parabolic. Taking exponentials of both sides suggests that the relationship of M_2 -at-length to $\ln(\text{length of prey})$ had the approximate shape of the Gaussian function. However, the relationship found between $\ln(M_2)$ and $\ln(Wt)$ in the MSVPA, and which we seek to mimic (see below), was linear. Clearly, for approximate compatibility between M_2 -values in the model and those observed from MSVPA, the M_2 -values over the length range of the model (5–130 cm) must represent the descending right-hand limb of the Gaussian curve. This in turn requires that M_2 peaks at or below the smallest size (5 cm), at intermediate exploitation rates when the size spectrum has a slope of about -0.1 . To achieve this required either that the size-preference parameters (μ and σ) be set higher than those observed (i.e. predators prefer smaller prey and/or a wider spread of prey), or that the power of the length term in Equation (6) for M_2 (ω) be set lower than 3. We adopted an ω of 2, a value consistent with the assumption that the consumption rates of animals are proportional to their surface area (Kooijman, 2000), and also close to the value expected should alternative scaling relationships link consumption rates and body size (van der Meer, 2006). This formulation leads to the desired pattern of Gaussian curves for M_2 by size that peak at small sizes (5–10 cm) for an overall F of 0.7, with reasonable values of μ and σ .

To convert lengths to weights, a common isometric length–weight relationship ($Wt = 0.01L^3$; Wt in g; L in cm) is assumed for all species.

Recruitment at 5 cm for each species was defined as a power curve of SSB, with an additional L_∞ correction term:

$$N_{5,S} = \rho L_{50,S}^\varphi \text{SSB}^\theta \quad (7)$$

For each species, the size at maturity h was taken to be $0.5L_\infty$, and SSB was the sum of the biomass of fish $> h$.

This simple model can be readily programmed as an EXCEL spreadsheet and (with suitable relaxation¹ of some sensitive terms such as M_2) converges rapidly to a steady state for a particular choice of parameters. Once it has converged, summary community information such as size spectrum slope and intercept, total biomass, catch, and consumption are calculated (Fulton *et al.*, 2005; Shin *et al.*, 2005).

The only source of compensation for reduced SSB structured into the model was via the power term (φ) in the stock-recruit relationship (Equation (7)). The model can provide insight into if and how the internal predation dynamics of the model (Equation (6)) might provide a second source of compensation, and hence greater stability, at the community level. Hence, φ was a key parameter in the model. Different values of φ would correspond to different levels of compensatory recruits-per-spawner (R/S; the single-species process). If comparable patterns in model outputs are observed across a substantial range of values for φ , then predation interactions are an important structuring property of the modelled community (the ecosystem process), in addition to the single-species R/S response.

Four simulacra were run covering a range of φ (0.25–0.95) to depict stronger or weaker compensation in the stock-recruit relationship, and to explore if and how community-scale predation mortality interacted with varying R/S. For each simulacrum, most parameters were held constant. However, to compensate for changes in φ , it was necessary to modify the ρ and θ parameters of Equation (7) and the ratio of M_1 to K (τ). For each simulacrum, these three parameters were chosen to produce a system as similar as possible to the exploited North Sea fish community in the 1980s, as described by multispecies VPA in ICES (1988) and Pope (1991). The key North Sea features that formed the constraints that each simulacrum tried to replicate were the following:

- (i) F was assumed to approximate the mean exploitation rate on fully recruited size classes of all species in the North Sea (0.7; ICES, 2004) with 50% selection at 30% of L_∞ .
- (ii) A $\ln(N)$ size spectrum slope of about 0.1 cm^{-1} that was linear over the 20–100 cm length range (i.e. with a Spearman's R^2 of >0.95).

¹ Changing a parameter value by less than the apparent step needed.

- (iii) M_2 such that a plot against weight (Wt) was as close as possible to the fitted relationship in ICES (1988, Figure 10.3.1): $\ln(\text{quarterly } M_2) = -0.268 - 0.386 \times \ln(\text{Wt})$.
- (iv) A total fish biomass of about 7 million t (approximating the value given for the North Sea by Sparholt, 1990), with both catch and fish consumption being about 3 million.
- (v) Catch of small species (those with L_∞ of 10 and 20 cm) to be about half of the total (roughly the part represented by the industrial catches for fishmeal in the North Sea in the 1980s; ICES, 1988; Pope, 1991).

Table 1 shows the parameter values adopted, and Table 2 is a summary of how each of the simulacra matched these constraints. In all cases, it proved impossible to match the biomass given the catch and F specified in the targets. Clearly these values were incompatible. However, the extent to which this problem is caused by the model underestimating the productivity of the North Sea or by inaccurate estimates of the constraints being fitted is unclear. Other constraints became more difficult to match in the more extreme runs (e.g. spectrum slope in scenario 4).

Finally, for each simulacrum, the effect of changes in the exploitation level was explored ($F = 0.0$ – 3.0).

Table 1. Symbols and values of input parameters for the four simulacra.

Constant					
<i>K/L_∞</i> relationship					
Constant	α				4.5
Power	β				0.6667
Fishing mortality rate					
Overall rate	F				0.7
Selection curve l_{50}/L_∞	δ				0.33
Selection curve slope	γ				0.2
Species selection modifier	λ				0.0035
<i>M₂</i> relationship					
μ	μ				5
σ	σ				1.699
Power of length	ω				2
<i>M₂</i> constant	ν				2E–13
Size at first maturity	h				0.5
Scenario					
		1 (key run)	2	3	4
Variable					
<i>M/K</i> ratio	τ	0.8	0.8	0.9	1.0
Stock recruitment					
Power SSB	φ	0.45	0.25	0.75	0.95
Power <i>L_∞</i>	θ	–3.55	–3.90	–3.10	–2.66
Constant	ρ	18.0	20.3	14.7	12.4

Table 2. Target values of the North Sea-like constraints and output values of the four simulacra.

Parameter	Target	Scenario			
		1 (key run)	2	3	4
Size spectra					
Intercept	Free	3401E ⁶	3029E ⁶	1497E ⁶	3821E ⁶
Slope	−0.100	−0.097	−0.092	−0.076	−0.049
r^2	>0.95	0.997	0.997	0.994	0.961
M_2 -values (y^{-1}) and $\ln(M_2)$ on $\ln(Wt)$ regression					
Maximum M_2	1.50	1.81	1.74	1.37	1.41
M_2 (10 cm)	1.50	0.78	0.86	0.85	1.41
Intercept	−0.27	−0.01	0.02	−0.05	0.05
Slope	−0.39	−0.45	−0.45	−0.41	−0.34
Catch, consumption, and biomass (million t)					
Catch <30 cm L_∞ groups	1.50	1.54	1.45	1.74	1.64
Catch 30–50 cm L_∞ groups	0.70	0.61	0.54	0.20	0.00
Catch 60–130 cm L_∞ groups	0.80	0.81	1.00	1.21	1.49
Total catch	3.00	2.97	2.98	3.14	3.13
Total consumption	3.50	3.50	3.46	3.48	4.00
Total biomass	7.00	5.04	5.14	5.60	6.07

Results

Scenario 1 – key run

As a key run, the simulation with a value of $\phi = 0.45$ was used, corresponding to a fairly modest rate of increase in R/S as SSB declined.

Across the 20–100 cm size range, the individual size spectra behave regularly and stay close to log-linear with increasing F . This size range corresponds to the lengths of fish sampled reliably with trawl survey gear, and was used as the standard to be fitted by model runs. For the key run, all r^2 -values are >0.975 for F -values ranging from 0.2 to 3 (only for $F = 0.0$, $r^2 = 0.84$). The best-fit spectra show a steady progression of slope and intercept (Figure 1). The slope varies almost linearly with increasing F (Figure 2a), indicating a gradual release from predation by large fish, while the intercept increases asymptotically, with notional numbers of size zero fish increasing quickly until $F \sim 1$, and much more gradually thereafter (Figure 2b). Therefore, the strongly non-linear increase in intercept in combination with a consistent, gradual change in slope indicates that the model initially responds to increasing F with the production of large numbers of additional recruits from fish with intermediate L_∞ whose SSB increases through release from predation, but this compensation attributable to increased production of recruits is reduced above $F \sim 1$. Summary figures from this scenario provide a number of insights into the dynamics of the community as F varies. For $F > 1$, the average Wt in the sea and in the catch are essentially identical, whereas the latter are greater for $F < 1$ (Figure 3a). Both metrics declined consistently with increasing F , but the average L_∞ of all fish in

the community >10 cm did not respond consistently to F , increasing to a maximum at around $F = 0.7$ and then decreasing (Figure 3b). Only when average L_∞ was calculated for all fish in size classes >30 cm did this metric decrease consistently with increasing F .

These results were not expected because, corresponding to the North Sea situation, fish with a relatively low L_∞ (sandeel-like) are fully exposed to fishing, with the same relative selection ogive applied as to fish with a larger L_∞ . Perhaps therefore only at low F are species with large L_∞ able to produce enough pre-recruits to constitute a noteworthy fraction of all small fish. Total catch from the modelled community increased with community-wide F nearly up to $F = 2$, and catches of different L_∞ groups show different, but individually consistent, patterns (Figure 3c). Total catch (i.e. from all sizes) of large species ($L_\infty > 60$ cm) peaks at $F \sim 0.5$ and declines steadily thereafter, whereas catch of those with L_∞ in the 30–60 cm range peaks around $F = 1$, although at a lower maximum value. Catch from the smaller species ($L_\infty < 30$ cm) continues to increase until $F \sim 2$, producing a much greater overall catch, but at F -values at which catches from larger fish are very small.

Changes in F also change the catch composition. For all F , catch is greatest from the 10 cm L_∞ group, reaching high levels at high F (Figure 4). At low F , the three largest L_∞ groups contribute more catch than any of the others except the 10 cm one. As F increases, progressively smaller L_∞ groups produce the greatest catch.

Changes in the abundance of predators of various sizes affect the rate of predation mortality in the community, and how it is distributed among different prey sizes. Understanding this relationship is crucial to evaluating indirect

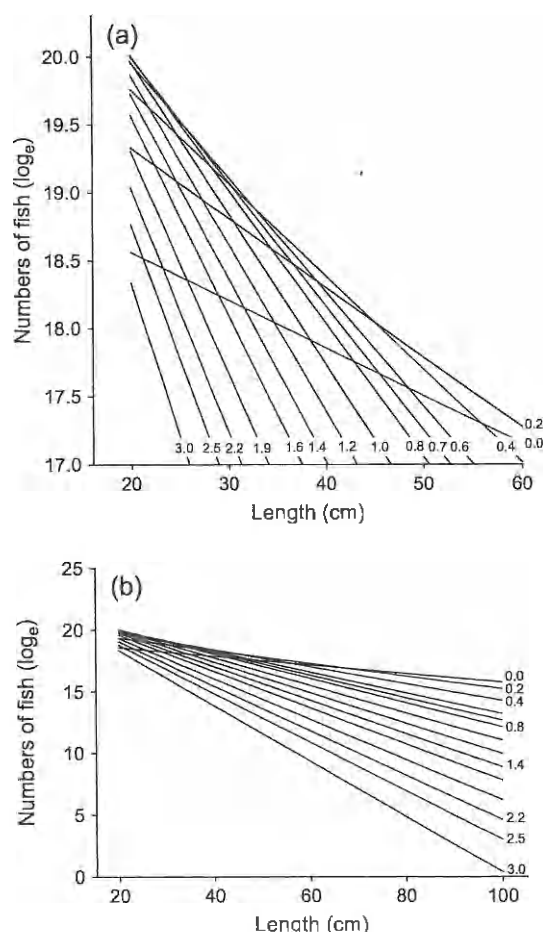


Figure 1. Best-fit log-linear regression lines for the simulated 13-species fish community, for values of fishing mortality (F) = 0, 0.2, 0.4, 0.6, 0.7, 0.8, 1.0, 1.2, 1.4, 1.6, 1.9, 2.0, 2.2, 2.5, and 3.0. (a) Detail and (b) full spectra.

fishery impacts in an ecosystem context. M_2 on 5 cm fish is high relative to M_2 on larger sizes at all F , but ranges from 1.8 when $F=0$ to 0.2 when $F=3$, illustrating that reduction of predators affects the survivorship of even pre-recruits (Figure 5a). The M_2 response to changes in F is very large for 5–15 cm fish, indicating that the trade-off in mortality between predation and fishing is an important dynamic component of exploited communities. For $F > 1.4$, essentially all mortality on fish > 20 cm is due to fishing. For intermediate F (~ 0.8 – 1.4), M_2 declines rapidly with prey size to nearly zero on prey > 30 cm.

The model also provides estimates of how total biomass and catch respond to the changing balance between F and M_2 (Figure 5b). Total biomass decreases consistently as F increases, and most rapidly as F goes from 0 to ~ 0.5 . Over this interval, removals by catch and predation combined decline marginally, because biomass no longer removed by predators is, nonetheless, removed directly by

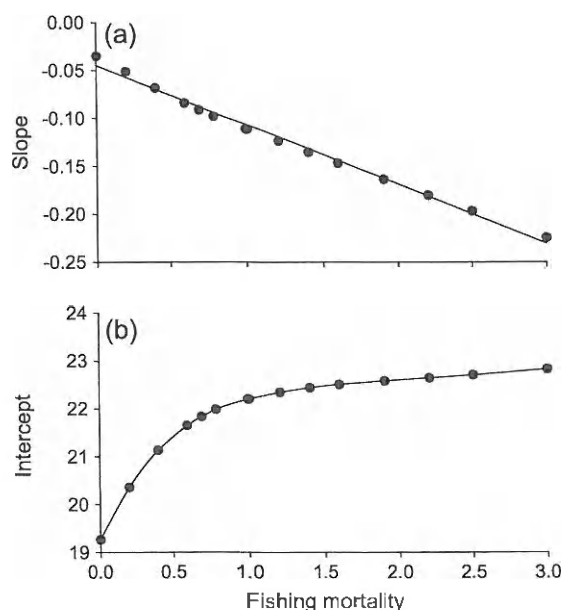


Figure 2. (a) Slopes and (b) intercepts of the key-run size spectra as a function of fishing mortality (F).

fishing, which takes larger individuals. Above $F \sim 1.4$, the catch stabilizes while biomass consumed continues to decline. Although total removals rapidly decrease, total biomass declines at a rate comparable with the decline in biomass eaten. At $F > 2$, catch, biomass consumed, and total biomass all decline, reflecting a community that is severely stressed.

The effects of fishing and predation on numbers by L_∞ group for two size classes (5 and 15 cm) are presented in Figure 6a and b. Fish with $L_\infty > 110$ cm decline at all values of F , and at faster rates for larger L_∞ . The small and intermediate L_∞ groups increase in the lower F -range but then decline, with the greatest response in the intermediate L_∞ groups. This change in community composition, a decreasing proportion of fish with the capability of growing to large sizes, is an important indirect effect of fishing, and is reflected in community metrics such as average L_∞ (Figure 3b).

The model also allows exploration of the recruitment dynamics of each species as it enters the fishery (Figure 6c). For $L_\infty < 30$ cm (the top three lines), recruitment is stable throughout. For species with intermediate L_∞ , recruitment increases substantially up to $F = 0.7$, and subsequently declines slowly. For larger species, any initial increase in recruitment is small in absolute and proportional terms, and peak recruitment is reached at a much lower F (less than $F = 0.5$ for all $L_\infty > 100$ cm).

The corresponding dynamics of SSB (Figure 6d) show a continuous decline with F for species with $L_\infty \geq 90$ cm, and progressively more steeply for larger species. For species with $L_\infty > 30$ and < 60 cm, the trend is dome-shaped.

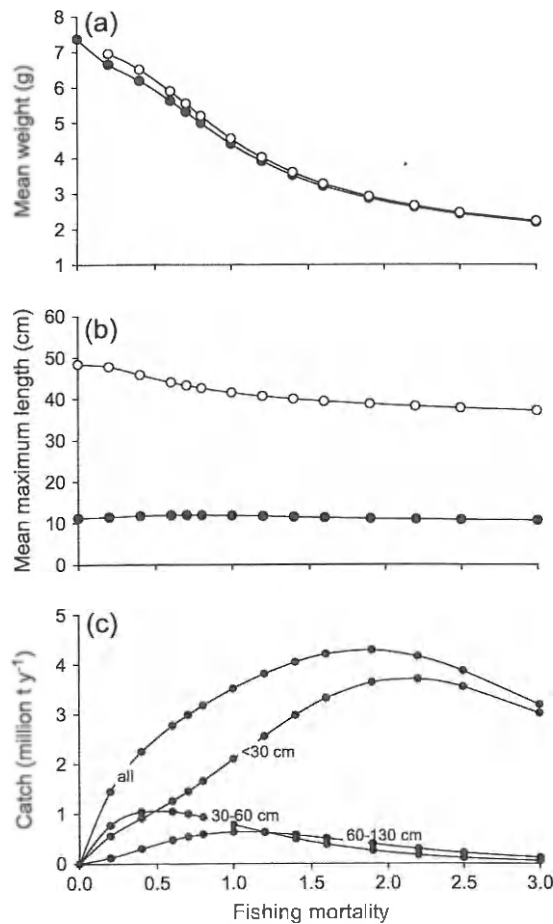


Figure 3. Key run: (a) mean weights of a fish in the sea (filled circles) and of a fish in the catch (open circles) for fish ≥ 5 cm, (b) average L_{∞} of all fish in the community within size ranges 10–130 cm (filled circles) and 30–130 cm (open circles), and (c) catch for various L_{∞} classes and total catch, all as functions of fishing mortality (F).

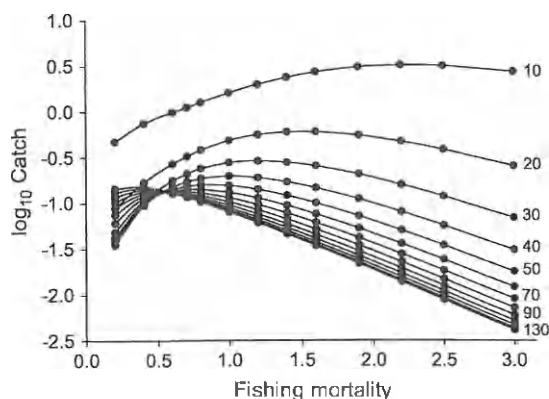


Figure 4. Key run: catch (million t) as a function of fishing mortality (F) for individual L_{∞} groups (10–130 cm; not all lines are labelled).

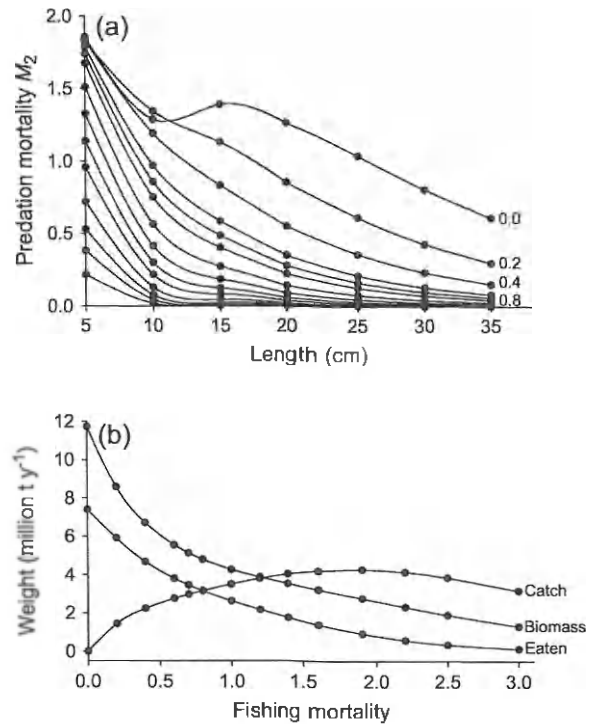


Figure 5. Key run: (a) predation mortality (M_2) by length class in relation to fishing mortality (F ; cf. Figure 1) and (b) trends in SSB (biomass), and removals by the fishery (catch) and by predators (consumed) as a function of F .

For the two smallest L_{∞} groups, the trade-off in community-scale F and M_2 produces a U-shaped response in SSB, apparently another indirect effect of fishing.

Alternative scenarios

The three alternatives to the key run were tuned to match as far as possible the same biomass, size spectrum slope, and other constraints at $F = 0.7$, but differed in the degree that R/S increased to compensate for declining SSB. The lower ϕ (scenario 2) makes recruitment decrease more slowly as exploitation and predation reduce the numbers of spawners. A higher ϕ (scenarios 3 and 4) makes recruitment vary more proportionately with SSB. Reduction of SSB by fishing will result in fewer recruits entering the community as small fish, but also fewer predators on the small fish. It should be noted that the four models have been parameterized differently, so the resultant communities at $F = 0.7$ are not strictly comparable, because they conform differently to the various constraints applied to mimic the North Sea. Therefore, the outputs are not strictly comparable in absolute terms, but the emerging differences in patterns in various metrics in response to variations in F may be attributed to the differences in the R/S parameter ϕ .

For all scenarios, the slope of the size spectrum becomes steeper as F increases (Figure 7a), but the pattern becomes

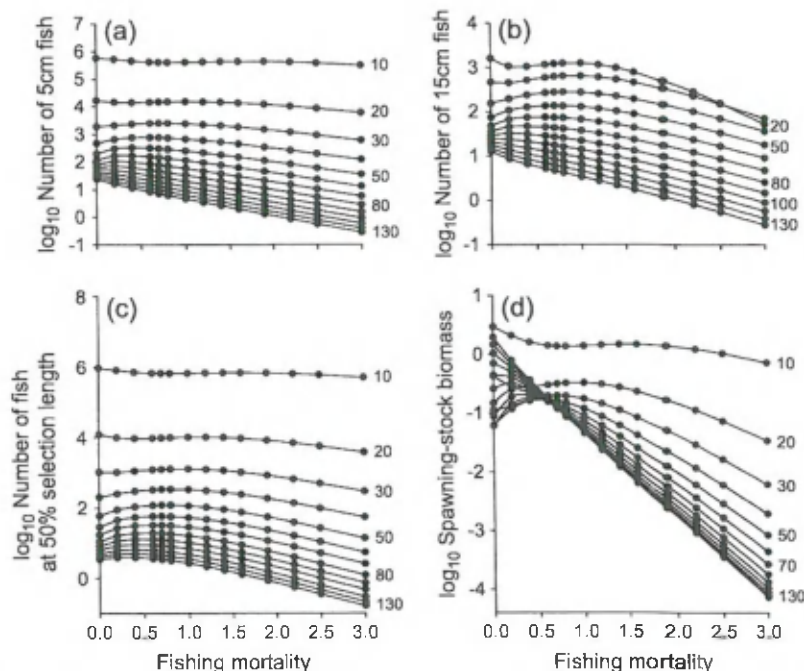


Figure 6. Numbers of fish (millions) in the (a) 5 and (b) 15 cm size class, and (c) at 50% selection length and (d) spawning-stock biomass (SSB, million t) as a function of fishing mortality for individual L_{∞} groups (a, c, d: 10–130 cm; b: 20–130 cm; not all lines are labelled).

more irregular if compensation is reduced (higher φ). At $\varphi = 0.95$, the alternating phases of gradual and steep changes in slope suggest that the community may have states where the changing recruitment rate controls the community

dynamics and states where predation mortality exercises the control, depending on the fishing mortality imposed.

In contrast to the relative stability of the changes in slope with F for different levels of recruitment compensation, the patterns for the spectrum intercepts varied greatly among the scenarios (Figure 7b). At $\varphi = 0.25$, the intercept keeps increasing even when $F = 3$. For $\varphi = 0.75$, the intercept increases until peaking at $F \sim 1$, at a value of only 60% of the intercept at $F = 1$ in the key run. If F is increased further, the intercept declines gradually. For $\varphi = 0.95$, the intercept hardly responds to increasing exploitation until $F > 1.3$. Above that value, productivity undergoes a collapse, dropping more than five orders of magnitude as F increases to $F = 2$.

With high compensation, the increase in R/S with declining SSB allows the community to continue to produce many small fish as stocks are depleted by fishing, and increasing numbers survive until size of recruitment to the fishery as predation mortality is reduced through the depletion of the predator field. As compensatory recruitment is weakened, the numbers of small fish can still increase at high F , because the reduction in M_2 by harvesting large predators is greater than the reduction in production of offspring by a diminishing SSB. This compensatory community-scale process is limited, however, and the effect of reduced SSB dominates if $F > 1$.

For scenarios 1–4, the maximum total catch is obtained with an F in the range 1.60–2.04 (Table 3). Catches of small fish dominate catches at most $F > 1.0$, and the maximum catches of L_{∞} groups > 80 cm were taken roughly at

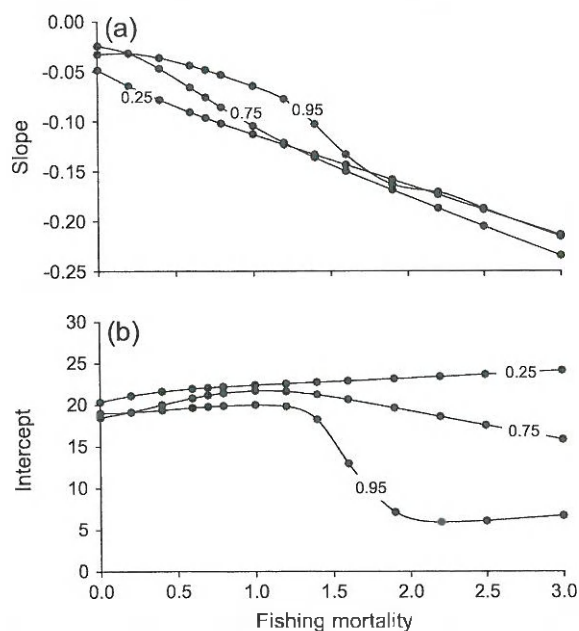


Figure 7. Relationships between (a) slopes and (b) intercepts of size spectra and fishing mortality (F) for three scenarios representing different values of the power term in the stock-recruit relationship ($\varphi = 0.25, 0.75, 0.95$; cf. Figure 2 for the key run – $\varphi = 0.45$).

Table 3. Values of selected community properties for the four simulacra.

Parameter	Selection	Scenario			
		1 (key run) ($\phi = 0.45$)	2 ($\phi = 0.25$)	3 ($\phi = 0.75$)	4 ($\phi = 0.95$)
Maximum catch (corresponding F -values in parenthesis)	Total	4.30 (2.02)	4.64 (1.85)	4.51 (1.75)	5.24 (1.60)
	$L_{\infty} > 60$ cm fish	1.04 (0.49)	0.98 (0.64)	1.34 (0.52)	1.53 (0.61)
	$30 < L_{\infty} < 60$ cm fish	0.63 (1.05)	0.71 (1.25)	0.41 (1.06)	0.03 (1.35)
	$L_{\infty} < 30$ cm fish	3.71 (2.25)	3.62 (2.50)	4.32 (1.77)	5.23 (1.68)
Total biomass	At $F = 0$	11.73	10.45	15.33	13.14
	At $F = 1$	4.27	4.78	4.14	5.01
	At $F = 1.9$	2.77	3.19	2.63	2.84
	At $F = 3$	1.32	1.82	0.45	0.01
Biomass consumed	At $F = 0$	7.39	6.99	8.99	9.38
	At $F = 1$	2.63	2.90	2.30	3.27
	At $F = 1.9$	0.93	1.24	0.45	0.64
	At $F = 3$	0.15	0.35	0.01	8×10^{-6}
Total catch	At $F = 0$	0	0	0	0
	At $F = 1$	3.51	3.81	3.40	3.82
	At $F = 1.9$	4.28	4.63	4.19	4.52
	At $F = 3$	3.19	4.08	1.11	0.23
M_2					
5 cm fish	$F = 0$	1.98	1.84	1.75	1.98
	$F = 0.4$	1.95	1.79	1.39	1.55
	$F = 3$	0.45	0.19	0.05	0.0
10 cm fish	$F = 0$	1.36	1.30	1.25	1.81
	$F = 0.4$	1.10	1.19	1.20	1.79
	$F = 3$	0.04	0.06	0.01	0.0
15 cm fish	$F = 0$	1.24	1.39	1.61	2.35
	$F = 0.4$	0.67	0.83	1.16	1.71
	$F = 3$	0.03	0.01	0.0	0.0
35 cm fish	$F = 0$	0.48	0.61	0.82	1.21
	$F = 0.4$	0.09	0.15	0.29	0.50
	$F = 3$	0.0	0.0	0.0	0.0

a value of F well below 1.0. With higher ϕ , the size composition of the catch increasingly develops a bimodal pattern. For $F < \sim 0.4$ most catch comes from the largest sizes, whereas for $F > \sim 1.5$, essentially all comes from the smallest sizes. The peak catch from the larger L_{∞} groups is taken at similar F , and catches drop rapidly once F exceeds 1. Likewise, catch from species with small L_{∞} peaks at lower F . Once the F producing this maximum catch is exceeded, however, catches drop rapidly. Catch from the intermediate species is low for all F , and negligible in scenario 4.

These patterns suggest that with weak recruitment compensation the community is becoming "wasp-waisted", with relatively more fish accumulating in the larger and smaller L_{∞} classes, whereas the intermediate sizes are

suffering combined effects of exploitation, low productivity, and some predation mortality.

In scenario 2, the community has a 15% smaller total biomass at $F = 0$ than in the key run. However, the decline with F is more gradual over the full range of F , such that there is $\sim 30\%$ more biomass in the community at $F = 3$. This is a consequence of productivity being maintained, not of reduced predation. In fact, the biomass consumed is only 5% different between scenarios 1 and 2 for $F = 0$, but declines more slowly in scenario 2 (Table 3); at $F = 3$, predators eat more than twice as much biomass at the lower ϕ .

Compared with the key run, total biomass starts out higher in scenarios 3 and 4, but declines more quickly with increasing F . The greatest biomass is reached in scenario 3, but all scenarios produce similar biomasses at

$F \sim 2$; beyond that, F -value biomass declines steeply as ϕ increases. At $F=0$, predators in scenarios 3 and 4 eat 20–30% more biomass than in the key run. However, as predator populations are reduced by fishing, the biomass consumed declines steeply, such that at $F=2$ it has fallen by 95% and at $F=3$ it is almost zero. When the stock-recruit relationship compensates weakly for decreasing biomass, the role of fishing quickly comes to dominate over predation at the community scale.

The interplay between catch and M_2 is clear from the differential impact of F on M_2 at length. For all scenarios, M_2 at $F=0$ is of a similar magnitude for the smallest fish (Table 3), but substantially higher for larger fish when stock-recruit compensation is weak (scenarios 3 and 4).

The interaction of compensation attributable to changing R/S and M_2 is clearly present in the patterns of SSB (Figure 8) and recruitment (Figure 9) as a function of F . For $\phi = 0.25$, the relationship between SSB and F is almost linear for all L_∞ groups, but patterns become increasingly more complex with higher ϕ (cf. Figure 6d). The peak SSB for a given L_∞ species also shifts to higher F with greater ϕ , while its absolute value becomes less, especially for larger species. Remarkably, at high ϕ , the biomass of the community becomes totally dominated by small and large species.

When ϕ is low, the numbers of different L_∞ fish in the 5 and 15 cm size classes show very little differential response to F apart from decreasing regularly (Figure 9). In contrast, there are more 5 and 15 cm fish with large L_∞ than with intermediate L_∞ at $F < 0.5$ in the higher ϕ scenarios, and this inequality increases as F declines towards 0. In scenario 4, both recruitment and SSB drop precipitously at $F > 1.3$ for all but the smallest L_∞ species. This indicates a dramatic change in a community whose aggregate SSB would have appeared resilient to exploitation up to that point, with several species increasing in SSB, and relatively abundant ones holding their own.

Applying differential F by size

In the scenarios discussed so far, F was applied to all size groups according to a linear multiplier rule. However, fisheries on different size groups may (at least partly) be managed separately, and there has been much debate about the impacts of industrial fisheries on ecosystems (Croxall *et al.*, 1992; Furness, 1999; ICES, 1999). The model allows differential F to be applied to large and small sizes of fish. The effect on several community-level outputs was evaluated for the key-run scenario ($\phi = 0.45$).

Simulations were made by maintaining the size-based selectivity for each L_∞ group, but setting overall F equal to 1 and modifying the species effort multiplier (λ) so that F for the 10 and 20 cm L_∞ groups (F_{small}) and the 30–130 cm L_∞ group (F_{large}) were independent. For both groups, F was varied from 0.0 to 1.5 in steps of 0.3 (36 combinations).

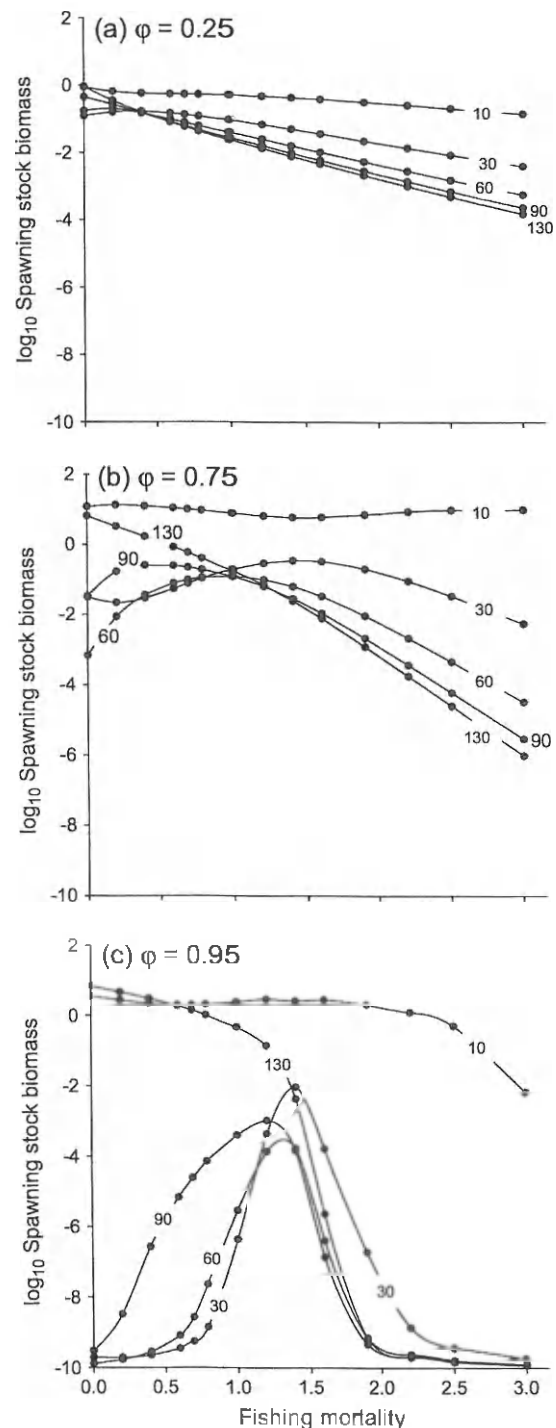


Figure 8. Spawning-stock biomass (SSB, million t) by selected L_∞ group (see labels) as a function of fishing mortality (F) for three values of the power term in the stock-recruitment relationship. (a) $\phi = 0.25$; (b) $\phi = 0.75$; and (c) $\phi = 0.95$.

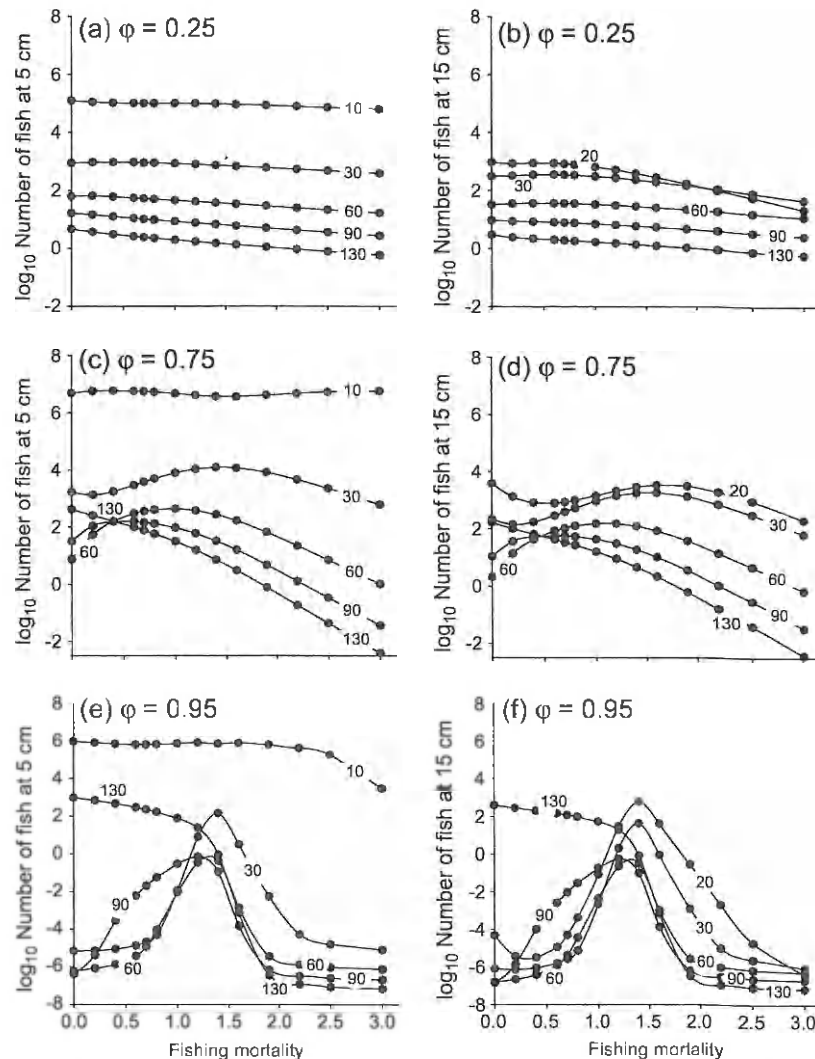


Figure 9. Numbers of fish (millions) in the 5 and 15 cm size classes as a function of fishing mortality (F) by selected L_∞ group (see labels) for the three values of the power term in the stock-recruit relationship; (a) 5 cm, $\phi = 0.25$; (b) 15 cm, $\phi = 0.25$; (c) 5 cm, $\phi = 0.75$; (d) 15 cm, $\phi = 0.75$; (e) 5 cm, $\phi = 0.95$; and (f) 15 cm, $\phi = 0.95$.

The slope is sensitive to F_{large} , but is insensitive to F_{small} (Figure 10a), whereas intercepts are sensitive to both (Figure 10b). The mediation of predation is apparent in the non-linearity of the intercepts, because at low F_{small} , even a high F_{large} does not produce a large intercept; the effect of increased F is compensated for by reduced M_2 . However, if F_{small} is high, then the intercept increases steadily with F_{large} and the entire community becomes more productive.

Both total catch (Figure 10c) and total biomass (Figure 10d) respond differentially to variations in F on the two size groups. The two responses are reciprocal, as expected, but catch responds more than biomass. Total catch is highest with high F on both size groups, whereas high catches from the community are not possible if F_{small}

is low. In fact, catch drops when F_{large} is high and F_{small} is low, whereas catch increases consistently with F_{small} , at all levels of F_{large} . Catches of large, intermediate, and small fish vary considerably depending on the relative and absolute values of the F on the two size groups. We omit the details here, but the patterns suggest that the interactions between size-specific F and M_2 are complex.

Biomass responses are less dynamic. Biomass is low with even moderate F_{small} , regardless of F_{large} , while total biomass is only high if F_{large} is low, even if F_{small} is substantial. This suggests a strong trade-off between the mortality caused by fishing and by predation in the community, when predator biomass is large.

The reciprocal effect of predation on the response of catches to varying size-specific F is clear from the contour

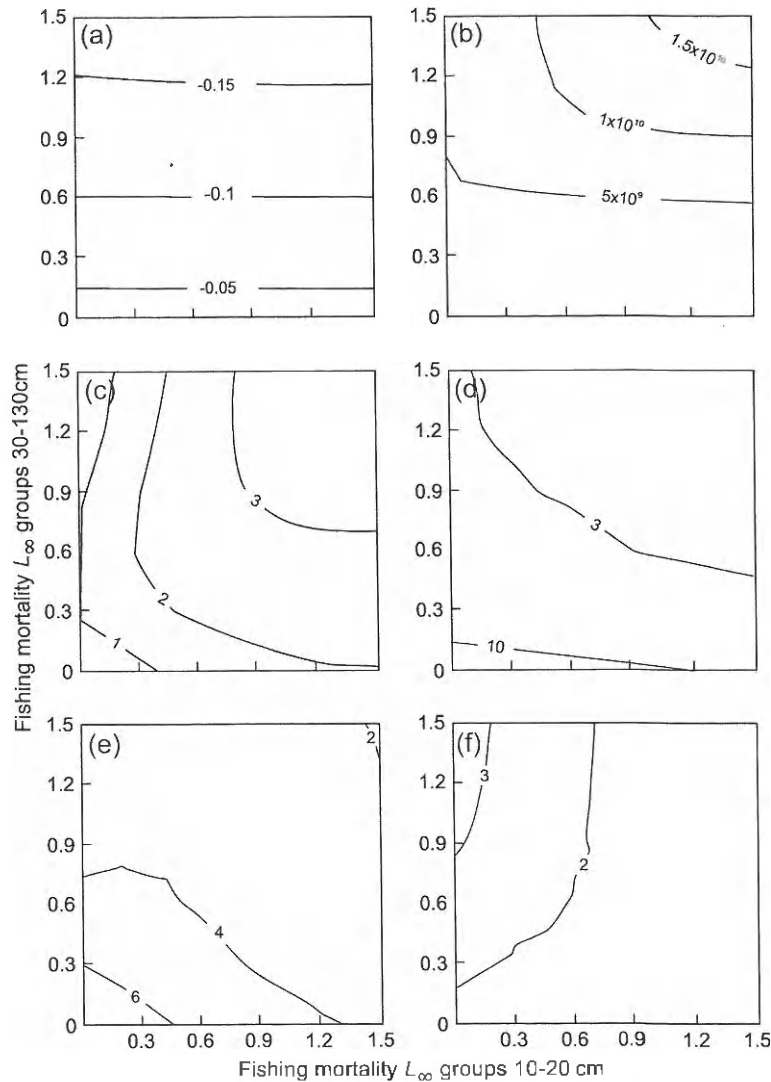


Figure 10. Contour plots of (a) slope of size spectra, (b) intercepts of size spectra, (c) total catch (million t), (d) total biomass (million t), (e) biomass consumed (million t), and (f) maximum predation mortality (M_2) as functions of fishing mortality (F) on small (<30 cm) and intermediate-large (30+ cm) species.

plots of biomass eaten (Figure 10e) and M_2 inflicted (Figure 10f). Biomass eaten is stable over a wide range of both F_{small} and F_{large} . However, when F_{large} is low, the amount eaten declines steadily as F_{small} increases, illustrating the partial trade-off of catch and predation when predators are not being exploited heavily. When $F_{\text{large}} > 0.6$, however, consumption remains fairly constant regardless of F_{small} .

The stability of consumption also translates into maximum M_2 -values that vary only gradually over a wide range of F_{large} . Maximum M_2 responds inversely to F_{small} , decreasing as biomass lost to fishing substitutes for biomass lost to predators. The trade-off becomes somewhat stronger as F_{large} increases.

Overall, the contour plots show that, although the dynamics of the predation interactions do not compensate

fully for changing rates and patterns of exploitation on fish of various size, there is some buffering. In particular, moderate fishing on small fish does not appear to jeopardize the catch of larger species.

Discussion

Model structure

The model structure has been chosen for its simplicity and for its parsimonious parameterization. It uses 15 parameters to describe a 13-“species” community, many fewer than required by MSVPA (Pope, 1991) and mass-balance representations (Christensen, 1995) of similar communities. This, of course, has limitations. For example, the model does not

account for the variations in mortality schedules, food size preferences, metabolic demands, and realized life-history trade-offs seen in real species, because these characteristics of "species" are defined only by their asymptotic size. Also, possible predator saturation effects have been excluded and more consideration should be given if, and where, it is necessary to conserve mass balance. Introducing mass-balance constraints will not be straightforward, however, because the biomass in the smaller size groups obtains much of their food from outside the fish community being modelled. Nonetheless, despite such limitations, the model behaves in a coherent fashion and describes broadly believable fish community responses to fishing pressure that are consistent with available evidence in the North Sea (Greenstreet and Hall, 1996; Rice and Gislason, 1996; Jennings *et al.*, 1999; Daan *et al.*, 2005).

A further development would be to adapt the model structure so that transitional situations can be simulated. This would provide additional insight into how a community might respond through time to exploitation change and augment the information on the steady states that the model currently provides.

Parameter choice

We chose to maintain a constant growth model across the various simulacra and to vary the stock-recruit relationship in a systematic fashion. Some other parameters are mostly concerned with establishing the appropriate scale of the simulated community and its balance between large and small species. Other parameters are adapted to keep M_2 within sensible limits, based on results obtained with multispecies VPA. Future work could modify parameter choices to adapt the model to simulate plausible communities with different characteristics, such as one dominated by clupeid-type species, or a characteristic of a different temperature regime or environmental forcing, to explore the generality of our findings.

Although not reported here in detail, we did examine the sensitivity of the model to the choice of all parameters. This was helpful in modifying the parameters to achieve simulacra that met as far as possible the pre-set constraints. Given the general exploitation pattern adopted for all four simulacra, either slope or biomass was in general less variable than the other constraints. Therefore, it is not possible to satisfy the biomass constraint, and not always possible to satisfy the slope constraint without larger violations of other targets. These two targets appear to be fixed largely by the imposed exploitation regime, the given balance of catches by size group, and by consumption level.

A more objective means of selecting parameter values could be developed to meet the constraints according to some objective measure of goodness-of-fit. Currently, it is not obvious how weights can be assigned to individual target constraints. Giving the relative deviation of the model from each constraint equal weight and using the Solver

function in Excel to estimate some parameters in the baseline scenario resulted only in minor changes. The most important were an increase in the preferred predator-prey size ratio μ by 21%, and a reduction in overall fishing mortality by 17%.

We also explored the alternative of taking as many parameter values as possible from independent literature sources, but existing overviews did not meet our needs. For instance, although the parameters in Charnov (1993) are internally consistent, natural mortality is represented as a single parameter, not disaggregated into predation and non-predation sources. Because the interaction of M_2 with stock-recruit dynamics was central to our investigations, these parameters could not be used directly as a starting point. *Ad hoc* efforts to overcome this shortcoming produced an alternative set of parameters that were explored in the model. Results of these exploratory runs were similar to the results presented in all major patterns, increasing our confidence that, within the limitations of our simple model, the life-history relationships are reasonably consistent with theoretical expectations.

Key patterns

The results are consistent with other work that indicates that the slope of the size spectrum is a good indicator of the level of F on the community (review by Shin *et al.*, 2005). This relationship applied well over the full plausible range of F in all four simulacra, suggesting that it is quite a robust indicator. However, there is no suggestion that a particular value for the slope should be desirable for all systems. Rather, changes in slopes provide relative and comparative information over a wide range of parameter settings.

Model results are also consistent with the emerging idea that the intercept of the size spectrum has informative dynamics, particularly when stock-recruit compensation is weak, although it is hard to estimate accurately for real data sets (Daan *et al.*, 2005). Measures of community productivity are particularly hard to acquire, while in our simulations it was possible to predict the F that would cause productivity to decline. Therefore, if the dynamics of the intercept do reflect impacts of fishing on the integrated productivity of the exploited community, this metric might be another useful relative indicator for management. However, other natural or anthropogenic factors may also influence the productivity of a fish community and hence the intercept of community size spectra in the sea.

For the simulacra with higher values of ϕ , the simulated numbers at size tended to become highly bimodal. This strong tendency had large impacts on catches and distributions of M_2 -values among the species. The patterns observed suggest that when recruitment compensation is weak, underneath a generally linear size spectrum the life-history composition of the community may change dramatically as F increases. The bimodality suggests some form of "wasp-waisted" community, but the pattern observed

here is not identical to the “wasp-waisted” systems *sensu* Rice (1995) and Cury *et al.* (2003), which refer to a limited number of species in the middle of a foodweb. Still, there may be functional analogies when being a species of an intermediate size class is a less viable strategy. It would be interesting to know if more natural communities could show this pattern of distribution of biomass into larger and smaller fish species, were F on the communities to be reduced substantially. Alternatively, these results might suggest that one should expect to see biomass distributed in a bimodal way more often in communities where there is little compensation of R/S with changing SSB .

Taken together the simulations have an important message. Even when the stock-recruit relationship provides little response of recruitment to changing SSB , predation dynamics maintain the linearity of the relationship between the spectrum slope and F . Communities with weaker compensation must start off more productive, and the productivity continue to increase until SSB of most large predators is depleted. Increasing exploitation beyond that point produces communities with much lower productivity, suggesting that if large predators have been fished out, fishing mortality should be lowered on the remaining smaller species, to avoid a community-scale decline.

In considering the relative role of stock-recruit compensation and predation in controlling community dynamics, it appears that at low F , species with intermediate L_{∞} pay a double cost of heavy M_2 on their pre-recruits while bearing some M_2 themselves. However, they are unable to compensate for the heavy M_2 with increased productivity as effectively as species with smaller L_{∞} . As F increases, stock-recruit dynamics rapidly take control over community dynamics, and the productivity of the intermediate sized species at low biomass becomes expressed according to its ability to compensate with increased R/S .

The compensation processes described lead to an important pattern in various size-based metrics that have been proposed as indicators of the effects of fishing, such as mean body size, mean maximum body size and, for a given mean μ , the change in mean trophic level (Shin *et al.*, 2005). Average weight in the sea and in the catch decreased consistently with increasing F in the key run, suggesting that these metrics had several properties of good state indicators (Rice and Rochet, 2005). However, when calculated for fish in all L_{∞} classes, average L_{∞} did not respond consistently to F , reflecting the effects of M_2 and F on abundance in intermediate size classes. At low F , intermediate size classes could tolerate F and benefited from reduced M_2 as their predators were depleted. Their abundance and the M_2 they inflicted on small size classes both increased, as did the average L_{∞} . At higher F , the intermediate size classes could not maintain their biomass, and average L_{∞} decreased. Only when average L_{∞} was calculated for fish in size classes >30 cm did it decrease consistently with F . This was due to the size range considered spanning approximately two rather than three trophic levels, such that there was a simple

relationship between increasing F and the consequent relaxation of M_2 . These results suggest that the size classes to be included when developing and interpreting indicators of community size composition need to be carefully considered in relation to the trophic structure and likely strength of the trophic interactions in the community.

Decreasing predation mortality acts to buffer the direct effects of increasing fishing on the various size classes in all four scenarios, but the nature and the magnitude of the effect depends both on F and on the degree of compensation. The effect was large for enough of the (F, ϕ) combinations to conclude that it would be unwise to ignore the potential interactions in an ecosystem management context. The size-structured simulation approach is particularly promising as a tool to inform management about possible risks and consequences of various multispecies harvesting strategies, because although effects of predation are indeterminate in species-based models (Rice, 1995; Bax, 1998; Yodzis, 2000), they can behave predictably in size-based approaches. For example, arguments that moderate fishing on small fish jeopardizes catches from larger fish species are not supported strongly by the results here. The relationships are complex, but only when F on larger fish is well above the F associated with highest catch does F on small fish affect catches from the larger fish, and the effect of exploiting the small fish, although weak, is actually positive on catch from the larger fish. Predation interactions are more important in the context of how catches of intermediate fish respond to the exploitation of fish of different size.

Processes structuring communities

In developing the model, some compensatory feedback (similar to density-dependent mortality on recruitment, but not necessarily acting as a density-dependent recruitment term) had to be present in the community dynamics, or the model tended to end up with all the biomass in one (or perhaps one large and one small) size class that had a particularly favourable balance of growth and mortality inflicted by fishing and predation. We structured species-specific compensation into the stock-recruit relationship through the power term, although it could have been placed in the growth parameter instead. The large impact of this parameter suggests that it would be important to examine data from real multispecies data sets, to see where compensation is actually expressed, and how strongly it is manifest in community dynamics.

The dynamics of the model included further compensation at a community scale, via the predation mortality inflicted by the predator biomass. The compensation in changing predation mortality can linearize the size spectrum even when the stock-recruit compensation is weak. We may therefore see the existence of compensatory feedback of two types: (i) a community-level compensation process based on the overall predation mortality at size that limits the ultimate size of the community, but places little constraint on

species and (ii) a species-level compensation attributable to stock recruitment or other species-specific processes that tends to limit the proportion of the total biomass that a species can represent. We suspect that the former process may dominate in lightly exploited communities and those with variable exploitation histories. This may be why other density-dependent controls are often hard to find.

Hypothesis testing

The chief purpose of developing the model was to test hypotheses about the processes that structure marine fish communities. Specifically, the model was designed to allow a partial test of the hypotheses that size spectra have broadly linear slopes in the main size range of target demersal species (20–100 cm) and are a function of exploitation rate of the community. The model has conspicuously failed to falsify these hypotheses, because slopes were linear over a wide range of F , for a variety of formulations that fit the constraints in Table 2. We also sought insight into the mechanisms that can maintain such linear slopes. Our results indicate that the density-dependent controls by predation mortality at a community scale and by recruitment–SSB relationships at a species scale are key mechanisms, with their relative importance depending on current fishing intensity and exploitation history.

To investigate whether a linear size spectrum was an inherent property of the model, we fitted a second order polynomial to the spectrum and used Solver to search for parameter combinations that would increase its curvilinearity. A curvilinear spectrum could be produced indeed if recruitment to the larger L_{∞} was significantly reduced by changing the L_{∞} power adjustment (ϕ), but this resulted in a community consisting almost entirely of fish with an $L_{\infty} < 40$ cm. Communities dominated solely by species of very small body size are not known in open marine environments, even when fishing has artificially modified community structure to favour small-bodied species (Bianchi *et al.*, 2000).

Further ideas may be tested, or at least explored, with appropriate extensions of the model. In this respect, the parsimonious parameterization is of great benefit because it does not use the whole data set available for model fitting (which would leave nothing for hypothesis testing). This is a rare virtue among multispecies models. For example, the numbers recruiting by L_{∞} group might be compared with numbers derived from multispecies VPA, to see how the model results compare with assessment results.

Examples of other ideas that might be explored would be the assumption of independence of various ecosystem descriptors, and the information content of the intercept (or midpoint) of the size spectrum. Foodweb theory predicts that the number of pathways through ecosystems is important to understanding the impacts of exploitation on community structure (Yodzis, 2001). Exploring hypotheses about changes in the diversity size spectrum under different

exploitation regimes, to complement these explorations of the dynamics of the abundance size spectrum, may provide a tractable way of looking at diversity aspects of community dynamics and management. Both these types of model investigations could be expanded by systematic exploration of the effects of variance in mortality schedules, food size preferences, metabolic demands, and realized life-history trade-offs within “species” defined by their asymptotic size. The outputs of size-based models of community diversity also may provide insight into why species rarity evolves in communities.

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