

This paper is not to be cited without prior reference to the authors

International Council for the
Exploration of the Sea

CM 1999/Z:01
Ecosystem Management

Harvesting a Size-Structured Ecosystem

Daniel E. Duplisea and Mark V. Bravington

CEFAS Lowestoft Laboratory
Pakefield Road, Lowestoft
Suffolk NR33 0HT
United Kingdom

fax: +44 1502 524511
e-mail: d.duplisea@cefas.co.uk
m.v.bravington@cefas.co.uk

ABSTRACT

Strategic decisions about fishing policy should entail multispecies considerations, and reliable management needs to be based on results that are robust to model uncertainty. Therefore, we considered two dynamic size-based models of hypothetical fish communities: (1) bottom-up, based on individual species (2) top-down, based on an aggregated community. The bottom-up model is a length-based version of Multispecies Virtual Population Analysis (MSVPA) where numbers of individuals in length-cohorts are tracked and species interactions are mediated by predation mortality. The top-down model is an energy flow model derived from biomass size spectrum theory which considers flow of energy through the aggregated community without regard to species. The effect of optimal size-based harvesting strategies on community properties such as stability and persistence of size-spectra, are compared between the two models. By comparing model results, we can identify which properties are robust to model uncertainty, and the processes, of which we know little, that can strongly affect results. These types of conclusions are needed both to direct further research and define the limits of management advice which can be derived from the models.

Keywords: size-structured models, optimal harvesting, robustness

1. INTRODUCTION

Ecosystem management is a concept that has found its way into the statute books before there is widespread agreement about what it means or how to do it. To be sure, there are some specific issues, such as conserving seabirds or sensitive benthic habitats, where fishery management can and has been modified to take ecosystem effects into account. But when it comes to the effects of fishing on the larger ecosystem, there is less scientific consensus about how to act. There are several possible reasons: two obvious candidates are the daunting complexity of interactions in an ecosystem like the North Sea, and the lack of any clear management objective for something as abstract as "the ecosystem". Despite the difficulties, though, fishery management will be compelled towards some kind of ecosystem management. Fishery science has a leading role to play in suggesting how this might sensibly be done.

The single-species management framework practised within ICES delivers numerous quantitative measures and targets. The apparent precision of these numbers is useful to managers in providing some objective justification for management actions (Gulland 1988). But the true precision is not as high as single-species models suggest. There are sometimes serious and unquantifiable data quality issues, particularly over the reliability of catch statistics; and then there are multispecies interactions. We know that multispecies interactions can be important, but we are not now, and never will be, certain about just how the interactions operate. Scientific integrity demands that our uncertainty be incorporated into assessment and projection models, but in doing so, we inevitably reduce the apparent precision. This has not endeared multispecies models to managers (Brugge and Holden 1991).

This problem really stems from a dependency on detailed species-level results. Even if data quality concerns were to vanish overnight, uncertainty about multispecies interactions will be with us for the foreseeable future. Since we are unlikely to be able to make precise predictions about single species, and since management often cannot control single-species removals very precisely anyway, it seems more sensible to consider management policies aimed at predictable composite properties of the ecosystem and the fisheries that exploit it. Such properties do exist: Dickie and Kerr (1982) cite a number of examples, including the stability of aggregate catch biomass compared to individual species catch, and the stability of catch revenue compared to catch biomass. Although stable aggregate properties are in principle susceptible to modelling, comparatively little research effort has been expended in this area.

There are two key points to be borne in mind when contemplating ecosystem management from a fishery perspective:

- Management must concentrate on inputs that can actually be managed. It is an old cliché, but true, that "managers control fishermen, not fish". There is little point in devising, say, single-species catch limits based on elaborate biological interaction models, if one is dealing with mixed-species fisheries that inevitably entail high by-catches.

- Management goals should centre on outputs that have clear interpretations, and which can be predicted reliably. Equilibrium yields of single species are interpretable, but not predictable in systems with strong multispecies interactions

With these considerations in mind, we consider in this paper a very simple set of controls (fishing mortality at size, independent of species) and simple outputs (yield in value or biomass). We present preliminary investigations of optimal yield strategies for the entire fished ecosystem, using two types of model: a species-level length-cohort model along the lines of MSFOR (multispecies forecast model) (Magnússon 1995), and a size-spectrum mass transfer model with no differentiation into species (Silvert and Platt 1981).

These models are quite different in scope and scale. The size-spectrum models represent aggregate group properties and spans at least 9 orders of magnitude in weight (Boudreau *et al.* 1991, Sheldon and Kerr 1972), while the MSVPA-type length-cohort model tracks individual 'species' and operates over about 3 orders of magnitude in weight. By using such different models, one can assess the robustness of management strategies and system properties, and identify important discrepancies which should guide the direction of further research.

2. METHODS AND RESULTS

For both types of model, we have investigated optimal fishing strategies over a range of "community types" or "ecosystem types". In the absence of analytical solutions to the optimal yield problem for these models, we have considered n -point fishing strategies, where fishing mortality is specified at 2, 3, or 4 body weights and interpolated linearly between these values. Optimisation then reduces to the problem of maximising the equilibrium yield over a 2, 3 or 4-dimensional parameter space.

2.1.1 length-cohort model methods

The length-cohort model is similar to MSVPA but it is length rather than age based. The model was set up in MS-excel to follow length-cohorts of individuals throughout their life. This model assumes that fish continue to grow throughout their lives, if only by small increments when large, and that this growth is not limited by any sort of resource. Ten species were set up initially which are distinguished by two independent life history parameters: r-K continuum classification and maximum size expressed as the von Bertalanffy L-infinity (Hilborn and Walters 1992). From these two independent parameters, three dependent parameters are calculated: von Bertalanffy growth rate, Beverton-Holt maximum recruitment level (Hilborn and Walters 1992), and Beverton-Holt slope at the origin. A species in the community is defined by the two parameters. Several other properties of the populations result from the species parameters such as predation mortality and residual natural mortality.

A baseline community was established which had roughly an equal mix of r-like and K-like species and a right-skewed L-infinity frequency distribution that corresponded to the English Groundfish Survey data for the North Sea. Different community types

were constructed by altering the component species or removing species, hence changing the species parameters.

2.1.1.1 predation mortality

Per capita predation mortality is calculated using the Holling Type II functional response of a predator on a prey population which is the same for as used in MSVPA (Hilden 1988). Type II functional responses divide a predator's foraging time into searching for and handling of prey and contains an attack rate parameter. In the present model, a predators handling time was made to increase with more K-like prey which is a reflection of evolved defences in these prey (e.g. spines). The attack rate was made to increase with more r-like prey as these prey are generally fast growing hence more active hence expose themselves to predation more frequently than less active K-like prey.

Per capita predation is multiplied by the number of predators to obtain total mortality on a prey (M_2). Predators are considered to be those fish in the two adjacent length classes that are two length classes larger than the prey. All species eat all others, including cannibalism. Two predators eating the same prey have the same per capita predation rate on a prey population but differences in numbers of these predators gives differences in the predation on the prey population between from the predator populations.

2.1.1.2 residual natural mortality

Residual natural mortality (M_1) is a U-shaped function (quadratic) of body length. That is, M_1 is high for fish at the extremes of their body size-range. High mortality in juveniles reflects dysfunctional birth attributes such that they die independent of predation. High mortality in large adult sizes reflects disease susceptibility of the older fish. The intercept of this quadratic is larger for more r-selected species.

2.1.1.3 stock-recruitment relationship

The Beverton-Holt formulation is used as the stock-recruitment relationship. The spawning stock is defined by setting a percentage of a species' L_{inf} at which it is considered mature. This percentage applies equally to all species in the system and is truncated to the nearest whole length class ≥ 1 . The maximum recruitment level is greater for more r-selected species which reflects the opportunist abilities of a r-like species.

2.1.1.4 relationship between natural mortality and growth rate

It has been shown that there is an empirical relationship between the von Bertalanffy growth parameter k' and the total natural mortality of fish stock (Pauly 1980). The value of M/k' ($M=M_1+M_2$) varies between about 0.3 and 5 for these various stocks. In this model, size specific M/k' varies between about 0.5 and 9. This difference between the model and the empirical relationship is small considering that a dynamic predation mortality and a varying residual natural mortality with body size is calculated in the model. For species with small L_{inf} and high rK classification, M/k' is quite large and vice versa, this is also found for some species groups (Pauly 1980).

Predation mortality is calculated with the assumption that all species prey upon all others, including cannibalism. If the food web input was altered, the constancy in predation mortality would vary considerably more across species hence the M/k' value would differ. This reflects the limitations of the original empirical relationship rather than a deficiency in the model.

2.1.1.5 value yield determination

A rough relationship was determined for value at size and species from MSVPA input data on value. The overall value of a species is a function of its maximum body size and the value of an individual of that species is a function of its body size. We determined the following relationship from MSVPA input data:

$$V_{il} = L_{infi}^{0.6} \cdot l^{0.42}$$

where V_{il} is the value of species (ECU/Kg) i at length l (cm), L_{infi} is the maximum length of species i and l is the length of the individual of species i .

2.1.2 length-cohort model results

The exploited baseline community numbers size-spectrum is generally linear but falls away from the linear trend at large body sizes (Fig. 1). The unexploited community numbers size-spectrum is far more linear throughout the body size range and the regression has an R^2 value near 1. The diversity size-spectrum is also linear with a

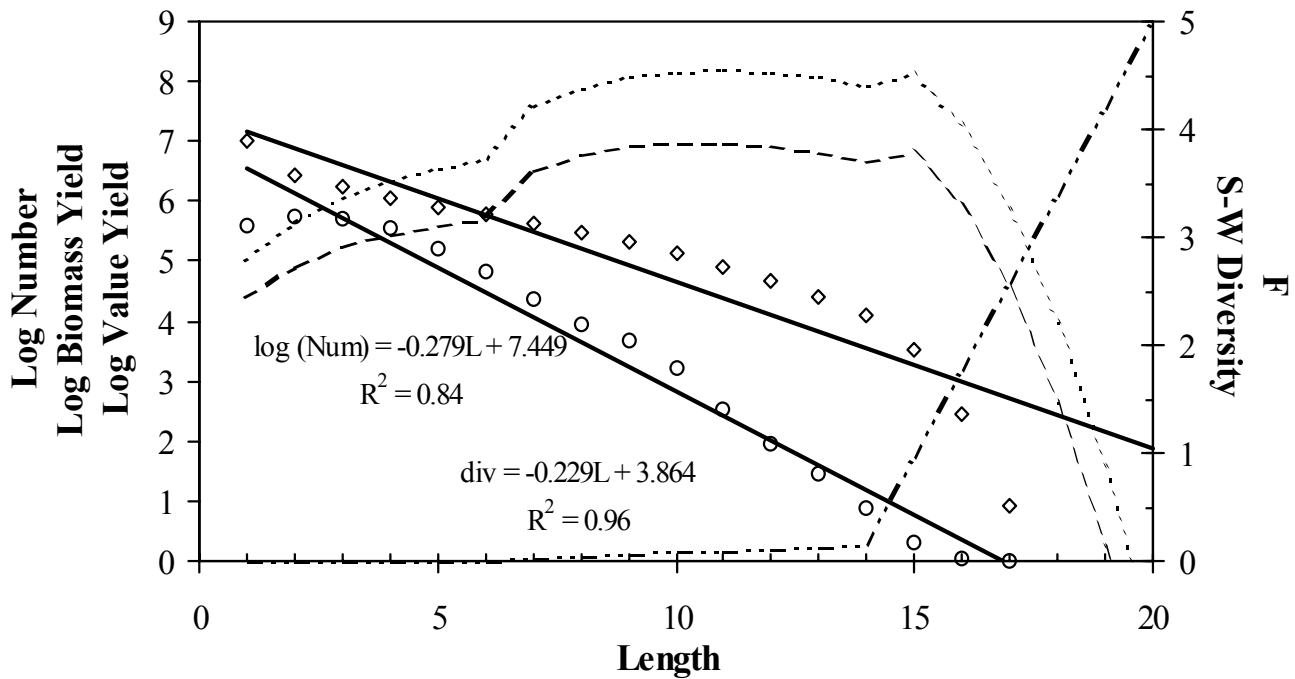


Figure 1: Numbers and Shannon-Wiener diversity size spectra, optimal equilibrium yield and F at size for the baseline community (Table 2, community 1). Triangles are the number size-spectrum, circles are the diversity size-spectrum, dotted line is the value yield curve, long dashed line is the biomass yield curve and the dashed-dotted line is the F at size curve. Linear regression equations for numbers and diversity size spectra. Units are arbitrary but internally consistent.

decreasing slope that does not differ much between the exploited and unexploited community. For the baseline community the optimal F at size pattern is with very low F at small size and large F at larger sizes. This exploitation pattern produces a hump shaped yield at size curve for both biomass and value.

In all the communities examined, the slopes of both the numbers size-spectrum and diversity size-spectrum are negative (Table 1). With fishing, these slopes steepen in all cases and the intercept increases for the numbers size-spectrum but is inconsistent for the diversity size-spectrum. Fishing steepens the numbers size-spectrum slope by 1.7 fold for the baseline community. The greatest difference in numbers size-spectrum slope with fishing occurs for the community where the three largest species are removed.

Table 1: optimal fishing strategies which maximise value yield for different communities using the length-cohort model. The baseline community is the reference for all other communities. Italicised values are those for the unfished community, other values are for fishing with at maximum equilibrium value yield.

community	size spectrum slope	size spectrum intercept	diversity slope	diversity intercept	system / yield value	system / yield biomass	min F	max F
1) baseline community	<i>-0.169</i>	<i>6.955</i>	<i>-0.196</i>	<i>3.767</i>	<i>12.0</i>	<i>260</i>	0	5.000
	-0.279	7.449	-0.229	3.864	104	6.47		
2) make the largest species extinct	<i>-0.230</i>	<i>7.170</i>	<i>-0.178</i>	<i>3.432</i>	<i>8.67</i>	<i>152</i>	0	5.000
	-0.367	7.651	-0.222	3.601	71.5	5.67		
3) reduces L_{inf} of largest species by 10%	<i>-0.208</i>	<i>7.146</i>	<i>-0.172</i>	<i>3.647</i>	<i>11.2</i>	<i>211</i>	0	0.288
	-0.340	7.682	-0.223	3.833	128	9.21		
4) make largest species pure r- selected	<i>-0.191</i>	<i>6.991</i>	<i>-0.189</i>	<i>3.752</i>	<i>11.6</i>	<i>214</i>	0	0.276
	-0.310	7.525	-0.235	3.856	158	10.4		
5) make largest species pure K- selected	<i>-0.191</i>	<i>7.000</i>	<i>-0.186</i>	<i>3.652</i>	<i>9.14</i>	<i>188</i>	0	0.165
	-0.340	7.660	-0.186	3.602	91.0	6.72		
6) make the three largest species extinct	<i>-0.255</i>	<i>7.082</i>	<i>-0.254</i>	<i>3.392</i>	<i>6.79</i>	<i>69.6</i>	0	3.395
	-0.540	8.035	-0.247	3.359	36.7	3.59		
7) change the community to small size and fast growing	unstable	unstable	unstable	unstable	unstable	unstable	unstable	unstable
8) change the community to small size and slow growing	<i>-0.281</i>	<i>7.244</i>	<i>-0.174</i>	<i>3.703</i>	<i>6.52</i>	<i>104</i>	0	1.243
	-0.461	7.722	-0.182	3.695	91.2	8.99		
9) increase recruitment potential	<i>-0.169</i>	<i>6.949</i>	<i>-0.194</i>	<i>3.755</i>	<i>12.0</i>	<i>260</i>	0	5.000
	-0.290	7.514	-0.232	3.866	188	11.8		
10) decrease recruitment potential	<i>-0.164</i>	<i>6.877</i>	<i>-0.184</i>	<i>3.623</i>	<i>10.6</i>	<i>255</i>	0	0.208
	-0.276	7.395	-0.224	3.731	189	11.9		

The difference in maximum yield of the system varies by two orders of magnitude between the different communities (Table 1). The greatest value and biomass yields occur for the baseline community (community 1) which contains a mixture of species with different life history parameters covering the range allowed in the model. The smallest maximum yield occurred in the system where the three largest species were removed (community 6), which was an order of magnitude less than the baseline. Making the largest species purely r-selected (community 4) did not increase the maximum yield in the system. In a community where species tended toward small L_{inf} and skewed toward the r portion of the r-K continuum (community 7) (as might occur in heavily exploited warmer seas), makes the community size-spectra unstable and no values could be reported. Similarly, instability occurs in a community of fast growing species with large L_{inf} .

Increasing and decreasing the recruitment potential of all the stocks (communities 9 & 10) did not substantially alter the slopes and intercepts of the diversity and numbers size spectra relative to the baseline community in both fished and unfished communities (Table 1).

F at size patterns for optimal value and biomass yield tends to be similar for all communities examined: no fishing on small individuals and heavy fishing on the large individuals (Table 1).

F/Mtot values vary between near 0 to 0.42, indicating that fishing can remove almost 50% of what natural mortality removes in each time step (Table 2). Generally, F/Mtot values are highest in species with large maximum body size (L_{inf}); however, F/Mtot depends on the growth rate (k'). The fishery has a relatively greater impact on slow-growing species rather than fast-growing species with similar L_{inf} values (Table 2).

Table 2: Characteristics of the baseline community at equilibrium under maximum exploitation rate. Parameters refer to those described in the methods. Mtot is the sum of predation mortality and residual natural mortality. F/Mtot for each species population was determined by the ratio of the sum of the products of population number and F and Mtot, respectively. Sums were computed only over the size range of reproductively mature individuals ($L \geq L_m$).

species	L_{inf}	k'	F/Mtot
1	22	0.036	0.234
2	7	0.033	0.007
3	6	0.036	0.005
4	18	0.017	0.429
5	8	0.035	0.006
6	9	0.030	0.013
7	13	0.031	0.103
8	17	0.028	0.313
9	5	0.038	0.004
10	12	0.033	0.063

1.1 size-spectrum model methods

Steady-state mathematical formulations for size spectra were developed first (Platt and Denman 1977, Kerr 1974), followed by a dynamic (time-varying) formulation (Silvert and Platt 1981), which we have taken as the basis for our model. In this simplified system, the only distinguishing characteristic of an animal is its body weight; this determines both what it is likely to eat, and what is likely to eat it. Predation is allometric (Thiebaut and Dickie 1992), so that all animals prefer to eat animals whose body weight is about a factor q lower than their own. Growth rate is proportional to ingestion rate, which in turn is proportional to the number and biomass of available prey, multiplied by a predation efficiency term which depends on predator size (Thiebaut and Dickie 1993). The model is assumed to start from an equilibrium solution in the absence of fishing, in which log biomass per log weight class varies linearly with weight.

The evolution of the ecosystem governed by a variant of Silvert and Platt's (1980) "master equation":

$$\frac{\partial n}{\partial t} = -\frac{\partial(ng)}{\partial w} - nz - nF \quad [1]$$

where t is time, n is number density, g is the per capita growth rate, w is individual weight, z is the natural mortality rate, and F is the fishing mortality rate. The quantities n , g and z are all continuous functions of both w and t , and F is a function of w alone. The number of animals between weights w_1 and w_2 at a time t is given by $\int_{w_1}^{w_2} n(w, t) dw$, and the equations for growth and mortality rates are

$$s(w, w')dw$$

$$g(w) = K\theta(w)\int_0^\infty w'n(w')s(w, w')dw'$$

$$z(w) = \int_0^\infty n(w')\theta(w')s(w, w')dw'$$

where K is production/growth/conversion efficiency, $\theta(w)$ is predator efficiency, and $s(w, w')$ is a prey selectivity function.

We ignore mortality from sources other than predation and fishing, and the influx due to reproduction. For the models considered, reproductive influx into a "typical" size class would be much smaller than influx due to growth from the next smaller class; and as Silvert and Platt note, reproduction considerably complicates the mathematics. Loss of parental biomass through reproduction is implicitly taken account of via the production efficiency. In order to keep the system going, we assume a constant rate of input of mass (i.e. primary production) in the lowest size classes.

Ecosystem dynamics are basically determined by three numbers: the production efficiency K , the size-spectrum slope at equilibrium ξ of $\log n$ on $\log w$, and the preferred predator-prey weight ratio q . Once these are fixed, the equilibrium condition allows us to calculate predator efficiency (attack rate), which also turns out to follow a power law in w (Thiebaut and Dickie 1993).

Some published estimates are available for K , ξ and q , although the estimates often pertain only to specific parts of specific ecosystems and it is a simplification to assume that fixed numbers are appropriate even within a single ecosystem. In this paper, we are interested in exploring the qualitative robustness of results, rather than in trying to obtain realistic results for any particular system, so the choice of parameters is not crucial. We used production/growth/conversion efficiencies of 20% and 10% (Straile 1997, Humphreys 1979), preferred predator-prey size ratios of 10^3 and 10^4 (Thiebaut and Dickie 1993, Hahn and Langton 1984), and slopes ξ of -2.05 and -2.10, corresponding to *biomass* spectrum slopes between -0.05 and -0.10 (Boudreau and Dickie 1992).

The prey selectivity curve must also be specified, although it has little effect on the equilibrium solution provided that the preferred predator-prey weight ratio q is constant. We used an allometric log-normal prey selectivity curve, so that the ingestion rate for a predator of weight w becomes

$$(2\pi\sigma^2)^{-1/2} \int b n(b) \exp\left\{-(2\sigma^2)^{-1}(\log_{10} b - \log_{10}(qw))^2\right\} db$$

The constant σ determines the effective range of prey sizes which are eaten; we chose σ so that selectivity falls to 10% of peak at weights about 1.4 orders of magnitude above the preferred range.

Equation [1] and its equilibrium solution assume that the size range is infinite. This is a convenient fiction for mathematical purposes, but presents difficulties from computational and biological points of view as the number of size classes needs to be kept finite. In practice, we assumed that the size-spectrum for animals below about 10% of the approximate weight of a fish egg, remains constant over time. At the other end of the spectrum, some assumption must be made about the size-spectrum above the largest modelled size class, since these animals must exert some predation pressure on smaller animals. To model very-large-animal dynamics parsimoniously, we assumed that their size-spectrum would maintain its equilibrium slope, but that their abundance (and hence predation pressure) would be proportional to the instantaneous availability of food relative to equilibrium.

We assumed that commercially valuable fish span two orders of magnitude in weight. Within this range, we took price per kilo proportional to $\text{weight}^{0.3}$; this is a reasonable "species-free" approximation based on the relationship used in the length-cohort model. Bycatch mortality of unsaleable small/large fish was assumed to fall linearly to zero between the smallest/largest targeted body weight and the weight half an order of magnitude below/above. This mortality was introduced mainly to avoid shock-waves in the numerical ecosystem!

To solve the partial differential equation [1], we used a first-order method in size-space and time, based on conservation of mass and numbers. The method is fast and numerically stable but not very accurate; an acceptable limitation for preliminary theoretical investigations. The time steps and size classes for solution were determined by numerical considerations, but the time scale was chosen so that "one

year" would produce natural (predation) mortality of 0.2 on an average-sized exploitable fish at equilibrium.

To measure the performance of a particular fishing strategy, one would ideally start with the ecosystem in its unexploited equilibrium, run the system under exploitation until a new equilibrium is reached, and evaluate yield at that point. However, there are alternative sinusoidal equilibria for equations like [1], with arbitrary peak-trough distances (Thiebaut and Dickie 1992). If equation [1] is projected indefinitely in time with any disturbance from the linear equilibrium, these sinusoidal features oscillate and grow without limit. In any case, unlimited oscillations obviously do not occur in real ecosystems. Stable dome-like features appear in empirical biomass size-spectra (Sprules and Goyke 1994, Boudreau et al. 1991, Rodriguez *et al.* 1990), and the exploited part of fish size-spectra shows a stable response to fishing pressure (Rice and Gislason 1996, Duplisea and Kerr 1995, Pope *et al.* 1988). The implication is that equation [1] must lack some important kind of feedback which operates over longer time scales which bounds oscillations. This area requires further work.

Over shorter time scales, though, equation [1] is still a plausible description of mass transfer in the ecosystem. It would be useful to have some proxy for "equilibrium yield under a more realistic model" that can be obtained from the simple equation [1]. We used the minimum yield over 30 years of exploitation, roughly the time required for one growth cycle through the exploited size range. Although this may not accurately reflect absolute equilibrium yield, it does provide a benchmark for comparisons between fishing strategies. The search for the optimal fishing strategy then becomes a minimax-- or more accurately a maximin-- problem.

We programmed the size-structured model in a mixture of Splus and Borland Delphi. The relationship between minimum yield and fishing effort is smooth on a large scale, but not necessarily on the very small scale used for derivative calculations by the standard optimisation routines in Splus, which expect continuous second derivatives and no local maxima. It would be more appropriate to use a derivative-free minimiser with simulated annealing to avoid local maxima. For the present, we have used grid searches to get reliable (but not very accurate) results.

1.1.1size-spectrum model results

One notable feature of our assumptions is that equilibrium growth rates generally seem too low in comparison to predation mortality. Over all the models considered, and at the weight where annual natural mortality is around 20%, the annual percentage growth is only about 15%-17%, a rate greatly exceeded by young recruited fish of many species in the North Sea. The time required to grow from egg to typical adult commercially-exploited fish, involving about a 10^6 -fold increase in body weight, is around 30-50 model years, i.e. 5-10 times longer than is seen in the North Sea. This slow-growth property is a consistent feature of models based on equation [1], at least within our chosen ranges of production efficiency, preferred predator-prey ratio, and

equilibrium slope. Conclusions must therefore be treated as tentative until more realistic models can be devised.

The optimal (or maximin) two-point fishing strategy is consistent across the ecosystem models considered: harvest large fish quite hard, and small fish quite gently. This is true for both value and biomass yield, though the optimal value yield is obtained at lower harvesting rates than the optimal biomass yield. Yields are fairly flat when fishing mortality on large animals is increased above the optimum, but decrease rapidly as fishing mortality on young animals is increased (Fig. 2).

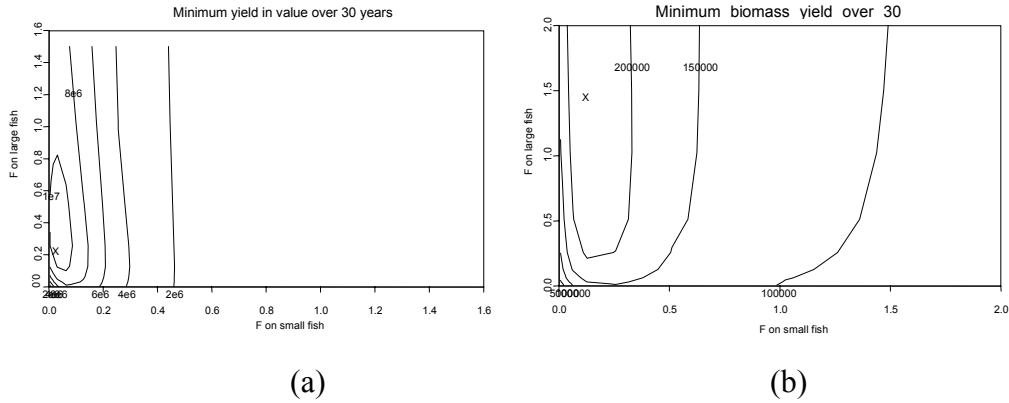


Figure 2: Contours of minimum yield in (a) value, (b) biomass for different two-point fishing strategies. X-axis is fishing mortality on smallest valuable fish; Y-axis is fishing mortality on largest valuable fish. The optimum (determined by grid search) is marked by a cross. Ecosystem parameters are $q=10^{-3}$, $\xi=-0.05$, $K=20\%$.

For the optimum two-point strategy in Fig. 2a, the state of the system at the year of minimum yield (year 11) is shown in Fig. 3. Compared to the equilibrium, the size-spectrum has steepened considerably in the exploited range, and the left-hand end point has been raised. The greatest part of the revenue is derived from mid-sized fish.

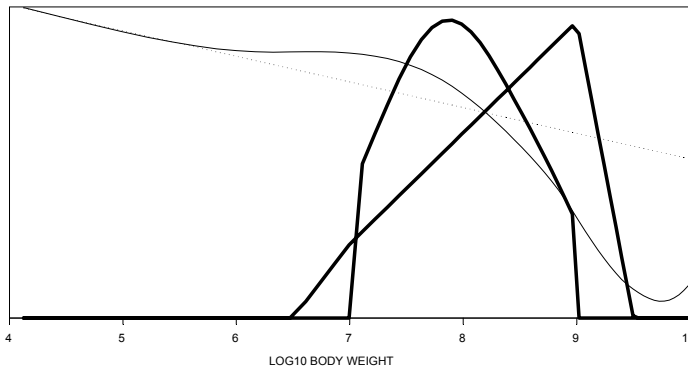


Figure 3: System state at year of minimum yield from optimal strategy in Fig. 2a. Thin lines are log biomass density before exploitation (dotted) and at year of minimum yield (solid). Thick pointed line is fishing mortality at size. Thick domed curve is realised yield in value, as a function of size.

With a three-point control strategy, the optimal F is smallest for mid-sized fish (Fig 4). Again, though, fishing mortality is greatest on the large fish.

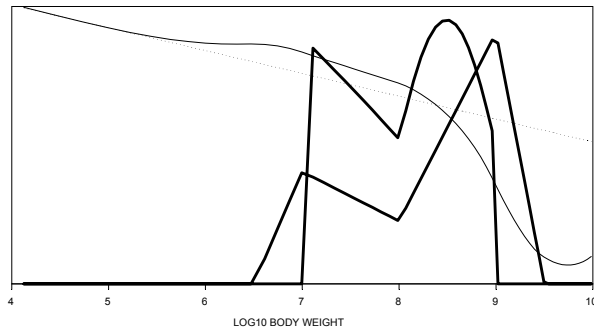


Figure 4: System state at year of minimum yield from optimal three-point strategy for ecosystem in Figs. 2 & 3

These results are typical of all the ecosystem parameter combinations used. For example, fig. 4 shows maximin system state for a two-point fishing strategy with the same ecosystem parameters as Figs. 1-3, except with predators taking smaller prey ($q=10^{-4}$). Indeed, the numerical values of optimum two-point fishing strategy itself are fairly consistent over the ecosystem parameters, at least to the accuracy considered in the grid search. Fig. 6 shows contours of minimum yield for the same model as Figs. 1-3, but with conversion efficiency reduced to 10%. The optimum strategy is about the same as in Fig. 2, but the yield falls off more rapidly with increasing fishing mortality on large animals.

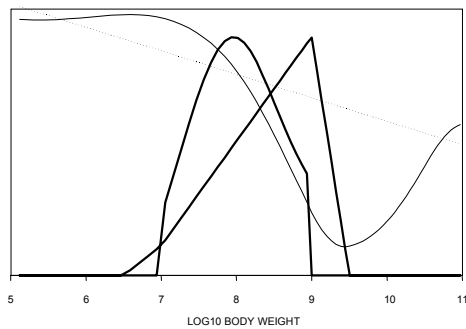


Figure 5: As Fig. 3, but ecosystem (and optimal strategy) has $q=10^{-4}$.

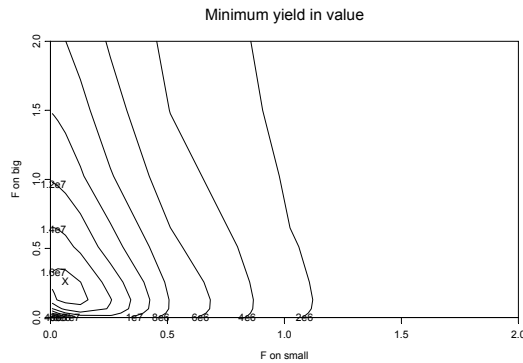


Figure 6: As Fig 1a, but with $K=10\%$.

3. DISCUSSION

Our models provide a preliminary answer to a question posed by Pope and Knights (1982): "*How should the size-spectrum of fish be most effectively exploited? Should fishing pressure be an increasing function of size, a decreasing function of size, or some discontinuous function?*". The answer seems to be that fishing pressure should increase with size overall, though not necessarily in all parts of the size-spectrum (cf. Fig. 4). The same general conclusion applies whether one is trying to optimise revenue or harvested biomass, though overall fishing levels are higher in the second case. These results are not immediately obvious, and "Eltonian pyramid" arguments of system biomass and production dictate that harvesting lower trophic levels will provide higher yields. Indeed, for the size-spectrum model, cohort biomass is a decreasing function of time in this model, so one might expect to maximise yield by fishing a cohort early and hard, before the biomass is dissipated through metabolism and trophic transfers. In practice this does not work well, emphasising the importance of feedback through predation and growth.

To validate our claim, there would need to be further systematic investigation with more realistic (but not necessarily more detailed) ecosystem models. Aside from introducing different types of model, both models used here need further development. The size-spectrum model shows some implausible behaviour, in that animals grow too slowly and equilibria are unstable; it is far from ideal to use minima as proxies for equilibria. One amelioration might be to allow some disaggregation, say into functional trophic-groups with different preferred predator-prey size ratios, or into different physical niches. There are several other glaring omissions, including reproduction and predator functional response in the size-spectrum model and seasonality. Neither model includes an optimal foraging mechanism taking into account both predator-prey body size ratio and prey density in the environment such as that described by K-lines (Kerr and Martin 1970). Technical interactions with multi-fleet fisheries are not accounted for in the models.

From a management perspective, better biological models are only part of the story. It is crucial to have models that reflect the kinds of management controls potentially (though not necessarily currently) available. For example, there is little point in devising an optimal size-based fishing mortality pattern if the mix of effort among existing fleets cannot be manipulated to achieve anything like that pattern. Also, economic considerations should play a much greater role, in particular with regard to substitution and elasticity across species and sizes. Achieving optimum total yield might mean that particular fleets would have to fish uneconomically, in effect providing subsidies to other fleets. Although this could be achieved in theory, say by using negative taxes, it may not be a feasible management option. In any case, optimum yield does not necessarily mean optimum profit, and optimum profit is not necessarily the overriding social goal. Furthermore, it is less important to identify optimal solutions precisely than determine the opportunity cost associated with following an existing suboptimal strategy, and of the directions in which the current strategy should be changed in order to do better.

If management is designed to deliver maximum yields or some other socio-economic goal, there is no intrinsic guarantee that the entire ecosystem will be safeguarded. For example, low-fecundity species, such as elasmobranchs, are liable to collapse under any management regime that has unavoidable technical interactions and an explicit or implicit goal related to overall yield or effort. Apart from specific and predictable single issues of this type, the precautionary approach demands safeguards to ensure reversibility in the face of possible unforeseen effects. For these reasons, there is always likely to be a need for additional measures such as closed (refuge) areas.

Apart from ensuring the reversibility of anthropogenic effects, though, it is difficult or impossible to agree what is desirable for ecosystem management-- a point which emerged from the "1999 ICES/SCOR Ecosystem Effects of Fishing" (EE) meeting held in Montpellier, France. Socio-economic criteria such as yield, while by no means easy to agree, are more easily understood, and have a track record of explicit or implicit use in fisheries management. At the close of the EE meeting, it was suggested that ecosystems would generally be in better condition-- regardless of how that is measured-- if existing single-species management concepts (implicitly relating to yields etc.) were properly applied. Given the difficulties associated with single-species management in multispecies contexts, it is tempting to suggest that ecosystems might fare even better under simple management schemes designed around aggregate system properties. This paper is a first step in showing how such management schemes might be devised.

REFERENCES

- Boudreau, P. R. and L. M. Dickie. 1992. Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can. J. Fish. Aquat. Sci.* **49**: 1528-1538.
- Boudreau, P. R., L. M. Dickie and S. R. Kerr. 1991. Body-size spectra of production and biomass as system-level indicators of ecological dynamics. *J. Theor. Biol.* **152**: 329-339.
- Brugge, W. J. and M. J. Holden. 1991. Multispecies management: a manager's point of view. *ICES Mar. Sci. Symp.* **193**: 353-358.
- Dickie, L. M. and S. R. Kerr. 1982. Alternative approaches to fisheries management. *Can. Spec. Publ. Fish. Aquat. Sci.* **59**: 18-23.
- Duplisea, D. E. and S. R. Kerr. 1995. Application of a biomass size spectrum model to demersal fish data from the Scotian Shelf. *J. theor. Biol.* **177**: 263-269.
- Gulland, J. A. (1988) Fish population dynamics: the implications for management. Wiley, Chichester
- Hahm, W. and R. Langton. 1984. Prey selection based on predator/prey weight ratios for some Northwest Atlantic fish. *Mar. Ecol. Prog. Ser.* **19**: 1-5.
- Hilborn, R. and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman & Hall, New York
- Hilden, M. 1988. Significance of the functional response of predators to changes in prey abundance in multispecies virtual population analysis. *Can. J. Fish. Aquat. Sci.* **45**: 89-96.
- Humphreys, W. F. 1979. Production and respiration in animal populations. *J. Anim. Ecol.* **48**: 427-453.
- Kerr, S. R. 1974. Theory of size distribution in ecological communities. *J. Fish. Res. Board. Can.* **31**: 1859-1862.
- Kerr, S. R. and N. V. Martin. 1970. Trophic-dynamics of lake trout production systems. In: J. H. Steele (ed) *Marine food chains*. Oliver & Boyd, Edinburgh. p 365-376
- Magnússon, K. G. 1995. An overview of the multispecies VPA -- theory and applications. *Rev. Fish Biol. Fish.* **5**: 195-212.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. int. Explor. Mer.* **39**: 175-192.
- Platt, T. and K. Denman. 1977. Organisation in the pelagic ecosystem. *Helgol. Wiss. Meeresunters.* **30**: 575-581.
- Pope, J. G. and B. J. Knights. 1982. Comparisons of length distributions of combined catches of all demersal fishes in surveys in the North Sea and Faroe Bank. *Can. Spec. Pub. Fish. Aquat. Sci* **59**
- Pope, J. G., T. K. Stokes, S. A. Murawski and S. I. Idoine. 1988. A comparison of fish size-composition in the North Sea and on Georges Bank. In: W. Wolff, C. J. Soeder and F. Drepper (eds) *Ecodynamics, Contributions to Theoretical Ecology*. Springer Verlag, Berlin
- Rice, J. and H. Gislason. 1996. Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES J. Mar. Sci.* **53**: 1214-1225.
- Rodriguez, J., F. Echevarria and F. Jimenez-Gomez. 1990. Physiological and ecological scalings of body size in an oligotrophic, high mountain lake (La

- Caldera, Sierra Nevada, Spain). *J. Plankton Res* **12**: 593-599.
- Sheldon, R. W. and S. R. Kerr. 1972. The population density of monsters in Loch Ness. *Limnol. Oceanogr.* **17**: 796-798.
- Silvert, W. and T. Platt. 1981. Dynamic energy flow model of the particle size distributions in pelagic ecosystems. In: W. C. Lerfoot (ed) *Evolution and ecology of zooplankton communities*. University Press of New England, Hanover, NH. p 754-763
- Sprules, W. G. and A. P. Goyke. 1994. Size-based structure and production in the pelagia of Lakes Ontario and Michigan. *Can. J. Fish. Aquat. Sci.* **51**: 2603-2611.
- Straile, D. 1997. Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator-prey weight ratio, and taxonomic group. *Limnol. Oceanogr.* **42**: 1375-1385.
- Thiebaut, M. L. and L. M. Dickie. 1992. Models of aquatic biomass size spectra and the common structure of their solutions. *J. Theor. Biol.* **159**: 147-161.
- Thiebaut, M. L. and L. M. Dickie. 1993. Structure of the body-size spectrum of the biomass in aquatic ecosystems: A consequence of allometry in predatory-prey interactions. *Can. J. Fish. Aquat. Sci.* **50**: 1308-1317.