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Exploration of the Sea

Information Content of Ecosystem Metrics and Reference Points

Report of a Private Working Group

Dreumel, The Netherlands, 20-25 September 2000
The Old Rectory, Beccles, England, 9-13 July 2001
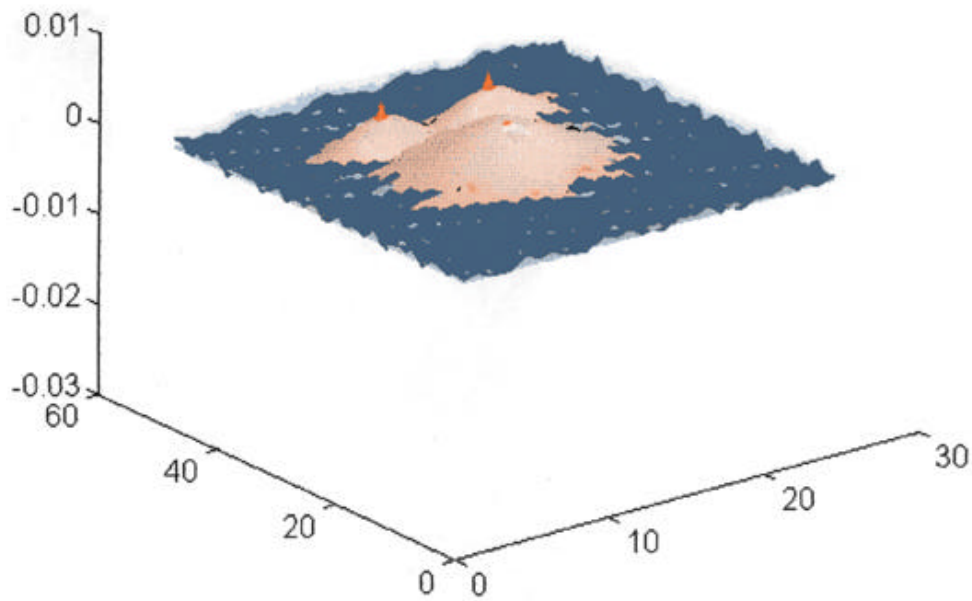
John Pope, Niels Daan, Henrik Gislason & Jake Rice

*Figure 0. One realisation of North Sea Fish Abundance according to Pope's Neutral Model,
or Emergent Properties of Mother North Sea*

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Abstract

We address the issue of wedding fisheries management to ecosystem management and in particular put forward ideas about the construction of neutral models for investigating community assembly rules and testing ecological hypotheses. To build a statistical model that mimics the North Sea fish community, we derived distributions of relevant parameters such as k-dominance curves, maximum length, log abundance and species richness from survey data. Subsequently, abundance and distribution of 100 species was modelled in MATLAB based on the lognormal distribution of species abundance observed in the North Sea and varying assumptions of annual variations in μ, s and in the centre of distribution. The hypothetical community was sampled annually to investigate temporal developments in emergent properties such as species richness and rarity indices and these were compared with survey estimates of the same parameters. In addition, an old idea of using MSVPA and MSFOR results to fit multispecies Schaeffer Models was elaborated, and some ideas are presented on possibilities to simulate multispecies, size structured communities and on potential measures of level of exploitation of fish communities as a basis for ecosystem comparison.

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1. Introduction

1.1. Terms of reference

The private Working Group set as its own TOR to have fun in the general area of multispecies models and ecosystem indices and more specifically to

- discuss the wedding of fisheries management to ecosystem management;
- provide Food for Thought on the issue of suitable community metrics for evaluating effects of fishing and anything else that came to mind and was found worth pursuing.

1.2. Participation

The first meeting was held from 20-25 September 2000 at Waaldijk 39, Dreumel, The Netherlands and was attended by

Prof Niels Daan	- The Netherlands
Prof Henrik Gislason	- Denmark
Prof John G. Pope	- Norway (Chair)
Prof Jake Rice	- Canada

As a follow-up, a second meeting was held from 9-13 July 2001 in The Old Rectory, Beccles, England. Regretfully, Henrik could not attend on this occasion.

2. Wedding fisheries management to ecosystem management

2.1. General musings

Earlier multispecies work within ICES (e.g. ICES, 1980 … 1997; Pope, 1989) focused on one process – predation -, and really one population dynamics parameter associated with that process – predation mortality M2. At the time, this was the right approach, because the primary goal was to feed information on internal consumption within the system into assessment tools of the day, and graft predation onto single-species fish population dynamics. The questions asked and uses made of the work were to improve advice on the sustainability of fisheries. Did fishing mortality F have to be adjusted in response to M2, in order to keep total mortality Z on any (or all) species sustainable? Of course we did other things than just estimate M2, but our work was structured around that focus.

The new generation of multispecies work still has relevance to the earlier class of questions, but enters a much larger domain of management concern for biodiversity. Advice covers much more than how F should be adjusted to keep Z sustainable. The advisory roles of fishery science expand in two ways: conservation questions are posed about non- target species of fisheries, and about perturbations other than fishing. The proximate example of such expansion raised at the meeting (Daan, 2001) was a desire by managers to have objective methods for identifying what was a truly rare species that warranted particular protection for conservation of biodiversity, and what areas were particularly important as hotspots of biodiversity.

Many other similar issues loom in the near future. Fishery science can make two general types of contributions to the scientific advice on these issues:
• Building up realistic, empirically based expectations of what can and does happen in marine ecosystems – so managers can know whether or not a particular problem really exists and in need of a solution;
• Testing the likelihood that management actions under consideration will actually improve an undesirable situation or cure a particular problem, if one has been shown to exist.

Both of these contributions require having a quantitative handle on (and subjective understanding of) what are "expected states" of vectors and processes, and "normal" rates and patterns of change in them, so Null Hypotheses can be tested, and deviations from "expected" conditions can be evaluated. Our ability to make important and unique contributions comes from three factors. We have access to and familiarity with important data sets, methods of data analysis, and modelling approaches and methods. These contrast markedly with the perspectives and tool-kits of "conservation biologists" coming into marine ecosystems from terrestrial ones, who are used to working in strongly habitat-o-centric contexts.

2.2. Musings specific to the PWG

Tasks considered worthwhile:
1) Refine the questions that ecosystem managers / biodiversity conservers, etc should be asking;
2) Move our modelling efforts to enable construction of neutral models for investigating community assembly rules and testing ecological hypotheses;
3) Determine what rules are necessary and sufficient conditions for simulating communities that are statistically indistinguishable from the available survey data for the North Sea; this will involve both the neutral modelling in (2) and some careful thinking about what statistical tests are actually appropriate for drawing inferences about how similar is similar "enough".

Pitfall:
Countless ecological questions, avenues for modelling, and opportunities for descriptive and sometimes even hypothesis testing data analyses arise. With all of us lacking infinite time with which to pursue things, which ones matter? Why do they matter?

Opportunities:
• Does the Daan (2001) rarity index (see section 5.1) have properties that are robust to sampling intensity and to different ways in which a species may be 'rare' (any µ & low ; low µ and any ;)
• Are there spatial hotspots for rarity? Is the index a good tool for picking them up? Is the suggestion that

rarity is more likely on the margins of the North Sea a process feature of the system or an artefact?
• Is the North Sea system being (has this system been) perturbed anomalistically in the recent (any) period, by intensification of F, climate change, etc? What degree of change would be expected without anomalous forcing? The latter question involves looking at inherent turnover rates of the system annually:

by species as present / absent
at IBM scale, dis-aggregated by species
at IBM scale, dis-aggregated by size class.
[NB. IBM – Individual-Based Model]

2.3. Narrative on neutral modelling – reasons, approaches, ideas

Why do we do it? We want to build non-biased and quantitative "expectations" of what the North Sea fish fauna would look like, and how it would change, given a known structure. The structure is known because we build it up from the bottom. The less structure that is hard-wired into its construction, the more powerfully it can test whether a particular process is necessary (or sufficient) to account for patterns observed (e.g., do we have to structure in a correlation between mean abundance of a species and breadth of its distribution before a fauna which "looks like" the real fauna can be simulated?). Do complex properties – like patterns of richness in space, and mixtures of common and rare species in plots – "emerge" from very simple rules, or must they be hard-wired in to be reproduced? In using models to increase our understanding of what really causes the structure and functioning of the North Sea, it is important to hard-wire in as little as possible – otherwise we get out what we structured in, and only prove that we can program correctly.

At the same time, neutral models are only informative if they DO produce reasonable behaviour. Hence it is important to think what constraints have to be met, before behaviour is considered "reasonable". We started fitting the k-dominance curve, but that only constrained us to get the abundance of the most common 5-7 species correct. We learned by doing that we should have a frequency distribution of numbers of species by (say ln) abundance class as a constraint, and fit the whole distribution (testable with a chi-square, as long as we are unrealistic about numbers of bins). We also chose, as a constraint, to fit the frequency distribution of numbers of species per rectangle (also testable with a chi-square) – get the right number of species with narrow distributions, wider ones, etc. Finally, during the simulations it quickly became clear that many models had difficulties reproducing the relationship between the number of rectangles occupied and ln(abundance), with breadth of distribution increasing more slowly with abundance in the models than was the case in the IBTS data. This also became a criterion for accepting a model as

a reasonable representation of the system. When constructing neutral models, it is always important to consider how many constraints are necessary before results of a simulation are "reasonable" enough to be informative about the real system of interest. We concluded that at least as a first step, we would have informative simulations just by fitting these two constraints. From simulated communities that met the specified constraints we could calculate rarity index values by species or rectangle, and with multiple iterations construct an expected distribution for this community parameter. Locating the observed values from the IBTS survey on the expected distribution from the simulations allows the probability of the observed values to be tested relative to the null hypotheses that neither specific species are more rare nor selected rectangles support more rare species than is expected by chance.

The utility of neutral model simulations in constructing expected distributions for community parameters is only one benefit of constrained neutral models, however. The work of developing simulations which fit the chosen constraints sheds light on a number of ecological questions about how the North Sea fish community is put together. For example, we should first ask if we can fit the constraints with μ's and 's in Section 2.2 drawn from specified and smooth distributions? By using the least amount of information from the actual observations, this would be hardest to do, but most general, indicating that there was a strong underlying regularity to the community as a whole. If we failed to fit the constraints assuming μ's and 's were drawn from some regular distributions, could we fit the constraints by re-sampling the vector of observed μ's and smoothly distributed 's (next hardest) or re-sampling independently on observed vectors of both parameters? If it was necessary to input the observed vectors of either μ or s in order to match the North Sea surveys, then we would have established that there was no underlying regularity to either mean abundances or breadths of distribution of the full community. However, we would have also established that μ's and 's are independent in the real North Sea; that is breadth of distribution is independent of abundance. If we still failed to fit our constraints with independent sampling of μ's and 's, then we would have established that is was necessary to force even more structure directly on the simulation. The first alternative would be by drawing μ's and 's from specified distributions, but with a correlation, or, if that simulation failed to fit the constraints, re-sampling the observed vectors with a structured correlation. Note that the sequence of simulations attempts to add as little structural complexity as possible at each step, so results are maximally information about the degree of underlying structure in the real community. These ecological insights are a valuable companion to developing the simulation tool needed to construct the expected distribution of the rarity index.

The stress on keeping the simulations as structurally simple as possible is only good science: many different and incompatible explanations that are more complex than the most parsimonious one can always be reconciled with a data set. However, the need for parsimonious models does not prevent the simulations from getting more complex over time. As we learn more from simple ones, we are likely to ask more complex questions. This is also good science, as long as we keep adding additional constraints, relevant to our new and more complex questions, so models with incorrect representations of the additional processes can be rejected efficiently. Two of the things which may be added early include capturing the patterns of length in community composition and simulating the effects of interannual variation around μ especially relative to the patterns produced by repeated annual realisations of . The former would require fitting some additional constraint regarding size-based properties of the community, whereas the latter would require fitting some interannual patterns in distributions of abundance, species per rectangle, or other relevant properties. Correlation of simulation parameters, and things like adding a contagion or exclusion parameter to placing centres of simulated distributions, are other directions of complexity likely to be explored in future. Further down the road, trophic roles, life history features, and similar things, may be explored.

The added structure to the simulations is not an end in itself – this is not a test of how many factors we can add to our model. Each step has to be preceded by careful formulations of what hypothesis we are trying to test, and what constraints are adequate to be confident we can reject incorrect model formulations. These tasks are not always straightforward. Just saying that our initial goal was to examine the reliability of the rarity index did not give us a clear idea of what simulations would do that task. However, as illustrated in section 6, the development of the simulations provided a number of insights into the structure of the North Sea fish community.

Such work is necessarily accompanied by giving a lot of thought to how existing data can be used to test against model simulations. This stimulates new ideas about how the survey data sets can be aggregated or broken down, re-sampled, and standardized. It also requires creative thinking about statistical tests that can be used in these multiple directional studies. These are both important additional benefits of undertaking a neutral modelling approach to exploring community structure. Particularly by stimulating to look at data in novel ways, we can get much greater mileage out of work already done. These tasks also require that we all have the data available in highly dis-aggregated form,

so they can be collapsed along different axes for different types of questions.

3. Using MSVPA and MSFOR results to fit Multispecies Schaeffer Models *(or a little knowledge of matrix algebra is a dangerous thing!).*

Simple representations of the yield surface (Pope, 1989) indicate how a multispecies Schaeffer model can be constructed using the values of changes in fleet and species yield $Y(s,f)$, for n species s and m fleets f. consequent on 10% increases in each of the fleets in turn as estimated from the MSFOR model. These are used as estimates of $Y(s,f)/E(g)$ where g can be any of the m fleets in the model.

We have from the multispecies Schaeffer model,

$$Y(s,f) = a(s,f)*E(f)+ \sum_{all} gb(s,f,g)*E(f)*E(g). \qquad [3.1]$$

Hence, if $g \neq f$ then

$$Y(s,f)/E(g) = b(s,f,g)*E(f), \qquad [3.2]$$

or if g=f then

$$Y(s,f)/E(f) = a(s,f) + 2 b(s,f,f)*E(f). \qquad [3.3]$$

If current effort is taken as unity (i.e. as a base line level) then with values at the current equilibrium denoted by prime' these equations become:

$$Y'(s,f) = a(s,f) + \sum_{all} g \, b(s,f,g), \qquad [3.4]$$

for $g \neq f$

$$Y'(s,f)/E'(g) = b(s,f,g), \qquad [3.5]$$

and for $g = f$

$$Y'(s,f)/E'(f) = a(s,f) + 2 b(s,f,f). \qquad [3.6]$$

Thus for an n species and m fleets there are n*m a(s,f) terms and n*m*m b(s,f,g) terms. These may be solved for using the n*m equations [3.4] above and the n*m*m equations [3.5] and [3.6] above. Note that equation [3.5] gives b(s,f,g) directly if $g \neq f$. Then the equations [3.4] and [3.6] are used to solve for a(s,f) and b(s,f,f). Alternatively these may be solved directly by linear algebra. The resulting multispecies Schaeffer model can be used to solve for MSY, F0.1 and other reference points (ICES, 1989).

The above approach draws on the equilibrium solutions available from MSFOR. However, it should be possible to calculate these directly from MSVPA results providing one is prepared to accept say a ten year average of biomass and yield as a steady state [we do so in grateful memory of Rodney Jones].

If we have n fleets such that

$$F'(s,a) = \sum_{all} f \, q(s,a,f)*E'(f), \qquad [3.7]$$

then if B(s,a) is the average annual biomass of species s at age a, we may write:-

$$Y'(s,a,f) = q(s,a,f)*E'(f)*B'(s,a), \qquad [3.8]$$

if $g \neq f$,

$$Y'(s,a,f)/E'(g)=q(s,a,f)*E'(f)* B'(s,a)/E'(g) \qquad [3.9]$$

or if g = f,

$$Y'(s,a,f)/E'(f) = q(s,a,f)*E'(f)* B'(s,a)/E'(f) + q(s,a,f)* B'(s,a). \qquad [3.10]$$

Thus, given estimates of $B'(s,a)/E'(f)$ we can estimate $Y'(s,a,f)/E'(g)$. These may be summed to give $Y'(s,+,f)/E'(g)$, where + indicates summation over the suffix. We may then use these to estimate the parameters of the multispecies Schaeffer model as with equations [3.4]-[3.6]. The attraction of the current route is we may include features such as stock recruitment not used in the existing MSFOR runs. What follows closely mirrors Pope's (1989) working paper going straight for the Jacobian (Jonesian?).

To estimate $B'(s,a)/E'(g)$ consider

$$B'(s,a,f) = Wt(s,a)*Recruits*exp(-cumF-cumM1- cumM2(s,a)), \qquad [3.11]$$

where cum denotes summation over all ages <a and allowing 0.5 *{F or M1 or M2} at age a, as an approximation to the equation of average biomass {i.e., taking exp(-Z/2) as an approximation to (1-exp(-Z))/Z}.

Further assume a power curve formulation of the stock recruitment relationship

$$Recruits= \cdot SSB(s) , \qquad [3.12]$$

$$|\{ B'(s,a)/E'(g)\}Y*/B'(s,a)|=| (s)|*|PropSSB(s,a)|* |\{ B'(s,a)/E'(g)\}/B'(s,a)|-|CUM|*|q(s,a,g)| -|CUM|*|M2(s,a,S,A)|* |\{ B'(s,a)/E'(g)Y*)P\}/B'(s,a)|, \qquad [3.13]$$

where:-

- $|\{ B'(s,a)/E'(g)\}/B'(s,a)|$ is a sa (the number of s,a combinations) by m matrix,;
- $|(s)|$ is a diagonal sa by sa matrix containing the S/R power value for species s,
- $|PropSSB(s,a)|$ is a sa by sa matrix containing a series of diagonally positioned square matrixes referring to each s block of ages and containing the proportion each of the species contributes to its SSB (i.e. terms of Wt(s,a)*Fecundity(s,a)*B(s,a)/SSB(s)).
- $|CUM|$ is an sa by sa matrix of sub-diagonal blocks of ones and diagonals of 0.5 (such as to sum up all ages ã<=a),
- $|q(s,a,g)|$ is a sa by m matrix of catchabilities.
- $|M2(s,a,S,A)|$ is a sa by sa matrix containing the current M2(s,a,S,A) of predator S,A on prey s,a.

This can then be solved as

$$|B'(s,a)/E'(g)| = -|B(s,a)|*[I-|(s)|*|PropSSB(s,a)| +|CUM|*|M2(s,a,S,A)|]-1*|CUM|*|q(s,a,g), \qquad [3.14]$$

with |B(s,a)| as a sa by sa diagonal matrix containing B'(s,a) and I as an identity matrix of dimension sa. These equations may be summed to give | B'(s)/ E'(g)| and these used in lieu of MSFOR estimates of gradient in equations [3.5] and [3.6].

Given estimates of a(s,f) and b(s,f,g) these may be summed for f to give

a'(s)=a(s,+)   [3.15]

and

b'(s,g) = b(s,+,g).   [3.16]

Because

Y(s,f)=B(s)*E(f),   [3.17]

using [3.1] we may write,

B(s)= a(s,f) + _all g b(s,f,g)*E(g).   [3.18]

Summing for the p(s) n cases where Y(s,f) 0, we obtain

|p(s)|*|B(s)|=|a'(s)| + |b'(s,g)|*|E(g)|,   [3.19]

where |p(s)| is a diagonal matrix of size n, where |B(s)| and |a'(s)| are column vectors of length n, where |b'(s,g)| is a n by m matrix and where |E(g)| is a column vector of length m. In the simple case where n=m and where |b'(s,g)| is non singular we may write

|E(g)|= |b'(s,g)|⁻¹*|a'(s)| - |b'(s,g)|⁻¹*|p(s)|*|B(s)|. [3.20]

Thus,

|b'(s,g)|⁻¹ *|a'(s)| = (s)   [3.21]

and

|b'(s,g)|⁻¹ *|p(s)| = (s,r),   [3.22]

the constants of the multispecies Schaeffer model as expressed in biomass B(s), B(r) terms. This formulation is also used in the AD model builder fits (section 4).

Where n<m or n>m or where |b'(s,g)| is singular, we will have to use pseudo inverses of |b'(s,g)| to obtain similar, but in the case of m<n, non-unique estimates of (s) and (s,r).

[NB. This may be related to the estimatability of the (s) and (s,r). If the fleets do not span the n dimensional vector space of species - because there are fewer distinct fleets than there are species - then we cannot hope to uniquely identify the (s) and (s,r), unless perchance the non-equilibrium case gives additional information. There would probably be utility in choosing as many fleets as there are species. Note that predators might be treated as an additional fleet.]

"And yet methinks, I own this hope as rare,
since non equilibrium doth but equilibrium repair?"

Given that we establish g(s) and h(s,r) (either via equations [3.4]-[3.6] or by [3.4], [3.10] and [3.13],

then we could enter the fitting procedure described in section 4 with specified values of these parameters and see how much they need to be modified to fit interactions to account for non- (or wrong) predation interactions and for climate effects on the model! The route through equations [3.4]-[3.6] is simpler but that through [3.4], [3.10] and [3.13] allows more flexible choice of fleets and also the inclusion of various stock recruitment relationships from constant to linear increases with a very minimal knowledge of the SR terms.

4. Using a multispecies surplus production model to describe population dynamics and species interaction.

4.1. Introduction

At one of the meetings of the Multispecies Assessment Working Group, a multispecies Schaefer model (Pope, 1979) was fitted to results from MSFOR predictions of +/-10% changes in fishing effort in the various North Sea fisheries. The model was subsequently used to predict changes in species and fleet yield as a function of effort and to estimate multispecies reference points (ICES, 1989). When the output was compared to MSFOR, the predictions from the two models were quite similar even for changes in fishing of up to +/-50% from the status quo. This raises the question whether simple biomass-based models can be used as a substitute for complicated multispecies models such as MSFOR when insufficient data are available to run the latter.

So far the parameters of the multispecies Schaefer model have only been estimated from MSFOR predictions for the North Sea. However, attempts to estimate the parameters of simple multispecies biomass-based models elsewhere (e.g. Collie and deLong, 1999) suggest that biologically meaningful values for the interaction coefficients can be derived from time series of yield and effort data. It was therefore decided to investigate whether the parameters of the multispecies surplus production model could be estimated directly from fishing effort, CPUE and biomass data from the North Sea.

4.2. Model structure.

According to Quinn and Deriso(1999) the single Schaefer surplus production model can be written as:

$$dB_i/dt = k_i(1-B_i/K_i)*B_i-F_i*B_i \qquad [4.1]$$

where B_i is the biomass of species i, k_i is an intrinsic growth parameter, K_i is the carrying capacity, and F_i is the fishing mortality.

Adding a species interaction term to this equation to account for predation and/or food dependent growth, and a term to account for the natural mortality caused by predators not included in the model, produces:

$$dB_i/dt = k_i(1–B_i/K_i)*B_i–F_i*B_i-\ \ d_{i,j}*B_i*B_j-OM_i*B_i \qquad [4.2]$$

where the sum runs over all other species groups, j (j i), and OM_i is the natural mortality of species i caused by other predators.

Schnute(1977) suggested to rearrange the equation to:

$$dB_i/B_i = k_i(1–B_i/K_i)*dt–F_i*dt-\ \ d_{i,j}*B_j*dt-OM_i*dt \qquad [4.3]$$

for which an analytical solution can be found.

By integrating from time t to t+1 and replacing the integral of B_i from t to t+1 by the average biomass, $B_{i,av}$, the solution can be written as:

$$Ln(B_{i,t+1}/B_{i,t})+F_i+OM_{i,t,t+1}=k_i–(k_i/K_i)*B_{i,av}-\ \ d_{i,j}*B_{j,av} \qquad [4.4]$$

or by substituting biomass by cpue, U, and F by effort, E, and adding an error term, as:

$$Ln(U_{I,t+1}/U_{I,t}) = k_i-k_i\,(U_{i,t}+U_{i,t+1})/(2q_iK_i)$$
$$-q_i(E_{i,t+1}+E_{i,t})/2-OM_{i,t,t+1}-\ \ d_{i,j}*(U_{j,t}+U_{j,t+1})/2+\ _t \qquad [4.5]$$

4.3. Parameter estimation

The model was written in AD model Builder and fitted to MSVPA estimates of log biomass ratios, average biomasses and average fishing mortalities for the period 1974-1994. Initially all 10 species were included, but although estimates of the (110) parameters could be derived, the associated standard deviations were high, and many of the parameters did not seem to have a biologically meaningful sign and magnitude.

Table 4.1. Parameter estimates from the simple 3 species groups model.

# Objective function value = 1.78621			
Maximum gradient component = 2.21109e-05			
# k:	0.61	0.23	1.41
# d:	0.05	-0.14	0.01
	0.17	-0.27	0.14
	0.92	-0.14	-0.24

According to Pope (1979), the sum of the Schaefer curves of individual species should conform to a Schaefer curve provided the fishing mortalities of the species are linearly related. The species were therefore grouped into roundfish (cod, haddock, saithe and whiting), pelagic (herring and mackerel), industrial (sandeel and Norway pout) and flatfish (plaice and sole). The model was fitted to ln biomass ratios using the sum of the removal rates (catches and other predation) and average biomass for each group. The parameter estimates for flatfish were highly variable and added little explanatory power to the overall model. This group was therefore removed leaving three major species groups to be modelled and 12 parameters, i.e. three k's and 9 d's (including the ki/Ki term), to be estimated. In addition, a run in which the k parameter was assumed to change gradually over time was attempted. In this run k was

modelled as a random walk and updated according to:

$$k_{i,t+t} = k_{i,t} * exp(k_i) \qquad [4.6]$$

where k_i is a normally distributed random variable with 0 mean and a variance which was assumed to be 5 times less that the variance of the log biomass ratios.

4.4. Results

Parameter estimates from the three species groups model are given in table 4.1. Some of these differ from expectations. The intercepts are all positive, but the diagonal in the d matrix, that expresses how the rate of biomass change depends on the biomass of the species itself (k_i/K_i term), contains negative values. A negative value in the diagonal introduces a positive biomass squared term producing a positive feedback on the biomass of the species itself. In the model, a negative value in the diagonal is therefore likely to lead to unstable population dynamics.

Table 4.2. Parameter estimates from the random walk model.

# Objective function value = 1.29		
Maximum gradient component = 8.14e-05		
# k: 0.62	0.29	7.34
0.63	0.29	6.79
0.63	0.29	5.76
0.61	0.29	5.07
0.62	0.29	4.94
0.61	0.30	4.90
0.62	0.30	5.06
0.62	0.30	4.62
0.63	0.30	4.89
0.64	0.30	4.52
0.64	0.30	4.71
0.65	0.30	4.32
0.65	0.29	4.46
0.64	0.29	4.34
0.63	0.28	3.94
0.63	0.28	4.01
0.63	0.28	3.91
0.64	0.28	3.91
0.66	0.29	3.97
0.67	0.29	3.96
0.66	0.29	4.11
# d: -0.002	-0.133	0.028
-0.159	-0.252	0.142
1.999	0.206	0.177

The observed change in average biomass over time is compared to the output from the simple model in Fig 4.1. For the roundfish and pelagic groups the model provides a fair description of the change over time, while the fit to the industrial species is less convincing.

When the biomass growth parameter, ki, is allowed to change over time, the fit to the biomass of industrial species improves considerably. In this run, the ki parameter for the industrial species declines over time to approximately half its initial value (table

4.2). For the roundfish and pelagic species the parameter stays reasonably constant and for these species groups the results change only slightly (Fig. 4.2).

The parameters are less unrealistic (table 4.2), but will still produce very low (and in some cases negative) virgin biomasses, in particular for the roundfish group.

4.5. Discussion

Unfortunately none of the models produced realistic parameter estimates. Several explanations are possible. The models may be too simple to capture the changes in biomass production that have occurred. Simple Schaefer models cannot capture fluctuations in recruitment success due to environmental changes and cannot account for the influence of changes in age composition on the rate of biomass growth. However, even when the instantaneous rate of biomass production was allowed to change with time, parameter estimates were still unrealistic. Another possibility is the lumping of species into larger functional groups (roundfish, pelagic and industrial). This is only valid if the fisheries for the individual stocks within each of these groups develop in parallel. Considering the changes in the North Sea fisheries that have occurred between 1974 and 1994 this is perhaps not a feasible assumption. Finally the time series of observations may have been too short and without sufficient contrast. Further analysis on a larger set of data will be necessary before the usefulness of the approach can be thoroughly evaluated.
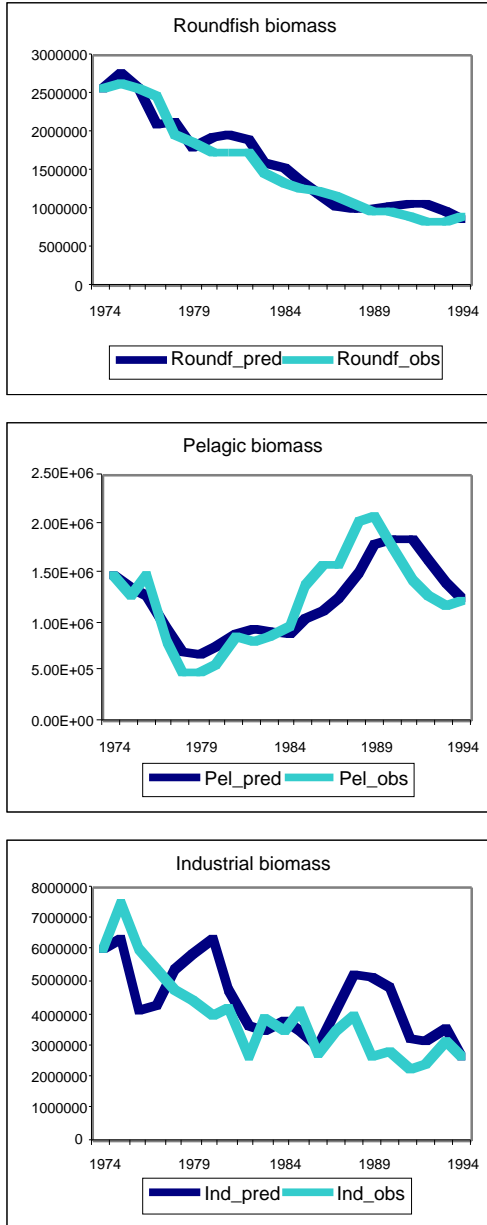
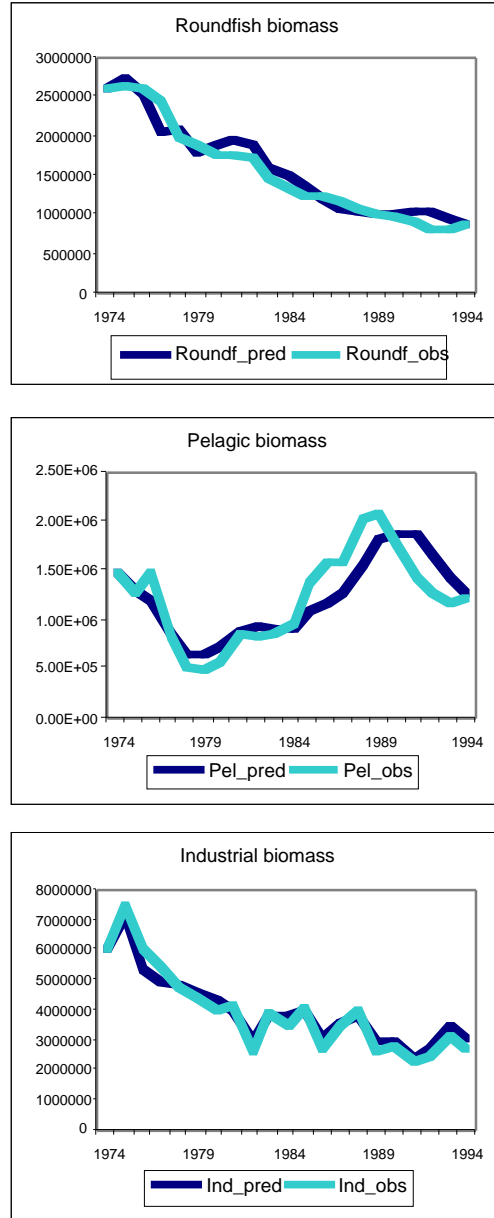Fig. 4.1. Predictions of biomass from the simple multispecies surplus production model.

Fig. 4.2. Predictions of biomass from the multispecies surplus production model with a time varying instantaneous rate of biomass growth.

5. The North Sea fish community as viewed by trawl surveys

5.1. Introduction

The concern of conservationists for maintaining or restoring biodiversity is directly linked to the issue of endangered species, which are defined either by intrinsic rarity or by declining trends. The traditional measures of biodiversity (species richness, Shannon-Wiener, evenness) are aimed to characterize communities in a way that allows comparison within and across ecosystems in terms of spatial and temporal differences, but have the disadvantage that they cannot be decomposed into the contribution of individual (rare) species. Actually, within an area, species composition might change completely without necessarily having an effect on the value of any of these indices, i.e. any metric may represent a large variety of community configurations. Similarly, the value itself does not give a clue as to whether the situation is satisfactory from a management point of view. In fact, although the general perception is that less interference of human activities will result in higher biodiversity, there are numerous examples where the observed effect is reversed. Altogether, they do not provide objective criteria that may be used unambiguously in management.

In response to a request to derive quantitative spatial and temporal measures of rarity of North Sea fish species, Daan (2001) developed a rarity index that takes into account both abundance and geographical extent of the distribution area of all species that composed the community. An important characteristic is that the index can be used to describe spatial and temporal differences in the contribution of rare species to the total community, but that it can also be decomposed in the constituting species. On the other hand, the index describes patterns within a particular data set (obtained with specific gears and thus reflecting all the problems generally related to variations in catchability: it characterizes the community as perceived through the gear!) and has no meaning for comparing different systems. An essential feature is that extensive data from routine monitoring programmes (fish surveys) are available, because paying extra attention to rare species requires that enough observations are available to estimate their rarity!

Although the analysis revealed some clear patterns in the geographical and temporal distribution of rare species, the question arises to what extent the index is affected by the existing geographical and temporal variations in sampling intensity, which are large. Our aim was to investigate this problem by simulating a North Sea fish community and then sample this artificial community to find out what kind of deviations might be observed in the index (see section 6).

However, the reconstruction of a 'typical' North Sea community requires that the simulation model should be parameterized according to features observed in the data. Apart from this specific application, such a simulation model might serve many other purposes.

This section provides information on the North Sea fish community that was considered pertinent to the modelling exercise. The database is the same as used by Daan (2001) and includes 24 412 valid hauls from 3 different surveys. The data set was restricted to 91 taxa comprising truly North Sea species (spawners and migrants). Vagrants as well as species with apparently a very low catchability were excluded. Species with major identification problems were grouped to the genus level.

5.2. K-dominance curve

K-dominance curves represent a measure of relative abundance and rarity of the species constituting a community. The estimated curve for the North Sea (fig. 5.1) shows a steeply ascending slope, that suddenly bends off into an extended flat tail. The six most abundant species make up more than 90% of the total abundance. These are all of commercial interest, although the dab is only marginally so. The 15 most abundant species out of 91 reported represent 99% of all fish caught.
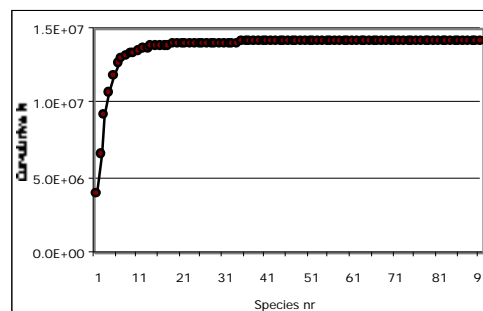

Fig. 5.1 K-dominance curve North Sea fish community.

5.3. Relation between range-size and density rarity

Daan's biodiversity index integrates two aspects of rarity that are not independent and therefore we investigated the relationship between the percentage of rectangles in which species have been caught and the average numerical abundance (fig 5.2). Although there is a clear overall relationship that can be described by a simple polynomial function, the scatter of points around the line is quite pronounced, especially in the mid-range of the observed abundance. This by itself is an indication that it is worthwhile to combine the two aspects into one integrated index.

The question arises, whether there are general biological characteristics of individual species that affect the estimated relationship. One obvious possibility is the size of the species, because

dispersion may be expected to depend on swimming ability. Therefore, the residuals from the fitted line were plotted against the maximum size of the individual species derived from Wheeler (1978) and Knijn *et al.* (1993).
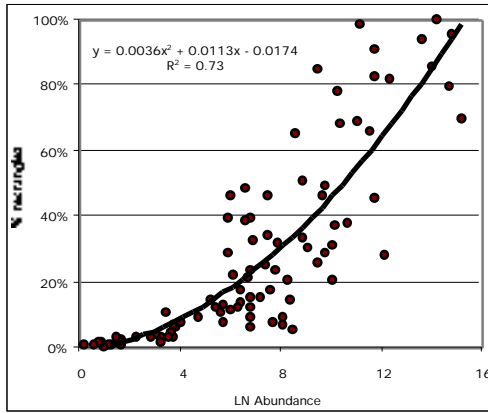

Fig. 5.2 Relationship between % of rectangles where observed and LN abundance with fitted polynomial.
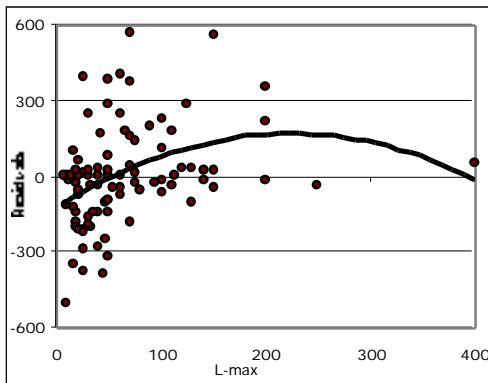

Fig. 5.3 Residuals of polynomial fit plotted against species L-max.

Fig 5.3 reveals that the residuals among the smaller species (roughly L-max <50 cm) were mostly negative, whereas they were mostly positive for intermediately sized fish.

Consequently, making a distinction between small and large fish revealed markedly different responses in the relationship between percentage of squares where species were caught and their numerical abundance: small fish species are found in larger densities over smaller areas than expected from the mean and vice versa for large fish (Fig. 5.4). In both cases, the variance explained increased significantly (R^2=0.79 and 0.81, respectively) compared to the total set (R^2=0.73).

A similar plot where pelagic fish were contrasted with benthic/demersal species revealed that the latter were more wide-spread in lower numbers (Fig. 5.5). Although this seems to be counterintuitive, there may be confounding with L-max, because many pelagic species are relatively small. The variance explained was high for pelagic species (R^2=0.87), but the value for

benthic/demersal species (0.71) was lower than for all species combined. No differentiation was observed between strictly benthic (e.g. flatfish) and demersal species (e.g. gadoids). However, the issue needs further investigation, because other aspects may be confounded with size as well, such as depth range.
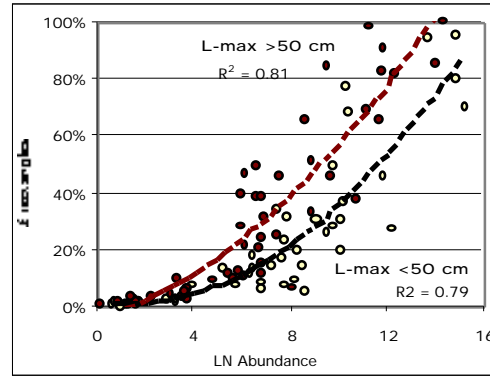

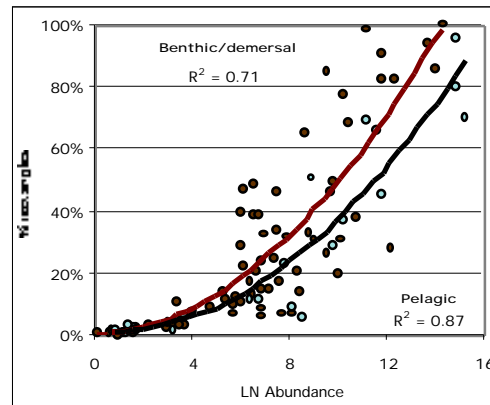Fig. 5.4 As fig 5.2, but for species with high and low L-max separately.

Fig. 5.5 As fig 5.4, but for benthic/demersal and pelagic species separately.

5.4. L-max

L-max is an important ecological parameter that is for instance related to predator-prey interactions and r/k strategy. Therefore, the frequency distribution (FD) of L-max among the species constituting a community would seem a relevant community metric (Fig 5.6). On an arithmetic scale, there is a marked dip just above 70 cm, but a LN transformation suggests a lognormal distribution.

It should be noted that L-max is a somewhat arbitrary measure based on hap-hazard observations. The Bertalanffy growth parameter L would seem more appropriate as a population average, but estimates are not readily available for many species. Moreover, both L-max and L may be biased when derived from heavily exploited populations that have little chance to reach their 'normal' size.
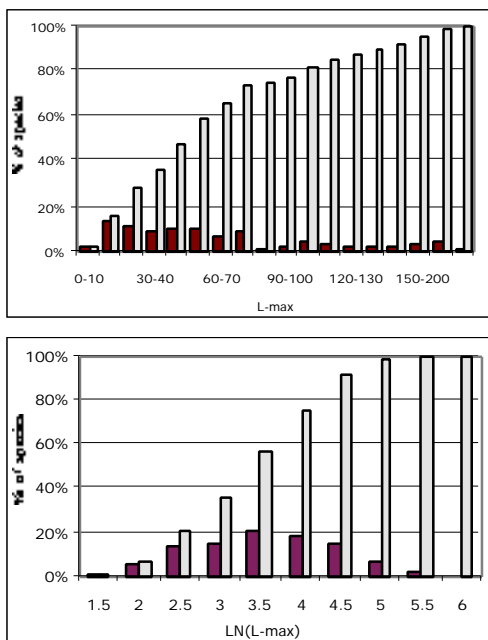
Fig. 5.6 FD of L-max among 91 North Sea fish species: (top) by arbitrary classes, (bottom) by LN classes).

5.5. *LN abundance*

Another important community characteristic is how the average abundance is distributed among the different species (Fig 5.7). Taking the overall mean abundance over 30 years (a) gives quite a different picture from the means of the annual FD (b). Although the pattern of the latter seems to be more regular, there is a clear over-representation of the lowest abundance class (i.e extremely rare species).
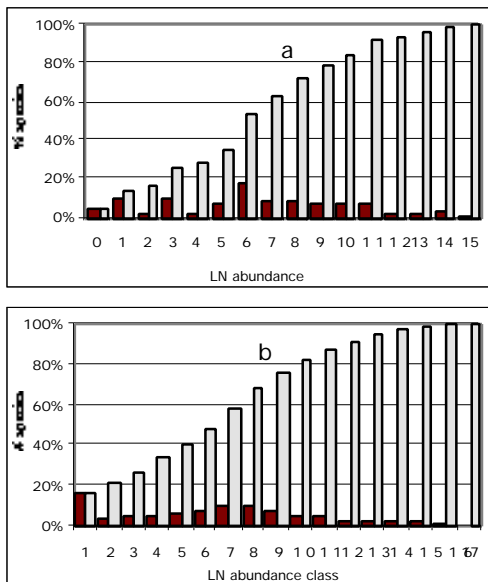

Fig. 5.7 FD of number of species (a) by LN mean abundance class and (b) by average LN abundance by year.

Based on the annual FD, we also related the standard deviation of the means to the mean LN abundance of all species (Fig. 5.8). For the rare species (LN abundance <4), the sd appeared to increase linearly with LN abundance (sd equal to the mean; i.e. Poisson distribution), while the sd clearly decreased for the more abundant species.
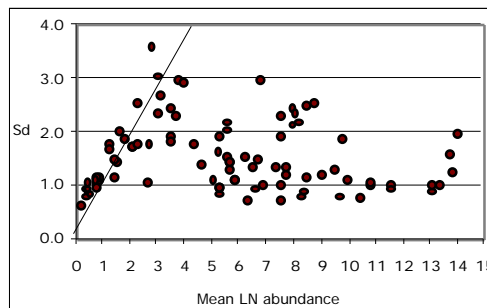
Fig. 5.8 Relationship between the standard deviation of the mean LN abundance and mean LN abundance by year.

5.6. *Species richness*

Fig. 5.9 presents the FD of the average percentage of rectangles fished that yielded a particular number of species. The top panel shows the raw data whereas the bottom panel is corrected for sampling intensity. The correction is based on 100 trawl hauls assuming a constant slope for the relationship between species richness and sampling intensity (see Daan, 2001). The difference signifies the importance of taking sampling intensity into account when dealing with species richness, but a more sensible correction factor might have to be based on bootstrapping.

Fig. 5.9 FD of % of rectangles with different species richness classes (a) uncorrected and (b) corrected for a standard sampling intensity of 100 hauls.

Another way of viewing species richness is how many species were found in which percentage of rectangles (Fig. 5.10). On an annual basis (a), a very high percentage is observed in a small number of rectan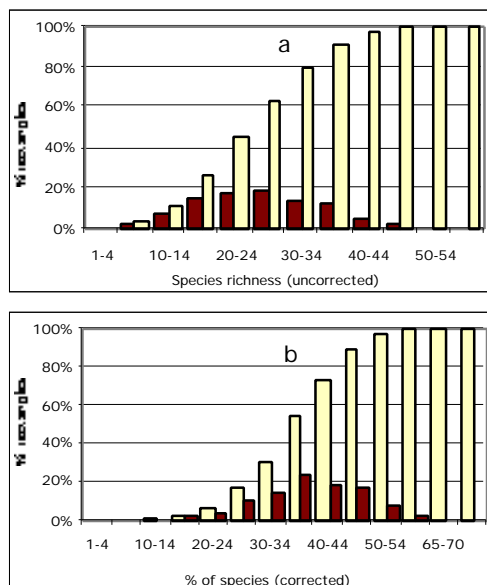gles and the distribution drops off rapidly, but the ranges observed in the (cumulative) annual FD (b) indicate that variation among years is rather small. The overall picture based on all data combined (c) is flattened compared to the FD based on annual data, which emphasizes that the distribution areas of all species are better defined when data are combined. If we could fish hard enough, all species might be encountered everywhere!

Obviously, species richness in the marine environment is not as straight forward as in terrestrial ecology, because we have only indirect observations that depend on limited sampling. While we can be confident that a nest of an osprey may not have been overlooked, catching the last mature skate is a different matter.
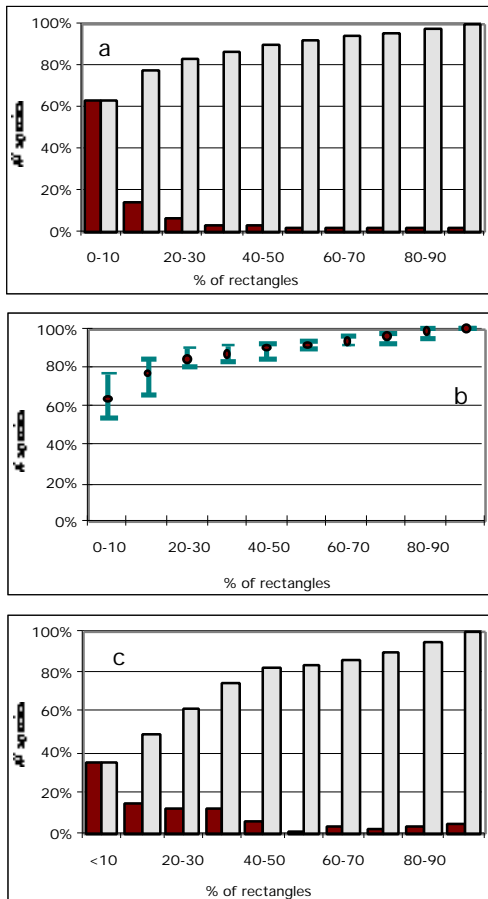

Fig. 5.10 FD of (a) the annual percentage of species observed in percentage of rectangles, (b) the range observed in these cumulative distribution.s, and (c) of the overall percentage combining all 30 years.

5.7. Species richness and LN abundance

A question arising was whether the number of species per rectangle is somehow related to the overall abundance of fish (Fig 5.11). Plots were made both for the uncorrected number of species and the number that would have been caught in 100 hauls in each rectangle. Although the correlation for the corrected richness is slightly lower, both are highly significant. However, the explained variance is low and the correlation appears to be driven largely by the lower end of the distribution of LN abundance, where actually the low number of fish caught might set an upper limit to the potential number of species caught.

It should be noted also that gear efficiency is partly a function of the catch. While a codend without fish may just swirl over the bottom, as soon as fish have been collected in the net, the gear assumes the shape that it has been designed for. This may bias survey data in areas where there are relatively few fish in the first place.
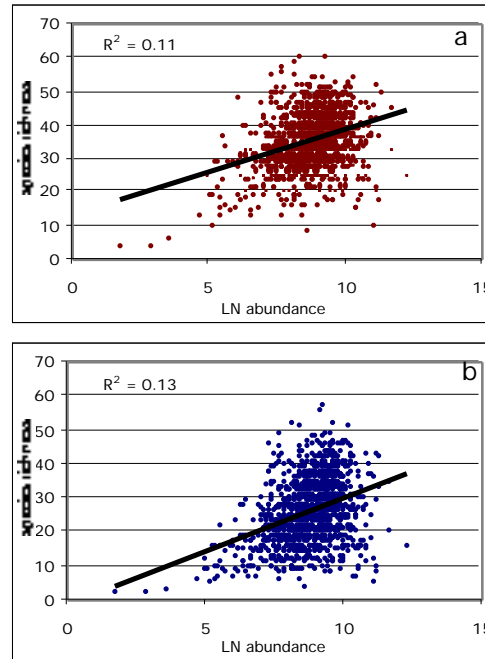
Fig 5.11 Species richness by rectangle vs LN abundance of all species combined: (a) corrected for sampling intensity (100 hauls), (b) uncorrected.

5.8. Discussion

The analyses presented here should be seen as a first attempt to describe the North Sea fish community in statistical terms. In fact, the most important reservation is that we can only see the community through the catches of the gear used, and we can be certain that catches of any gear will never mirror the true abundance in the sea. Among all commercially exploited species, sandeels yield the highest catches and probably represent the

single-most abundant taxon in the North Sea fish community. Nevertheless, they do not show up in large numbers in our catches. Whether this matters depends on the questions asked. If one wants to model the food web quantitatively, it is obvious that each species should get the proper weight to allow predictions of what effect exploitation may have on the system. However, it is an equally valid, and much easier, approach to model the system as we can view it through the catches of a survey gear and try to understand what has caused the changes observed. Of course, our picture will be biased, but our perception of the changes may not be. From a management point of view, it would seem useless to try to manage things, which cannot be seen and more appropriate to concentrate on those things that can be observed, even if this does not mirror the true world.

However, one important restriction of accepting bias is that the bias should not vary. In practice, this means entirely consistent data collection: doing things wrong is not bad as long as you do it consistently. In the past, much effort has been spent on ensuring standardisation of gears and catch procedures among nations participating in routine surveys in the North Sea. However, little attention has been paid to things like species identification. Daan (2001b) showed severe inconsistencies in the temporal and geographical distribution of a variety of less common species reported by individual countries participating in the International Bottom Trawl Survey in the North Sea. This immediately affects all of the community metrics presented here to characterize the North Sea fish fauna as viewed through scientific survey gear.

Nevertheless, it would seem unlikely that the major statistical properties of the community derived could have been flawed by such inconsistencies in data collection, because they are unlikely to cause anything but random noise on the estimated frequency distributions. More important effects can be expected on temporal changes in community metrics.

We were surprised to see how many metrics could be derived from survey data, that are pertinent to statistical modelling of a community and that at the same time have been so rarely addressed in the past. Still, this analysis is by no means exhaustive and in fact raises more questions about potential interdependencies of different metrics than it resolves. Our main conclusion is that there must be a wealth of significant information still burrowed in data sets around the world, that could be used to make intercomparisons between fish communities across different ecosystems and to identify common anthropogenic causes of observed changes.

6. A neutral model of the NS fish community

6.1. Introduction

The search for suitable metrics for evaluating ecosystem effects of fishing is severely hampered by the lack of established theory on how ecosystems operate. Although a variety of metrics has been proposed, with a few exceptions (e.g. size spectra) there is uncertainty how these metrics might be influenced by fishing. Also, lack of information on their variability hampers the development of quantitative criteria that could be used to evaluate hits, false alarms, misses and true zeros in the context of signal theory (Helstrom 1968). The rarity index developed by Daan (2001) evokes similar questions as many of the other metrics:

- when are observed differences in rarity value between species, rectangles or years significant and
- when do they matter for management?

In ecology, the first question can be addressed by neutral modelling; that is, simulating a community on the basis of known, explicit rules and investigating the empirical distribution of a metric based on repeated sampling from such a community (Lockwood et al., 1997; Belyea and Landcaster, 1999). There are many options here. At one extreme one might construct a completely arbitrary and hypothetical community, which bears no relationship to the real world. Although this would allow investigations of the variability in particular metrics, this would not give much guidance for evaluating empirical metrics when applied to a particular community (c.f. Colwell and Winkler 1984; Connor and Simberloff, 1984). It is well established in impact assessment (Lockwood, 1997; Beyers, 1998) that the usefulness of a simulation increases as it approximates an existing community as closely as possible without structuring into the simulation exactly the assumptions about possible interactions that one wishes to test. Correspondingly, we used available empirical survey information (section 5) as the basis for constructing a neutral model that broadly mimics the structure of the resident North Sea fish community (excluding vagrants).

6.2. Materials and methods.

Mean abundances for 100 species were assigned by resampling from the smoothed frequency distribution of mean relative abundances (Fig. 5.7b) of the 91 species observed in 30 years of North Sea research vessel surveys (Daan, 2001). For each species, the latitude x and longitude y of the centre of distribution were chosen at random on a 25 by 50 grid representing the North Sea (1250 squares; corresponding to 1323 squares sampled in

the North Seas when each ICES rectangle is divided in 9 sub-rectangles). A standard deviation sigma, representing the extent of range (equal in all directions), was chosen with distribution 5+5*r where r is distributed uniformly in the range 0-1. The mean of the parameter sigma was tuned to make the frequency distribution of species richness by rectangle match the observed frequency distribution in the surveys (cf. Fig. 5.10; ^{2}=11.95, df=9, 0.30>P>0.20).

[NB. Here we want P>0.05 to show that our simulated community did indeed match the true North Sea community, at least with regard to the number of species with various breadths of distribution.]

At the beginning of the simulation, individuals of the species are distributed across the 25*50 rectangles according to a bivariate normal distribution centred on x,y with sigma multiplied by the species abundance. Thus, the simulation makes the abundance of each species highest in the centre of its circular range, and abundance declines symmetrically in all directions, with 95% of its total abundance within 2 sigma of its centre. Each species had a unique value of sigma, which was held constant for an entire simulation.

Each year, these distributions are "surveyed" with a chance of observation chosen from a Poisson distribution with a mean related to the abundance in each rectangle. Species with low abundance in a rectangle thus have a possibility of having zero catch. A low abundance in a rectangle can result either from a low mean abundance (a species that is "rare" even in the centre of its distribution) or because a rectangle is far (relative to sigma) from the centre of distribution of a species with a high mean abundance (a rectangle that is on the "edge of the range").

The base run (table 6.1) held mean abundance and location of the centre of distribution fixed for all years, so the only stochasticity was in the probability of observation. This situation would mimic resampling a fish community within the same year. Alternative runs added interannual variance separately or combined in the two key features: µ and X-bar, Y-bar (table 6.1). The mean abundances could be perturbed by a random factor chosen on the interval of half to double. The centres of distribution of species could be perturbed by a random factor of between –3 and +3 rectangles in all directions. These sources of stochasticity reflect, respectively, changing abundance over time or changing area occupied.

Resulting survey catches are then processed to provide:

1. a rectangle dominance curve (cumulative curve of aggregate survey catch by rectangles ranked in order of catch per rectangle) showing what percentage of the rectangles contain what percentage of the total catch;
2. a histogram of the numbers of rectangles occupied by species;

3. a histogram of the species count per rectangle;
4. plot of rectangles occupied by species versus log species abundance;
5. Daan's Z measure of rarity by rectangle;

The simulation was programmed in MATLAB. The code is shown in annex I.
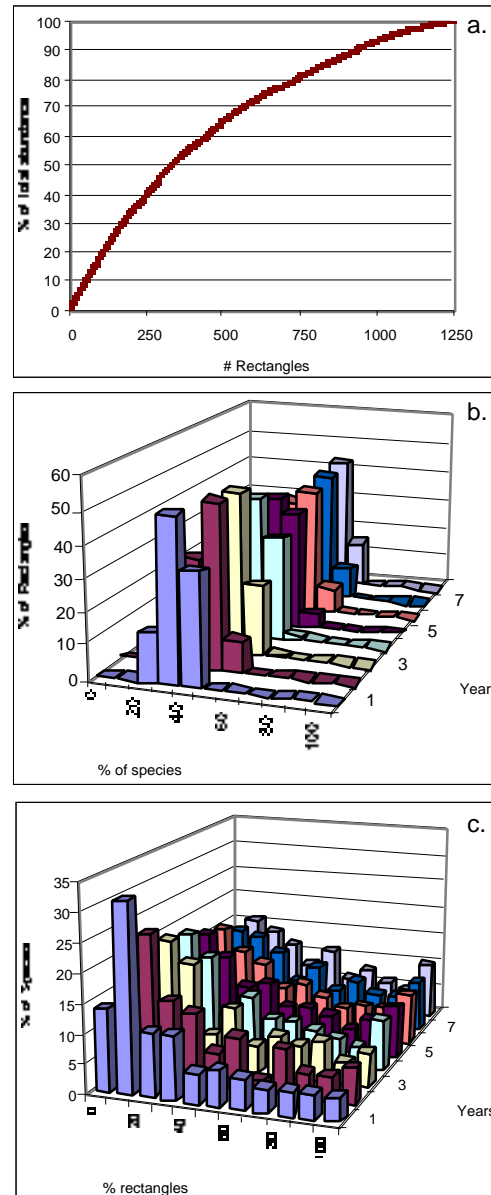
Fig. 6.1. Base run: (a) rectangle dominance curves (% of total abundance by rectangle sorted in descending order), (b) % frequency of rectangles observed with different percentages of species after 1 to 8 years (cumulative) and (c) a similar plot for the % frequency of species observed in different numbers of rectangles (expressed as % of 1250 rectangles).

6.3. Results

Most of the performance measures from the simulations proved rather insensitive to the different runs: allowing variance in annual

abundance and/or centre of distribution did not alter the average of any of the metrics. Fig. 6.1 shows some results for the base run. The rectangle dominance curves (a) by year were indistinguishable among years and among runs. These curves simply reflect the overall lognormal abundance distribution, which is not changed in response to the various ways that the lognormally distributed set of species is distributed over the grid cells. No data were available from the survey to check the result against survey data, but this should be possible in due course.

The frequency distribution of rectangles with the cumulative observed number of species over the 8 years (b) and the frequency distribution of the cumulative number of species observed in each rectangle (c) varied more among the runs, but the patterns were similar.

Apparently, such measures of species richness are useful only under special conditions, because they keep changing as more years of information become available. It is of course well known that species richness depends on sampling intensity and therefore should always be expressed relative to some measure of sampling intensity (e.g. per x hour fishing).

However, these simulations are able to partition the effect of mere increased sampling effort in a single survey (run 5) from the additional increase in the number of cells in which a species occurs over time caused by sampling in different years. The latter effect could be due to either varying mu (with constant sigma, in years of high abundance a species has a marginal occurrence in cells from which it is essentially absent in years of low abundance), or varying X,Y (shifting centre of distribution results in new cells being "colonised" over time).

Fig. 6.2 provides plots of the number of rectangles in which each species has been observed against the observed ln(abundance) for 2 different runs (cf table 6.1). These plots may be directly compared with similar information derived from the North Sea surveys (Fig.5.2). The similarity between the observed and simulated sets is striking, although the larger spread in the North Sea data at intermediate abundance suggests that the simulated variability should be increased. However, from the comparison of the relationship after the first year and after 8 years of simulation, it is clear that the steepness of the curve keeps changing, as it should, because catches of ever more species may be expected in individual rectangles by sampling more years. Again, constrasts among the simulations allow the effect of simply increased sampling to be partitioned from the effects of variation in abundance, variation in range, and variation in breadth of occurrence.

The differences between the base run without annual variation and run 8 with maximum annual variation are slightly counterintuitive, because the overall relationship seems hardly affected. In contrast, fixing sigma at a constant mean value (run 4) for all species clearly reduced the variability. However, this run was only included to clarify baseline conditions, but was not intended for comparison with real data sets. For example, Fig. 5.4 suggests that small and large species are characterized by different breadth of distribution for a given abundance. This alone should correspond to different species having different sigma, independent of their abundance as simulated in the base run. There is, of course, the possibility that μ and co-vary; that is, breadth of distribution increases non-linearly with abundance. That effect is being explored in further simulations.

Finally, fig. 6.3 provides the spatial distribution of rectangle rarity values following Daan (2001) for the base run and the run with maximum variability, both after one and after 8 years of observation. Increasing variability seems to spread out rarity values among more rectangles. This is not unexpected because the square where the probability of observing a less abundant species is highest changes from year to yearin this case. It is also clear that the scale of variation among species is reduced when more observations are added (more species have values larger than 1 and no species has values higher than 10 after 8 years).

6.4. Discussion

The model was originally intended to evaluate variation due to sampling in a specific metric (Daan's rarity index). However, constructing the model turned out to be a rewarding experience in itself, because it compelled us to evaluate a wide range of distributional properties for characterizing the fish community (section 5). Features such as the lognormal distribution of the abundance of individual species might otherwise have remained hidden.

The model signifies also the interpretational problems that we face in sampling a fish community with large differences in abundance and distribution among species, because nearly all metrics vary with the amount of information that becomes available. Moreover, several different properties of the community could change (mu, sigma, X,Y among runs 6, 7, and 8), yet very similar patterns were observed in our performance measures. Even when we have documented that "change" has occurred, there will be serious challenges determining exactly what aspect(s) of the community structure have changed.

The sensitivity of our metrics to sampling intensity, and their low diagnostic value will greatly reduce the possibilities for making comparisons of communities among ecosystems. The sampling problem is serious because not only survey gear but also sampling intensity and length

of time series are bound to vary. The fact that many different factors can produce the same patterns in the metrics is serious, because in real data we will not have *independent* knowledge of the underlying distributions of mean abundances, variances in abundances, and centres of distribution. Nevertheless, the simulations are only a first step. Many more scenarios are planned for intersessional work, and many more metrics can be explored for the various outputs. The simulations do more than just highlight where problems lie. They can also be research tools to obtain more stable metrics that account for sampling intensity and number of surveys, and display distinctive patterns when specific properties of community structure have changed.
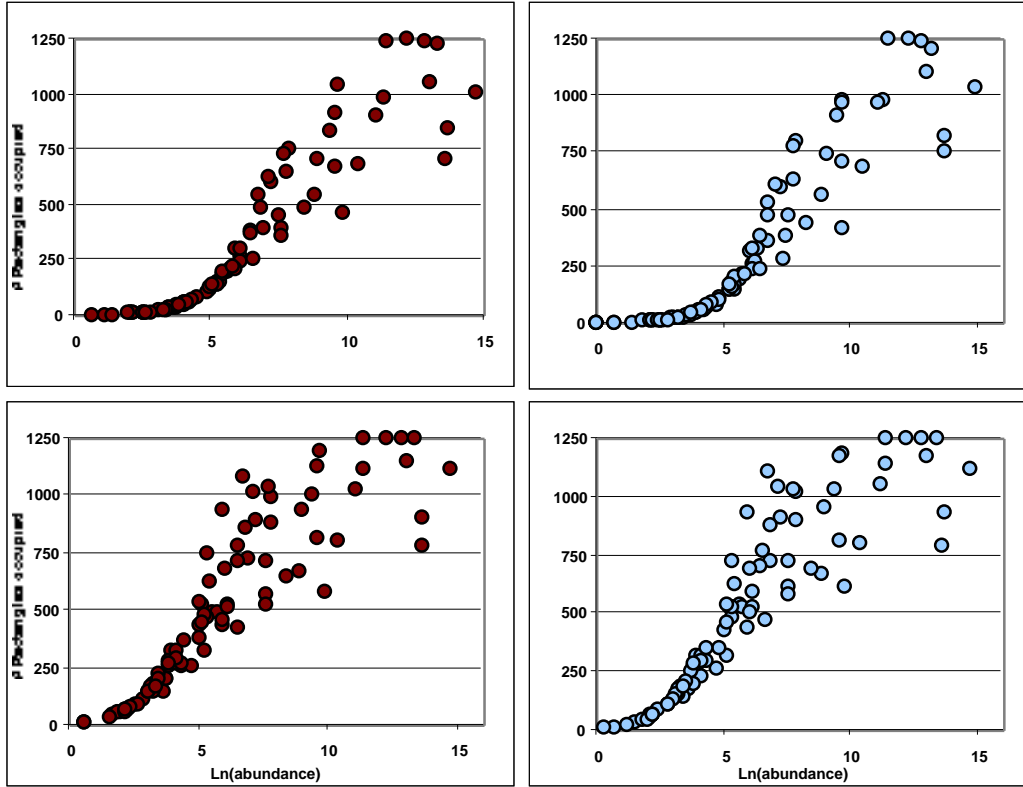

Fig. 6.2 Relationship between the number of rectangles occupied per species vs ln(abundance) after (top panels) one and (bottom panels) after eight years of sampling for the base run (run 5; left panels) and the run with random variation in μ and in the centre of distribution (run 8; right panels).

Table 6.1. Specification of runs with the MATLAB simulation model of the North Sea fish community.

| Run	Mu	Sigma	X-bar, Y-bar	Rational
4	fixed μ	fixed at 7.5	fixed to initial rand	no variation in parameters
5	**fixed μ**	**5+5*rand**	**fixed to initial rand**	**base run (sigma species specific, range 5-10)**
6	μ*exp(-0.7+1.4*rand)	5+5*rand	fixed to initial rand	annual variation in abundance (50-200%)
7	fixed μ	5+5*rand	initial rand-3+6*rand	annual var. in distribution centre (± 3 rect.)
8	μ*exp(-0.7+1.4*rand)	5+5*rand	initial rand-3+6*rand	all parameters except sigma vary by year
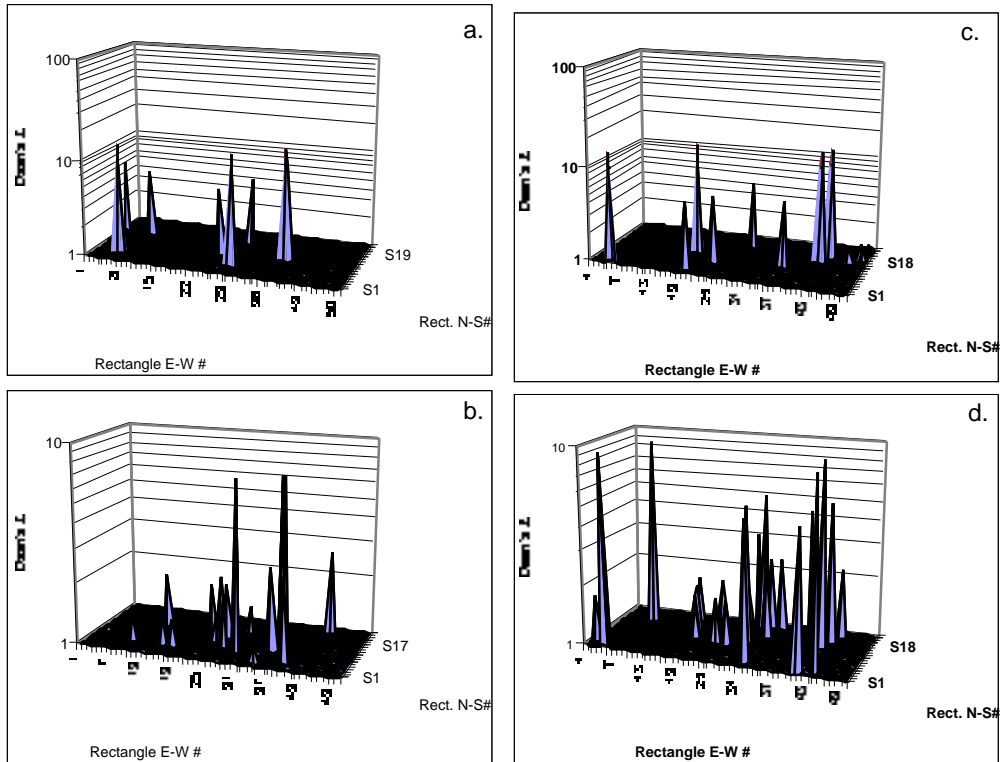
Fig. 6.3. Daan's integrated rarity index (abundance and distribution) after (top panels) 1 year and (bottom panels) eight years for the keyrun (5; left panels) and the run with maximum variation (8; right panels).

7. Simulation of multi-species, size-structured communities.

7.1. Rationale

The linear size spectrum of the fish community has interested fisheries scientists for two decades. Interpreting changes in slope of the size spectrum as a consequence of fishing is supported by both survey data from real ecosystems, and simulation studies of moderate sized sets of species interacting as predators and prey in an MSVPA-type way. Despite the body of evidence supporting the use of change in the slope of the size spectrum as an indicator of past fishing, there is concern that no one is quite sure why it works. We identified two possible explanations of very different complexity, and therefore likely to be of very different consequences for comparative studies and for management advice.

• The "ecological hypothesis" presumes that the linearity is a consequence of processes that act to produce an orderly decline in abundance with size. Temporary irregularities, for example a bump caused by the influx of an exceptional number of recruits, are rapidly smoothed out by ecological processes. For instance, large numbers of recruits attract more predators that may graze down the bump. Density dependent processes, particularly growth and survivorship, or the effects of one year class on the succeeding one, could easily be built into plausible mechanisms for smoothing bumps. Likewise, if a temporary dip were to occur in the linear size spectrum (for example by excessive fishing of one intermediate size interval) plausible arguments about density dependent survivorship, competitive release, etc, could provide a process-based explanation for preserving the linearity of the size spectrum of fish abundances. Such process-based explanations are attractive to many ecologists and fisheries scientists.

• The "aggregate hypotheses" is much simpler, invoking no process-based ecological interactions in producing the size spectra with negative linear slopes. It aggregates some simple single-species patterns that must exist, across all the species in the community. The first pattern is that regardless of what size a fish species may reach, it starts off small and can only stay the same size or get larger over time. Correspondingly, even though individuals of a species that is small (small Lmax) may never be large, all individuals of a species that is large (large Lmax) will begin their life small, and move through all the size intervals in the size spectrum. (It is true that some fully grown fish can lose body condition, and possibly even a little length, under particularly unfavourable feeding conditions, but this is unlikely to be common enough to negate the general pattern invoked here.). The second general pattern is that cohorts can only decrease in abundance over time, and are always equally or less (often much less) numerous as they increase in size. Combining these patterns means that:

• the smallest sampled size interval should have all the species observed in all larger size intervals,

• numbers of contributing species will decline over size intervals

• on average each species should tend to become less numerous over size intervals.

It is possible that aggregating these patterns across species will produce linear size spectra with negative slopes, without invoking any further biological processes.

[NB. Variation in cohort strength means that the latter pattern will not strictly hold for every species at all times, but it will be true on average. Moreover, some species with small Lmax are very numerous in the smallest size intervals, and decline in abundance quickly across increasing size intervals. This factor could mask a great deal of the variability in abundance of cohorts of species with larger Lmax, when they are small. Complicating factor: species where the adults migrate into an area, appearing for the first time at intermediate sizes in the range being sampled.]

If the aggregate hypothesis is sufficient to account for the size spectra constructed from real samples of fish communities, then the impacts of fishing on the fish community can be accounted for fully by the impacts of fishing on the individual species killed by fishing. (This will usually be a longer list than the list of target species, of course, because of by-catch and incidental mortality of non-target species.). If the aggregate hypothesis does not account for the observed linear pattern, then the impacts of fishing on the fish community will be moderated by interactions among species. This will make the ecosystem effects of fishing much more difficult to track. However, it is worth noting that if the consequence of the interactions is to maintain a linear slope to the size spectrum, then they will act to compensate at the community scale for the effects of fishing, buffering not amplifying the effects. This won't make them any easier to predict, or necessarily lead to more desirable (from whatever standpoint one may have) community configurations, but they will act to retain ecosystem structure in the face of perturbations by fisheries, and not dissipate it.

It may be possible to differentiate among these two hypotheses through simulating fish communities, and contrasting properties of the simulated communities with properties of real communities. The patterns expected under the aggregate hypothesis should be straightforward to reconstruct, making a small number of assumptions about single-species properties. If the aggregated patterns from the simulation match the patterns seen in real communities, then there is no empirical justification for invoking the much more complex interactions that constitute the ecological hypothesis. If the patterns from the aggregate simulations are unable to match patterns seen in

real communities, then there is justification to conclude that specific interactions occur in real communities to preserve the linear size spectrum. It is possible (although not certain) that the ways in which the simulated community fail to match the real communities may shed light on the nature of the structuring interactions. That is, of all the possible complex interactions that could be added to the aggregate simulation, a small number of them might correct the lack of fit most parsimoniously.

7.2. Concepts to be captured in the aggregate simulation

One specifies/assigns:
• **N species**, where the necessary N is somewhat larger than the actual number of species observed in a typical survey. (NB. This is Preston's "Veil Line" once again. Some species will be assigned parameters that result in them being so rare that they are unlikely to be taken in simulated "samples". Likewise, in real communities some species are so rare that they have not appeared in any samples by the time a survey has been completed.).
• A **mean and variance in cohort strength** for each species. This applies to the cohort strength when it enters the smallest size interval included in the survey data. Based on previous work, this might best be done drawing means from a lognormal distribution, and variances from a normal (or lognormal) one. The parameters of the distributions of means and variances can be estimated from the community to be matched, or one can just tune values iteratively. Alternatively, one can accumulate the actual distributions of mean abundances and variances in abundance across all the species in the community to be matched, and just resample from the observed distributions. These options for parameter choice will be available for all of the subsequent parameter sets. In all cases the strategy of drawing from a specified distribution is more general and flexible. However, it requires motivating use of some specific distribution. The alternative re-sampling strategy ensures that the true distribution of means and variances in the community to be matched are represented in the simulated community. In that case any lack of fit between the observed and simulated patterns is definitely due to the absence of one or more processes in the simulation, and not to just getting the distribution of means slightly (or greatly) wrong. In either case allowance must be made for the "veiled species" issue.
[NB. In community simulations there is often an issue of whether or not means and variances of abundance/cohort strength are independent or correlated. It is always good practice to begin the project by assigning means and variances in cohort strength independently for each species, but it can be useful to have the simulation constructed so that a correlation between mean and variance of each species' cohort strength can be specified.]
• Parameters to control the **rate at which the cohort moves through the size intervals**. There are several options, each seeming to need two parameters:
- Give each species a von Bertalanffy growth pattern. This means specifying a **k** and **L$_\infty$** for each species. As with the mean and variance of cohort sizes, the sampling distribution for k and L may be either lognormal (as a convenient first guess) with parameters from the real community, or the distribution of observed k's and L 's bootstrapped from the real community. The degree to which pairs of growth parameters should be correlated should be determined by the knowledge of the system to which the simulation is being compared. If the simulations should be able to include the possibility of density-dependent growth, then selection of one or both of the growth parameters has to be able to be made conditional on assigned cohort size.
- Make pre-terminal **stage residency** and **terminal stage** as a transition matrix with parameters assigned for each species. Random assignment of transition rates would produce all possible combinations of fast growing (fast transitions across pre-terminal stages) and slow growing (slower transitions across pre-terminal stages) species, and small (early terminal stage) and large (late terminal stage) species. It would seem to be appropriate to have transition rates decelerate as a species moved through the larger stages, but it should start as a common factor for all species (as the vonB growth curve is a common functional form). The same considerations apply to sampling distributions of the transition matrix values as for the von Bertalanffy case. It would be interesting to see if it was necessary to specify correlations between transition rates and terminal stage parameters (that is, do individuals of species which are destined to be large move through small size classes faster than individuals of species whose terminal size is small.). The simulation should definitely be able to explore the impacts of such correlations.
Whichever option is used, there should be some provision for intra-cohort variance in the rate at which the cohort moves through size classes. A transition matrix approach should intrinsically be able to smear a cohort across adjacent size intervals over time, but a vonB growth model will require a variance term. Should it be a simple (normal) random variable from a universal (same sampling distribution for all species) distribution, from a species specific distribution, or should intra-cohort

variance in growth rate be correlated with either (or both) cohort size and L ? In the transition matrix approach there should be some way to explore the effect of (and need for) species-specific matrix values to covary with cohort size as well as terminal stage attained.

• A parameter for **natural mortality rate**. This again could be done in a couple of different ways:

- **Species-specific M**: would almost certainly have to be correlated with L (or terminal stage). M could apply to the species over its entire life span, although for species with high L M for the first few size classes might need some multiplier. Sampling distribution for M would follow all the considerations above, although the "theoretical" distribution across species is unclear, if the choice is not to resample.

- **Size specific M**: Same considerations apply as for species specific M, but there would be fewer parameters in the total simulation, as long as there were fewer size intervals than species. If there was to be some variance among species in their rate of decline over size intervals, it should probably be assigned once to each species at the beginning of the simulation, rather than assigned independently at each size interval. The proper (data determined) sampling distribution for variance in M would be interesting.

• A parameter for **fishing mortality**. This will be specified as a forcing process in the simulations, and set on a scenario-specific basis. Considerations include:

- The simulation design will have to allow F to be set separately (if desired) for each species, and to vary in planned ways across size intervals.

- One proposal of interest was to have knife-edge vulnerability at a specified percentage of L for every harvested species.

- Setting F to match the fishery for target species should be straightforward. The fraction of species with high, moderate and low L that are fished in the real community can be known, and the simulation will have to include a step to ensure that can be preserved. An approach may be to rank species by their L value in the set-up pass, and have a Heavyside function for whether each will be fished or not, with mostly 0's for small L and increasing 1's for large L values. This Heavyside vector can be matched to a vector of F's, so it would be possible to adjust separately targeting among large and small species, and the intensity of F for different large and small species. This still leaves the question of how should by-catch mortality be handled?

7.3. Simulations

Set up:
• Specify number of species.
• Assign mean and variance in cohort size per species (initially uncorrelated).
• Assign growth parameters or transition matrix entries per species.
• Assign M per species (or size interval) correlated with maximum growth parameter or terminal size.
• Specify fishing mortality matrix by species and size interval.

Year 1:
• Specify cohort size for each species
• If assuming density dependent growth, adjust growth parameters / transition rates for realized cohort sizes.
• Let each species grow.
• Kill off each species with species or size specific M + F. (If a species is growing through several size intervals in one time step, it is necessary to account for all mortality correctly).

Year 2 –
• Repeat year 1 for cohort size and growth rate of recruits to smallest size interval.
• For recruits plus last year's survivors by species and size class, grow and kill off.
[NB. QUESTION: Once more than one cohort of a species occurs in the same size interval, do the density dependent growth and/or mortality parameters (if they are being used) remain the ones initially assigned given the initial cohort sizes, or are they readjusted to reflect the current density of conspecifics of similar size? This is important, because it will be a different simulation if cohorts keep their growth and mortality parameters through life (so all cohorts should be tracked individually until they reach their terminal size), or if conspecifics are pooled within in each size interval at each time step and what happens to them next would be determined by those local conditions.]

Repeat Year 2 until essentially all species have reached their L . This becomes the initial condition for the simulation. At this point, you continue simulation in the same way, but can begin to track yield and estimate the size spectrum parameters.

7.4. Further thoughts

The first simulations should be without the density dependent linkages of growth and mortality parameters to cohort size, if only because this is the simplest case, invoking the fewest processes. If the simulations fail to fit the real data, then adding the intra-specific density dependent factors should be the next level of complexity explored. If it is still impossible to fit the real surveys, then inter-specific density dependence may be the next case to explore. Here the intra-specific formulations may provide the right model to follow, with the degree of inter-specific impact increasing as species have increasingly similar L 's. At this point

the simulation would almost certainly have to be designed so that the density dependent adjustments were made size interval by size interval, not cohort by cohort. That structure would be necessary in order to examine community responses to size-and-species-selective fishing, where relative abundance of cohorts of different species might be changed abruptly when the cohort was part-way through its total scope for growth.

Thought should be given to what properties are to be compared between simulated and real survey communities. Total species richness, yield, and size spectra parameters are the minimum. Is it necessary for communities to match on more properties, though, such as

• Richness per size interval
• Distributions of abundances across species within size intervals
• Initial distributions of cohort strengths across species on a year by year basis.

8. Exploitation level of ecosystems

8.1. Introduction

One problem in evaluating effects of fishing at higher levels of aggregation than the single species such as the fish community is that the single species measures of exploitation (i.e., F) cannot be readily aggregated or averaged over species. If different ecosystems - or features of the same ecosystem at different times - are to be compared in terms of responses to exploitation, some quantitative measure of exploitation level of the total ecosystem is needed, because it will make a difference whether only one or the majority of species is overexploited. Also, exploitation of forage fish may have a different impact on the community than exploiting predators. It seems doubtful whether one single measure could capture all aspects and therefore we may need several measures, which together reflect total impact. We explore various optioms.

8.2. Yield/biomass and yield/production ratio

Potentially useful measures that have been or could be applied to single species and which could easily be aggregated over species are the percentage biomass removed each year and the yield/production ratio. However, this is not a simple matter, because reliable data are generally only available for commercially important species and very little is known about the biomass or production of other species that are landed, discarded or not caught with the existing gears. Although survey data might be used for swept-area estimates, differential catchability among species is likely to distort the picture obtained relative to the true biomass composition, because gears have been developed to catch commercial species and their

catchability is therefore probably higher than for other species. Jiming (1982) and Sparholt (1987) are among the few who systematically addressed this problem, but the wealth of survey data presently available and often obtained with different gears should make it worthwhile to update and refine these analyses.
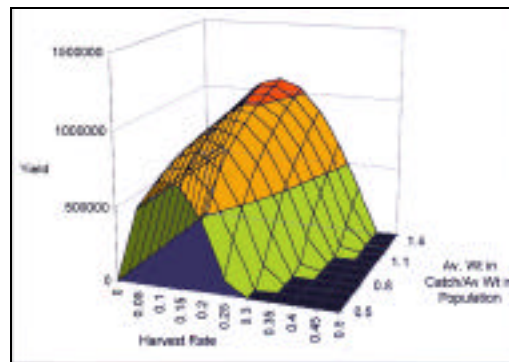

Fig 8.1. Bulk biomass steady state isopleth surface of yield vs harvest rate and w_c/w_s ratio.

8.3. Weight-in-the-catch weight-in-the-sea ratio

While catch/biomass ratio is potentially a useful measure of overall exploitation, it does not differentiate exploitation of different size classes. One possible measure of the size selection is the average weight-of-fish-in-the-catch (w_c) relative to the average weight-in-the-sea (w_s). Again, this idea has been tried out on Northeast Arctic cod. Fig 8.1 presents the steady state yield isopleth surface as a function of harvest rate (yield/biomass ratio and the associated w_c/w_s ratio, based on a bulk biomass model for the stock. By increasing the harvest rate from zero to half, the weight ratio drops to about 1/3 of its original value. This suggests that it could be a sensitive parameter for changes in exploitation.

Fig. 8.2 provides time series data of w_c, w_s and their ratio for the same cod stock. While weights in the catch may be considered empirical observations based on market sampling, weights in the stock were constructed from length at age data and VPA estimates of stock size age 3 and older cod. Although there is obviously quite a bit of short term variability that is related to recruitment of good or bad year classes, there is a clear long-term increasing trend in the ratio that matches the increase in fishing mortality as estimated by VPA (ICES, 2000). While average weights in the catch could be aggregated over species, an index of the mean weight of fish in the sea might be derived from survey catches for all species combined. Potentially, this may produce a useful measure of exploitation of the entire community.
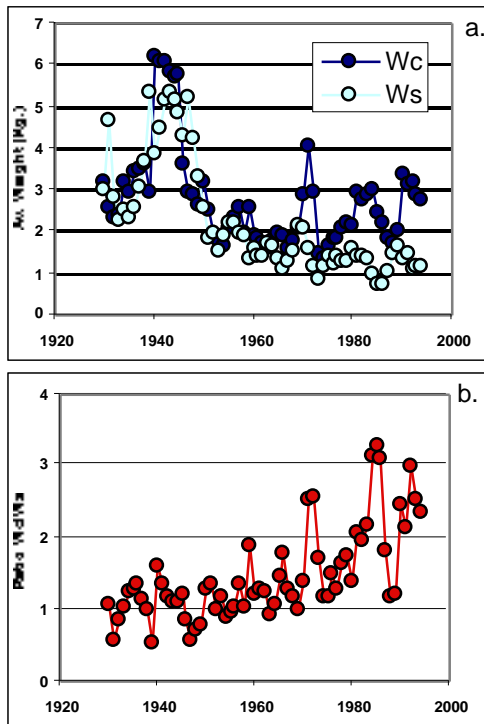
Fig. 8.2. Time series of (a) weight in the catch (w_c) and weight in the sea (w_s) for Northeast Arctic cod and (b) the ratio between these two (w_c/w_s).

8.4. Length-stratified distributions of ln(N)

During the exploration of the proper distribution of mu's across all fish species in the North Sea [Section 6], mean abundances across the community could be approximated by a log-normal distribution. Although this was only explored in some depth for total abundance, there were some indications that the abundances followed a log-normal distribution when dis-aggregated by length interval as well. At the smallest well-sampled length intervals there would be more species, and the range of ln(abundances) would also be broader (reasons for this are developed more fully in section 7). Hence, as size increases the peak of the length-stratified log-normal distributions would move towards the origin on the ln(abundance) axis, and the ascending limb of the distribution would become progressively more truncated. Contours of particular percentages of all species would be expected to follow lawful patterns across the surface of this family of probability density functions.

There are several reasons why the length-stratified distributions of ln(abundance) could be sensitive to exploitation rate. As fishing pressure increases, at least initially ln(abundance) of all exploited length classes would decline. Three processes should make the effect stronger at higher length intervals. First, fishing itself would likely be size-selective within species and overall, with

fishing mortality usually asymptotically highest at the larger sizes attained by each species. Second, a higher proportion of species are expected to be exploited from higher length intervals than lower length intervals (both directed and as by-catch), so the abundances of more species in larger length intervals would be reduced by fishing. Third, in the long run production of individuals in shorter length intervals could be stimulated through exploitation of larger length intervals, either by reduction in predation mortality or compensatory increases in production (*sensu* Schaeffer).
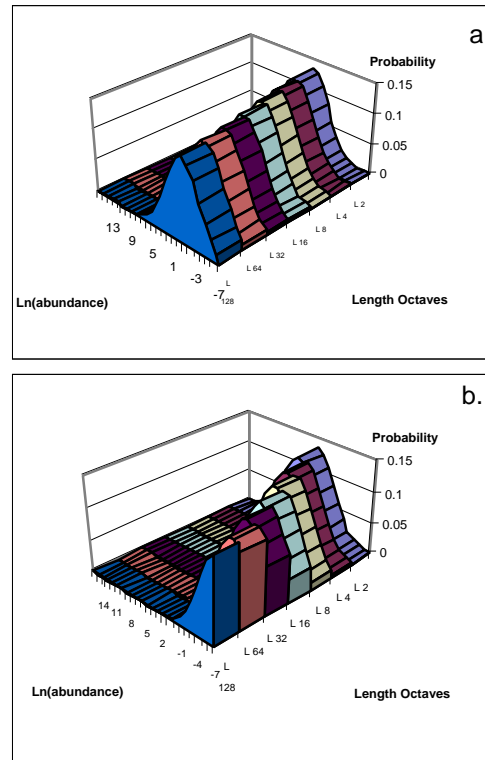

Fig. 8.3. Distribution of ln(abundance) at length octaves for (a) a simulated unexploited community and (b) a heavily exploited community.

These patterns, if confirmed by more intensive analyses of survey data, would offer another potential tool for measuring community-scale intensity of exploitation. If it is possible to estimate both virgin biomass (B_o) and L for all species in a community, with reasonable assumptions about growth it should be possible to reconstruct estimates of the distribution of abundances by length interval for an unexploited community. At the least, given a time series of survey data during a period of increasing (or decreasing) fishing effort overall, it would be possible to estimate the distribution of abundances across species by length interval for the earliest period. This family of length-stratified distributions would be contrasted with the same family of distributions after a period of exploitation.

Changing slopes of various contours along the distribution, as well as the trajectory of the peaks of the distribution, would be potential quantitative indicators of the community scale impact of fishing. Simulated data for an unexploited suite of species and the same suite of species subjected to heavy exploitation (Fig. 8.3) illustrate the type of pattern that might occur. Results of this preliminary simulation are sufficiently encouraging that we feel this type of analyses should be pursued further for data sets providing size composition data for most (if not all) fish species in a community over time.

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Annex I. MATLAB code for simulating the North Sea fish community.

```
10%dist1.m is a script file to simulate species catch distribution over a 50 by 25 rectangle
grid.
Murange=[2118.741      400.8973       49.21935       583.4292       73.44769      ...
18797.32       12.40647       703.5578       0.668664       341.4263      ...
70.94638       363.3153       506.5686       0.191772       41.88106      ...
0.095249       174.9356       328134.3       191.5823       525.5121      ...
502.1311       948.0459       12.90904       1061.022       5566943       ...
161.6698       90.55344       0.083326       0.152089       56.762        ...
130831.9       547501.8       11.71147       65.20542       13762.71      ...
276.8308       1149.21        0.657203       1385.711       0.126283      ...
10.02747       18450.05       0.499205       1.454931       660.3638      ...
24510.01       97.4651        72.09501       8.217466       3170.617      ...
1028242        9582.622       4.871136       0.349855       9109.401      ...
29518.53       159.7109       1187.203       268.9741       123389.2      ...
2144.668       293.3998       253.2517       35.68984       458160.3      ...
1785.773       1634259        17.05746       35.76972       120128.3      ...
1302.321       75.53079       170.0227       1.488706       0.150808      ...
46.12436       4224.979       95.25508       1.529151       16.57292      ...
15.56597       2029.592       93587.37       3060.986       35.25514      ...
476.5384       28619.45       2511.215       0.831986       2954.723      ...
29.59972       71.449         42.09216       35.9646        10.01292      ...
325.7231       1042321        62.69502       13.32592       0.159615]
xcount=zeros(25*50,100);
norec=zeros(8,100);
zrem=zeros(8,100);
remscsq=zeros(8,1250);
remlco=zeros(8,100);
remsr=zeros(8,1250);
remspr=zeros(8,100);
cou=zeros(25,50);
for i=1:100
xbar(i)=50*rand;
ybar(i)=25*rand;
sigma(i)=5+5*rand;
end
for y=1:8;
y
cou=zeros(25,50);
for i=1:100
prob=zeros(25,50);
prob=norman(xbar(i)-3+rand*6,ybar(i)-3+rand*6,
murange(i)*exp(-1+2*rand),sigma(i));
m=i;
for k-1:25
for l=1:50
n=(k-1)*50+1;
pr=prob(k,1);
co=poisson(pr,floor(25+3*pr));
xcount(n,m)=xcount(n,m)+co;
cou(k,l)=cou(k,l)+co;
end
end
end

figure
surf(cou)
hold on
title('summed species abundance per rectangle')

count=xcount/y
sqco=count*ones(100,1);
spco=count'*ones(1250,1);
sumsp=sum(spco);
lcount=count>0.001;
sprec=lcount'*ones(1250,1)
lll=sprec(95:100,1)'
z=1250*ones(100,1)./((sprec+1).*sqrt(spco+1));
zsum=sum(z);
z=z*1000/zsum;
zrem(y,1:100)=z';
cou=zeros(25,50);
invco=z./(spco+1);
zrec=count*invco;
```

```
for k=1:25
for l=1:50
zz(k,1)=zrec((k-1)*50+1,1);
end
end

figure
mesh(zz)
title('Daans z assigned to rectangle')
ylabel('rect count W-E')
xlabel('rect count S-N')
zlabel('Z score per rectangle')

cumsq=cumsum(flipud(sort(spqo)));
cumsq=100*cumsq/cumsq(1250,1);
figure
plot(cumsq,'or')
remcsq(y,1:1250)=cumsq';
title('Rectangle dominance curve')
xlabel('rectangle rank')
ylabel('% of Cum count of individuals)

figure
hist(sum(lcount));
norec(y,1:100)=sum(lcount)
title('Histogram of rectangle occupied per species')
xlabel('rectangle occupied')
ylabel(species frequency')

figure
hist(sum(lcount'))
remsr(y,1:1250)=sum(lcount');
title('Histogram of species per rectangle')
xlabel('number of species'
ylabel('species frequency')

figure
logco=log(spco);
stem(logco,sprec,'.r')
remlco(y,1:100)=logco';
remspr(y,1:100)=sprec';
title('rectangles occupied by species versus log(species abundance)';
xlabel('log(species abundance')
ylabel('rectangles occupied')

save a:\zz.dat y –ascii
save a:\zz.dat zz –ascii
end

figure
save c:\matlab\remcsq.dat remcsq -ascii
save c:\matlab\remlco.dat remlco -ascii
save c:\matlab\remsr.dat remsr -ascii
save c:\matlab\remspr.dat remspr -ascii
save c:\matlab\norec.dat norec -ascii
save c:\matlab\zrem.dat zrem -ascii
save c:\matlab\xcount.dat xcount -ascii
save c:\matlab\lcount.dat lcount -ascii
save c:\matlab\cou.dat cou –ascii
```