

REPORT OF THE  
**Study Group on Age-length Structured  
Assessment Models**

**Bergen, Norway  
3–6 June 2003**

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## **1 INTRODUCTION**

### **1.1 Participants**

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Stéphanie Mahevas, France  
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### **1.2 Terms of Reference**

It was decided by Council (C. Res. 2002/2D07) at the 90th Statutory Meeting, 29 September to 9 October 2002 that:

The study group on age-length structured assessment models [SGASAM] (Chair: Dr. K Guldbrandsen Frøysa, Norway) will meet in Bergen, Norway from 3-6 June 2003 to:

- a) investigate process model formulations, goodness of fit and model sensitivity in age-length based models;
- b) evaluate the usefulness of such tools in specific case studies on stocks with differing life-histories, data availability and quality, such as sprat, anglerfish, blue whiting, *Nephrops*, Greenland halibut and deepwater species.

SGASAM will report for the attention of Resource Management Committee and ACFM.

### **1.3 Scientific justification by ICES**

The Study Group will address problems that come from introducing length structure (in addition to age structure) and see how these problems may be solved in practical use. By using tools such as Fleksibest, the potential of an age-length model as an assessment tool for a wide range of stocks will be explored.

A resolution for the establishment of this Study Group was approved at the 2001 ASC but due to unforeseen circumstances the scheduled meeting had to be postponed.

The Study Group expands upon the ICES Workshop on Fleksibest – an Age and Length Based Assessment Tool held in Bergen, Norway, 16-19 January 2001 (ICES C. M. 2001/D:10).

## **2 BACKGROUND**

Despite the existence of a diversity of available model types, for largely historical and institutional reasons, catch-at-age models are by far the most widely used assessment approach within the ICES context (ICES C. M. 2003/D:03). SGASAM investigates and evaluates the use of length-structured and age-length-structured population models in fish stock assessment. In this introductory chapter the utility of length-structured population models is reviewed. Firstly, the various reasons for the use of such models are discussed. Secondly, cases where such models have been used for specific stocks are listed.

## 2.1 Why use length-structured population models?

The reasons for using length-structured population models broadly fall into two classes:

- It is thought that such models are a better representation of biological and fishery related processes.
- Problems with age determination do not permit the use of age-structured models or make such models less reliable.

Age-length-structured models may have a higher degree of complexity. The final choice of model will depend on the question asked and often be a trade off between the desired complexity and the availability of data.

### 2.1.1 Better representation of processes

Many biological and fishery-related processes (e.g. maturity, fecundity, growth, natural mortality, predation, selectivity of the fishery) are better described by length than by age. It has been noted that for some fish stocks in boreal systems applying age-length structured assessment models is especially relevant because such stocks experience large inter-annual variation in growth (Mehl and Sunnanå 1991; Mehl 1991). Further, intra-annual variation in growth can be explicitly included in length-structured and age-length-structured models (e.g. *Nephrops*). Changes in demographic characteristics (e.g. length-at-age, weight-at-age, mean age) have been noted in a number of stocks in recent time, and may be a response to high levels of exploitation or environmental fluctuations. Especially in rapidly developing fisheries the length-at-age distribution is unlikely to be in equilibrium and consequently variables such as maturity-at-age and selectivity-at-age are unlikely to be constant.

Mortality processes are one class of biological processes that are size dependent rather than age dependent. Evidently, natural mortality through predation is size based. Cannibalism is of special concern and for many species, for example cod, has an important role for the regulation of abundance. Usually the maximum size of prey, which is suitable for a predator is equal to half the length of predator. Consequently, the faster young fish achieve a size at which they can avoid predation, the greater will be their chance for survival. As a result natural mortality from predation depends more on length than on age. Fishing mortality is in effect a special case of predation, and obviously selectivity due to mesh size is dependent on fish size.

Several studies on reaction norms of maturation have highlighted that maturation is likely to be size as well as age dependent (Heino *et al.* 2002a,b,c; Grift *et al.* 2003). For example, in North Sea plaice, the length at which the probability of maturation is 50% decreases with age; conversely, maturity-at-age depends on length-at-age (Grift *et al.* 2003). Therefore, given a particular distribution of maturation reaction norms, any change in mean growth rate (e.g. related to temperature or food availability or stock density) leads to a change in mean maturity-at-age.

The ICES Study Group on Growth, Maturity and Condition in Stock Projections (SGGROMAT, ICES C.M. 2003/D:01) is concerned with incorporating knowledge on biological processes into methods of stock projections. This study group noted that the incorporation of biological processes often requires length-structured population models because the biological processes eventually resulting in numbers of recruits (e.g. fecundity, egg quality) are size dependent.

Resultant effects on the biological and fishery processes noted above are likely to be better accounted for by age-length structured models than by age-structured methods.

Recently implemented recovery plans for a number of depleted stocks have included a wide range of technical measures including changes in mesh sizes, coupled with spatial and temporal closures. Evaluation of the implications of changes in mesh sizes is also better served by the application of age-length- rather than age-structured models. Recent work on Northeast Arctic cod evaluated the effect of changes in gear selectivity on the stock size and stock composition (Kvamme and Frøysa, submitted).

### 2.1.2 Problems with ageing

One of the most important reasons why scientists may require length-structured or age-length-structured models is uncertainty in age determination. The ICES Working Group on Methods of Fish Stock Assessment (WGMG, ICES C. M. 2003/D:03) questioned whether age-structured methods were always the most natural choice, particularly in cases where ageing is difficult, e.g. in *Nephrops*. Age-reading problems have severe implications for the quality of the assessment in different parts of the world. For example, discrepancies in age reading of the cod in the Baltic between

the readers from different countries results in significant uncertainties in the stock assessment and management recommendations (ICES C. M. 2001/ACFM:18; Reeves, 2001; Radke, 2001). Based on these reasons the ICES Working Group on Fish Stock Assessment in the Baltic (WGBFAS) recommended investigation of the applicability of the alternative methods for eastern Baltic cod assessment.

The same problems have been recognized in CECAF (Northeast Central Atlantic) for pelagic fish species – sardine, horse mackerel, and sardinellas (FAO, 2002). The age reading comparisons between different readers showed such high discrepancies that it became necessary to reject age-structured models and use dynamic production models, which gave only a very rough description of the dynamics of these stocks. Even if the problem with age determination could be solved it will be necessary to wait many years before the database of age-structured data permits use of age-structured models again.

For the resources assessed by the Antarctic Commission (CCAMLR) the problem of age determination is very important (CCAMLR, 2002). Little direct age determination is carried out for most important fish species and krill. Usual practice includes age determination on the basis of length data using mixture distribution (de la Mare, 1994). This procedure is applied for estimation of the recruitment and age-structured indices of abundance for toothfish, icefish and krill.

A similar procedure is widely used for age determination from length composition for some Atlantic tuna stocks (Fournier *et al.*, 1990).

Assessment of *Nephrops* is hampered by the fact that there are no reliable and routine ageing techniques so *Nephrops* are assessed using a standard age-structured framework after applying a length-slicing procedure to transform catch-at-length to catch-at-age data (ICES C.M. 2003/ACFM:18). *Nephrops* and *Pandalus* are the only crustaceans regularly and formally assessed under ICES auspices, but the constraints on using age-structured methods apply to other important crustacean stocks in the ICES area and elsewhere.

### **2.1.3 The choice of model: trading off complexity of model and data availability**

Age-length-structured models are likely to be more realistic than models structured only by age or by length. Models of such kind have advantages because they can better reflect biological and fishery-related processes (as discussed above). However, age-length-structured models tend to be not only more realistic, but also more complicated, demand more data and require estimation of more parameters (Section 3.1). For these reasons results of assessment using these models may have more uncertainty in comparison with age-structured or length-structured models and therefore their advantages may be lost. Furthermore, multispecies models are more complicated than single-species ones.

Selection of structure of model (length-, age- or age-length-) should correspond to available data and should be a compromise between what is desirable and what is possible.

The ability of length-structured models to adequately capture information on year class strength depends on the clarity of modes in the catch-at-length distribution data which may not be apparent in species which are either slow growing or have high variability in growth rate. Such problems may be overcome by the incorporation of auxiliary information on recruitment, for example survey data. In these situations, it is also important to have good estimates of growth. Length-based methods are often used because animals are difficult to age and these are precisely the cases where estimates of growth parameters are few and may be (out-)dated. These problems remain a significant disadvantage for the application of length-structured methods.

The ICES Working Group on Methods of Fish Stock Assessment (WGMG, ICES C.M. 2003/D:03) suggested that the choice of the most appropriate assessment model structure for a given stock: “should be governed by both theoretical and practical considerations. The different models should be examined from a mathematical point of view, to see which assumptions are made and how the assumptions influence the resulting model. Particular effort should be directed at clarifying the implicit assumptions and how they influence the results. It should also be made clear what assumptions are made concerning the data structure. The theoretical studies should be combined with practical studies on simulated and real data sets. The artificial data sets used in these studies should represent the characteristics of the stock and the real-world data, and provide a known outcome against which the model estimates can be evaluated”. The use of artificial data sets has the advantage that the different perceptions on a stock by the various assessment models can be directly compared with ‘the true state’ of the artificial population (whereas ‘the true state’ of real stocks remains hidden from us). An example is shown in Section 3.3. Another advantage of the use of artificial data sets is that it allows identification of artefacts resulting from particular choices of assumptions in the model (Section 3.5).

## 2.2 ICES stocks for which length- or age-length structured models are applied in the assessment

The Study Group collated information about the use of length- or age-length structured models in stock assessment and projection performed by ICES Working and Study Groups. Such models are presently used for (at least) the following stocks:

- *Sebastes marinus* in Subareas V, VI and XIV (BORMICON, age-length structured) (Björnsson and Sigurdsson, 2003; ICES C.M. 2003/ACFM:24)
- Anglerfish on the Northern Shelf (Combined IIIa, IV and VI) (length structured) (Dobby 2000, 2001, 2002, Section 4.2; ICES C.M. 2003/ACFM:04)
- Northeast Arctic cod (Fleksibest, age-length structured) (Frøysa *et al.*, 2002; ICES C.M. 2003/ACFM:22)
- Barents Sea capelin (age-length structured without dynamic length structure\*) (Gjøsæter *et al.*, 2002; ICES, C.M. 2003/ACFM:23)
- Capelin in the Iceland-East Greenland-Jan Mayen area (age-length structured without dynamic length structure\*) (Gudmundsdottir and Vilhjálmsson, 2002; ICES C.M. 2003/ACFM:23)
- *Crangon* (age-length structured) (ICES C.M. 2003/xx, in prep.)

The size transition matrix approach has been applied to anglerfish (Section 4.2) and adapted for spiny dogfish (*Squalus acanthias*) in subareas IV, VI and VII (ICES C.M. 2002/G:08) and *Nephrops* in the Firth of Forth (Dobby, 2003). The ICES WG on the Assessment of *Nephrops* stocks (WGNEPH) (ICES C.M. 2003/ACFM:18) commented that the development of dynamic size-based methods, that avoid the problems of deterministic ‘slicing’ of length compositions into ‘age’ compositions, is difficult but highly desirable. WGNEPH found the results shown by the size transition matrix to be very promising, and recommended that this approach continue to be pursued with a view to WG application in the future.

The *Crangon* model is a female-only stochastic per-recruit model projecting daily cohorts forward with a daily time step (Lüthke, in prep.) building on a model developed by Temming and Damm (2001). Egg and larval development and growth at all stages are temperature dependent and growth is modelled in length. Moults and spawning frequency are modelled in terms of age in moults. Although still under development the model was used to explore the potential effects of some management options at the ICES *Crangon* WG (ICES in prep.) and the approach is being investigated further in Germany and the UK.

## 2.3 Examples of other stocks for which length-structured models are applied in the assessment

In New Zealand there are some invertebrate stocks that have been assessed for several years using length-structured models. They have all been developed using ADMModel Builder© libraries (Otter Research Ltd.):

Rock lobster (*Jasus edwardsii*) (Breen *et al.* 2002, Starr *et al.* in press)

Paua (an abalone) (*Haliotis iris*) (Breen *et al.* 2001, Breen *et al.* in press, Breen and Kim in press)

Cockle (a bivalve) (*Chione stutchburyi*)

Scallop (a bivalve) (*Pecten novaezelandiae*)

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\* The two capelin models are only used for stock projections, as the assessment of current stock size of those stocks is based only on acoustic surveys. At present, the stock projections (at least for Barents Sea capelin) are made for half a year ahead, and length growth does not occur in such projections. We thus describe these models as ‘age-length structured models without dynamic length structure’. The length structure is used e.g. in the modelling of maturation, which is assumed to be length-dependent. Work on making medium-term projections for Barents Sea capelin is in progress. Such projections will include a dynamic length structure.

### **3 PROCESS MODEL FORMULATIONS, GOODNESS OF FIT AND MODEL SENSITIVITY IN AGE-LENGTH BASED MODELS**

#### **3.1 Appropriate Complexity in Fisheries Modelling**

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##### **3.1.1 Abstract**

The ideal in any modelling exercise is to select the simplest model that adequately represents the important features of the studied system. The words 'adequately' and 'important' are subjective and will depend heavily on the system being studied and the goal of the modelling exercise. Furthermore 'adequately' will also be constrained by data availability. The correct choice of model structure and complexity is vital for successful modelling studies. However it is not always trivial to identify which factors influence the appropriate choice of model structure in any given situation. The extra complexity inherent in age-length models makes the correct choice of model structure and complexity of particular importance in these cases.

Complexity in a model can relate to a number of different factors. An increase in 'complexity' implies an increase in the flexibility and/or realism of the model. This may arise from a more sophisticated model structure or process sub-models, or from the parameterisation of the model. A more complex model has the potential, if correctly specified, to better simulate the processes in a given system. However more complex models also tend to demand more data in order to constrain their results. There is thus an optimum level of complexity for any given situation, dependant on the modelling goal, the system modelled and the data available.

##### **3.1.2 Sources of complexity**

Model complexity can arise from several different sources. The most obvious is the number of parameters to be estimated in the model, with a higher number of parameters producing more flexibility in the model. However, it may be possible to reduce the number of parameters without reducing the flexibility of the model. Modelling time-dependant processes with a time-dependant function can produce a considerable amount of flexibility in the model, without introducing many parameters to be estimated. The choice of parameters can thus be as important as the overall total. The choice of model structure will also have a direct impact on the level of complexity. For instance, an age&length-structured model contains inherently more complexity than an age-structured model. Selecting multispecies or multi-area models will also increase complexity. Within a given overall model structure the choice of processes to model, and the sophistication of each process sub-model, can also be varied. It is possible that a model with a relatively simple overall structure may include detailed or highly parameterised process sub-models. For instance an age-structured model may use a large number of parameters to estimate fishing selectivity, while an age-length structured model may be able to reduce this to a smaller parameter set. The overall complexity of the model is thus a result of the selection of the model structure, the process sub-models within that overall model, and the parameterisation of the model.

Studies have tended to indicate that there is a humped form to the relationship between model complexity and performance (Costanza and Sklar 1985, Håkanson 1995). Too much complexity leads to too much uncertainty and problems with interpretation of the model's dynamics and predictions, while too little detail results in models that cannot produce realistic behaviours. Thus, there may be an 'optimum' level of model complexity and this may be substantially below the maximum possible. Indeed, complexity introduced for the sake of completeness may be counterproductive if the resulting model is actually of poor quality. The key challenge facing modellers is therefore in striking a balance between complexity and uncertainty.

Because there is an 'optimum' in any given situation, it is often not possible to add all the complexity to the model that may be desired. In general certain processes will be more important to the biology or modelling goal than others. Some processes can therefore be fixed externally or highly simplified, while others can be fully simulated. In this way overall model complexity can be limited, with the focus of the modelling effort directed to specific processes within the system.

##### **3.1.3 Model Selection**

*Goal*

The critical factor in selecting model structure will be which question(s) the model is designed to answer. This may be highly specific and directed (e.g. investigating the likely effects of closed areas or gear selectivity on stock size) or more general (e.g. a desire to have a new model which can be compared against existing models). In either case the question

to be answered will have a large influence on the structure of the required model. It is also important to bear the overall goals in mind during the development of sub-models within the overall structure.

### *Processes*

The processes operating in the system will have an influence on the model structure (e.g. differing growth before and after maturation would indicate a need for mature and immature individuals to be modelled separately). Processes known or suspected to be operating in the real world may violate the assumptions of simple models (e.g. that age is a good proxy for length, that fishing of one species has no impact on other species). In these cases extra complexity may be demanded in the model to handle these processes.

### *Data*

Data availability will constrain the degree of model complexity possible (Schnute, 1987). Specific problems with the data can preclude or limit certain types of models. For example, poor age data will often preclude the use of an age-based model. More generally poor, sparse, or unreliable data will limit the total complexity possible in the model. Conversely abundant, rich, data sets, or diverse types of data, can indicate the sort of dynamics which require a more complex model.

The types of data required by complex models include some or all of: abundance data, length-, age- and age-and-length-distributions, level of fishing, selectivity of fishing, stomach contents data, migration data and mark-recapture data. Availability and quality of these data sets will have an influence on model selection.

### *Other information*

In the absence of suitable data for use as input into a model, it may still be possible to make use of a variety of different information sources. Such information can either be used in a Bayesian approach or to externally determine parameters. Data from other years or similar areas can be used in this manner to partially compensate for lack of data. Laboratory or field experiments can, for instance, provide parameters for growth or selectivity functions. Care must be taken when using this approach however, and wherever possible all data should be integrated into the model data sets.

## **3.1.4 Parameterisation**

The number of parameters estimated in a model will impact on the fit between model and data. Increasing the number of parameters increases the model flexibility, and therefore can fit the model more closely to the data. However this produces a danger of over-parameterisation. Model building should be considered an exercise in parsimony and conducted by starting with a simple model and investigating the effect of adding different parameters. In this case a benefit of the method of maximum likelihood is that the overall likelihood score can indicate in numerical terms the benefits to be gained in terms of overall fit to the data from adding extra parameters. Statistical tests exist which can evaluate the significance of adding additional parameters (McCullagh and Nelder, 1989) or structural changes (Akaike, 1974) to the model.

It is important to consider the individual likelihood components and the response of the modelled population as well as the total likelihood score. Different sets of parameters can produce similar improvements in the total likelihood by affecting different processes in the model. In this case the user must select between them based on factors other than the total likelihood score. This will require human discretion and cannot be fully automated. An example is given in Table 3.1.1 where increasing flexibility in growth rates, recruitment length or recruitment weight all give similar improvements to the likelihood score. In each case the parameter chosen was allowed to take a different value for each year, rather than using a single value for all years (as in the standard haddock model presented in Section 4.3).

The choice of which parameters to choose must thus be made by the modeller based on knowledge about the modelled system and the aims of the study, rather than simply on the total likelihood score. An examination of the responses of the different likelihood components indicates which processes in the model benefit from each increase in flexibility, and which do not. For example increasing flexibility in either starting length or starting weight of the haddock produces a better fit for adult fish, but a worse fit for newly recruited fish (as seen by the increase in likelihood component *si10*, the survey index for 7.5-12.5cm fish). The overall improvement in the fit of large fish has outweighed the errors introduced into the smaller fish. In contrast increasing the flexibility in starting length produces a greater improvement in the fit for small fish than for large ones. Which improvement is more important is a subjective decision, and will depend on the goals of the modelling study. It can also be seen in the table that adding several different parameter sets at once

produces a relatively small further increase in model fit. The modeller must therefore also choose the appropriate trade off between parsimony in the model parameters and goodness of fit to the data.

	ORIG	Recruit S.D.	Recruit Length	Recruit Weight	Yearly Growth	LEN & WT	LEN & Growth	Growth & WT	All
Extra parameters		22	21	21	21	42	42	42	85
<b>Likelihood</b>	<b>100</b>	<b>95.4</b>	<b>88.0</b>	<b>87.1</b>	<b>88.5</b>	<b>78.9</b>	<b>83.1</b>	<b>84.5</b>	<b>77.5</b>
<b>meanl.sur</b>	<b>100</b>	<b>99.5</b>	<b>76.2</b>	<b>60.6</b>	<b>63.8</b>	<b>53.6</b>	<b>62.3</b>	<b>53.7</b>	<b>50.4</b>
<b>meanl.catch</b>	<b>100</b>	<b>98.9</b>	<b>78.7</b>	<b>67.7</b>	<b>74.5</b>	<b>66.0</b>	<b>76.5</b>	<b>66.4</b>	<b>68.7</b>
<b>ldist.sur</b>	<b>100</b>	<b>87.1</b>	<b>78.1</b>	<b>89.7</b>	<b>98.4</b>	<b>62.9</b>	<b>77.7</b>	<b>82.0</b>	<b>53.1</b>
<b>ldist.catch</b>	<b>100</b>	<b>100.4</b>	<b>101.8</b>	<b>100.7</b>	<b>100.6</b>	<b>100.3</b>	<b>100.8</b>	<b>99.4</b>	<b>100.3</b>
<b>alkeys.sur</b>	<b>100</b>	<b>96.5</b>	<b>76.7</b>	<b>72.5</b>	<b>77.2</b>	<b>71.7</b>	<b>74.1</b>	<b>73.0</b>	<b>71.1</b>
<b>alkeys.catch</b>	<b>100</b>	<b>99.1</b>	<b>93.3</b>	<b>91.3</b>	<b>93.0</b>	<b>92.0</b>	<b>92.7</b>	<b>90.8</b>	<b>91.7</b>
<b>survey Index</b>	<b>100</b>	<b>82.2</b>	<b>76.1</b>	<b>81.4</b>	<b>82.2</b>	<b>52.2</b>	<b>60.3</b>	<b>76.0</b>	<b>47.2</b>
Si10	100	2.6	41.2	120.8	120.5	21.2	16.2	125.0	0.9
Si15	100	95.7	80.8	65.2	71.1	54.6	64.5	54.8	76.0
Si20	100	101.0	80.4	83.0	87.7	16.4	66.1	79.1	4.4
Si25_45	100	94.2	74.8	64.7	58.2	62.1	55.3	52.3	56.6
Si50_60	100	99.2	105.7	80.9	84.0	82.4	86.3	73.0	81.8
Si65_75	100	101.3	98.1	95.7	114.0	100.5	114.4	107.6	111.1

**Table 3.1.1** Improvement in likelihood score in the haddock model obtained by allowing various parameters to vary on a yearly basis.

ORIG is the standard 37-parameter model described in section 4.3, likelihood scores are normalized to 100. Recruit S.D. is standard deviation of length at recruitment. Recruit Length (LEN) is length at recruitment. Recruit Weight (WT) is weight at recruitment and Yearly Growth (Growth) is annual growth rate.

For each column the indicated parameters were allowed to vary on an annual basis, rather than have the same value for all years. The number of parameters added is indicated in each case. The resulting normalized likelihood is shown, as well as the individual components. Components:

meanl.sur, meanl.catch: mean length in the survey and catch;

ldist.sur, ldist.catch: length distribution in the survey and catch;

alkeys.sur, alkeys.catch: age-length keys in the survey and catch;

Survey index: survey index, aggregated by length.

si10, si15, si20, si25,45, si50\_60, si65\_75: Survey index split into 5cm length classes, mid points of the class given in the names.

### 3.2 Relating model variables to observations in age-length structured models (last part of WD2)

*Bjarte Bogstad, Institute of Marine Research, Bergen, Norway*

The last part of WD2 describes which observations and model variables could be compared. This is given for various classes of observations: Survey data, commercial catch data, stomach content data and mark-recapture data. The observations and corresponding model variables, which can be related using observation models, are spelled out in detail. WD2 presents observation models (e.g. a linear relationship between survey index and population abundance) for all these classes of observations. Many parameters in the observation models are assumed to be constant in time. For fisheries and survey-related parameters such as survey catchability and fleet selectivity one may want to allow for a time trend or to divide the observation data set into several periods and allow these parameters to vary between periods.

Other important issues to consider when relating model variables to observations include:

- At which aggregation level (space, time, age-length cells etc.) is it appropriate to compare model variables and observations?
- Choice of likelihood functions
- Choice of weighting factors

WD2 does not address these issues.

Below, the data types available for each main class of observations are listed:

#### *Survey data*

Trawl survey indices (numbers at length, age distributions for each given length group)

Acoustic abundance indices (total acoustic back-scattering area, length distribution, age distributions for each given length group)

Estimates from sightings surveys

#### *Commercial catch data*

Total catch in tonnes

Length distribution of catches

Age distribution for each given length group

Catch per unit effort

#### *Stomach content data*

The Gadget model calculates consumption, while the observations reflect stomach content at a particular point in time. In order to make a comparison, it is necessary to convert between these two entities. Converting from stomach content to consumption requires an evacuation rate model (e.g. Jones, 1974; dos Santos and Jobling, 1995), while converting from consumption to stomach content requires a feeding model in order to transform consumption rate to a distribution of stomach content. Since these transformations generally will be non-linear, it is important to have data from individual stomachs available. The conversion from stomach content to consumption is at present implemented in Gadget. This implies that model results are compared to transformed data. The theory for transformation of consumption rate to a distribution of stomach content is under development (Magnússon and Aspelund, 1997). This will allow model results to be compared directly to actual untransformed observations.

Three ways of comparing stomach content observations and models are currently implemented in Gadget:

Comparing absolute biomass consumed

Comparing ratio of biomass consumed

Comparing ratio of numbers consumed

#### *Mark-recapture data (under development)*

**3.3 CALEN – an age-length structured population model***D.J. Gilbert, N.M. Davies & J.R. McKenzie  
National Institute of Water and Atmospheric Research Ltd  
Wellington, New Zealand*

##### **3.3.1 Introduction**

We present a selective account of some aspects of our age-length structured model CALEN that we think may be of interest to those who already have an understanding of the concept of age-length structured modelling. The essential feature of such modelling is that the population state is described by a matrix of numbers of fish at age and length. Our development of CALEN used an extensive age, size and abundance dataset from the New Zealand Hauraki Gulf/Bay of Plenty snapper (*Pagrus auratus*; Sparidae) stock. CALEN is based on annual time steps and 1 cm length-classes. We briefly describe model processes with particular reference to the growth functions used. We discuss useful parameterisations and diagnostics. This account is based on a report provided under contract to the Ministry of Fisheries, New Zealand (Davies *et al.* 2002).

##### **3.3.2 Model structure and specifications**

#### *Recruitment*

Fish enter the age-length matrix at age 0 y. The entry length-class is an estimated parameter. The year class strength parameters are multipliers of a mean recruitment parameter. We estimate 17 year class strength (YCS) parameters (1980-1996) but for other years we predict YCS from summer sea surface temperature (SST). The YCS parameters were constrained to have a mean of one. There is no stock-recruitment relationship.

### *Mortality*

Natural and fishing mortality are modelled as deterministic processes with constant natural mortality and known annual landings. We use a catch equation where catch is removed instantaneously after a specified period of the year, and this can be solved explicitly for the exploitation rate. Our selectivity curves are length-based and we have one for each of six gear types (including research and recreational). They are made up of the left- and right-hand limbs of different normal density functions. There are three parameters: the join length, where the maximum selectivity is one, and the left and right lengths at which selectivity falls to 0.5. This parameterisation reduces correlation between the parameters.

### *Initialisation*

The model was run for 1970 – 2001, but starts from an estimated non-virgin state. This initial state was generated using two total annual fishing mortality parameters,  $F_1$  and  $F_2$ .  $F_2$  applies to an early period and  $F_1$  to the 20 years before 1970. We also determined YCS's and growth in the initialisation state from the SST relationships.

### *Growth*

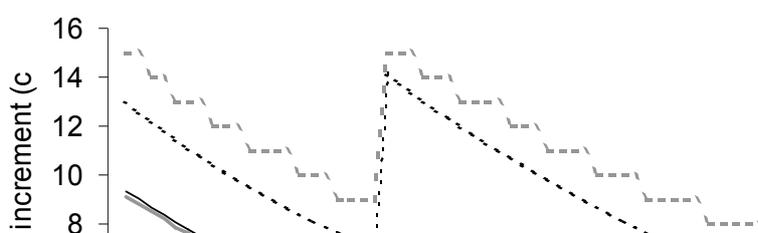
An age-length structured model requires a growth increment function that moves fish through the age-length state matrix. This must describe the mean increment for each age-length cell in the state matrix. It must also describe the variation around the mean. In CALEN the main determinant of growth increment is length, but a small age-length effect was also found to improve the fit to the snapper data. We modified our mean increments with annual growth factors that scaled the whole mean increment versus length curve. We also used SST predictors for YCS and the growth factors.

The exponential mean increment function fitted better than the (linear) von Bertalanffy function and better than several others we tried (Figure 3.3.1). We parameterised the functions with  $\mu_{10}$  and  $\mu_{30}$ , the increments at lengths 10 and 30 cm. These parameters are usually almost uncorrelated, unlike the conventional von Bertalanffy parameters  $k$  and  $L_\infty$ . This can considerably improve the reliability and speed of negative log-likelihood minimisation. The parameters  $\mu_{10}$  and  $\mu_{30}$  can be used under different functional forms of growth while still retaining the same meaning.

Millar *et al.* (1999) found that mean SST was significantly related to mean snapper growth. We found significant differences between the SST-based growth factors and those estimated as free parameters in some years.

The model failed to satisfactorily fit the growth of a few “stunted” or “giant” fish. We added a factor that depended on how much a fish's length differed from the mean length at its age i.e., an age-length dependent function. This factor made fish that had got ahead of their cohort tend to continue to grow faster than their equal-sized, older peers, and those that had fallen behind, to tend to continue to grow slower. It made a modest improvement to the fit, but adds substantially to computational requirements, because a different transition vector for every cell of the age-length matrix must be calculated.

The growth increment variation was modelled using the lognormal distribution. This fitted better than the normal distribution. The age-length samples showed that there is a marked increase in the spread of length-at-age between lengths 20 to 25 cm. We found that a stepwise increase in individual growth variability at 22 cm significantly improved the fit. This corresponds to the age of 50% maturity (Crossland 1977). We truncated the tails of the lognormal distribution to avoid unfeasibly large growth by a few individuals. This had the unfortunate effect of causing a downward step in the mean growth increment at length 22 cm (Figure 3.3.1).



**Figure 3.3.1** Mean annual growth increment at length calculated from an exponential function (solid) showing 5 and 95 percentile bounds for lognormal individual growth variability (dashed), and mean annual growth increment after discretisation and truncation (solid grey) with the minimum and maximum growth (dashed grey).

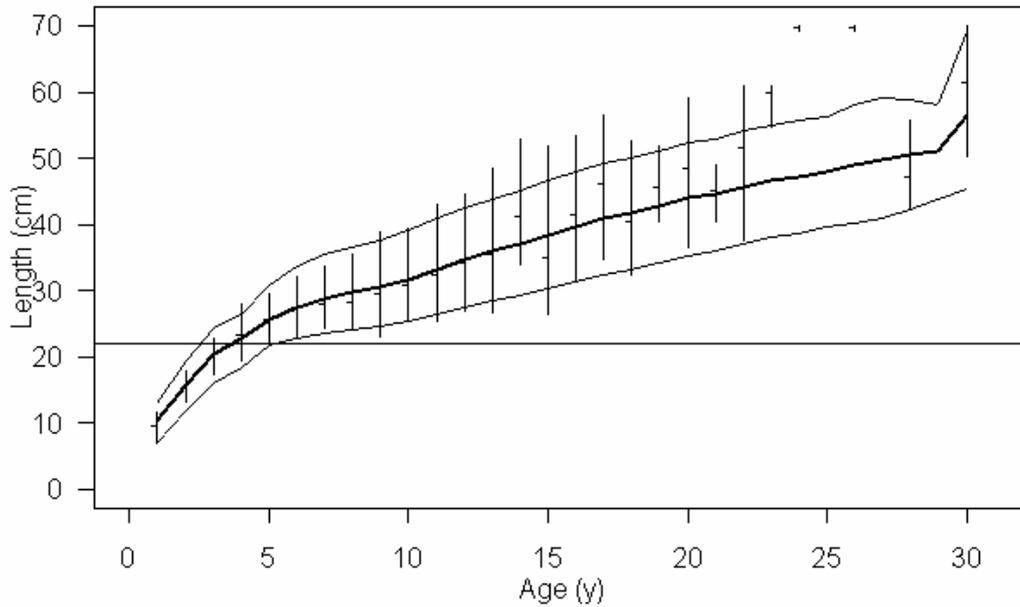
### 3.3.3 Parameter estimation

We estimated 50 free parameters, the maximum allowed by our minimiser. Multinomial, lognormal, and normal likelihood functions were employed for different data types. We fitted the model to estimated proportions of fish caught at age and length by 4 gear types as well as proportions caught-at-age by Danish seine, a longline catch per unit effort (CPUE) index of abundance, and population numbers at length estimated from tag-recapture experiments in 1985 and 1994.

The variability in distributions of age and length samples is greater than would be predicted by simple random sampling. We treated these estimates as though they came from simple random samples, but with smaller effective sample sizes. Effective sample size was obtained from an arbitrary function of the contributing number of landings, number of research trawl hauls, number of otoliths aged for the age-length key. Because the same age-length key is used, the data from different gear types is not independent and hence the effective sample size was made to be an inverse function of the number of gear types.

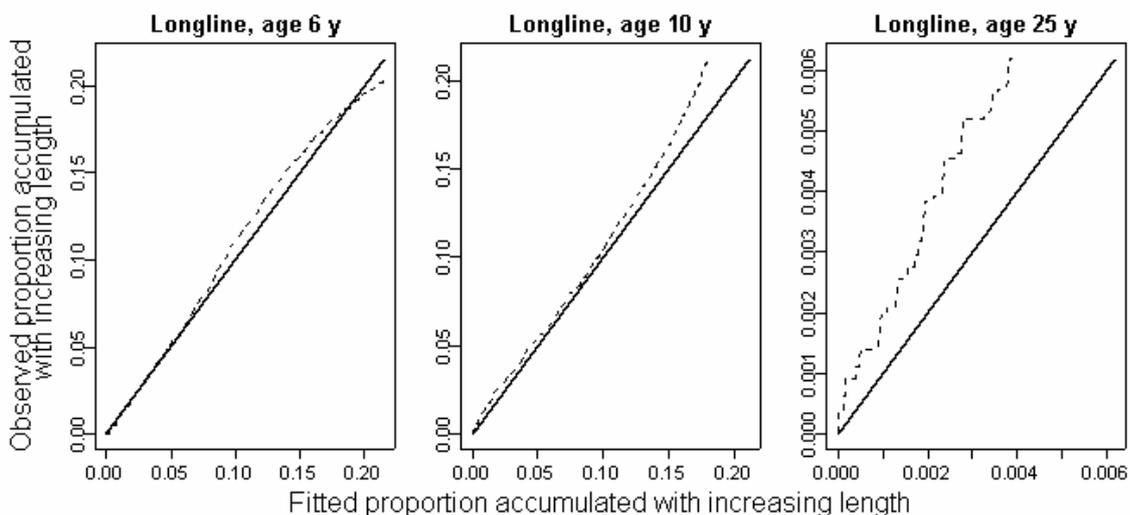
### 3.3.4 Diagnostics

The observed age-length matrix can be displayed as mean length and 90 percentile bars of length-at-age (Figure 3.3.2). The fitted means and 90 percentile lines can be displayed on the same plot. The fit to the age-length observations can be shown via observed and fitted marginal distributions, i.e., the age-length matrices can be summed over length or over age.

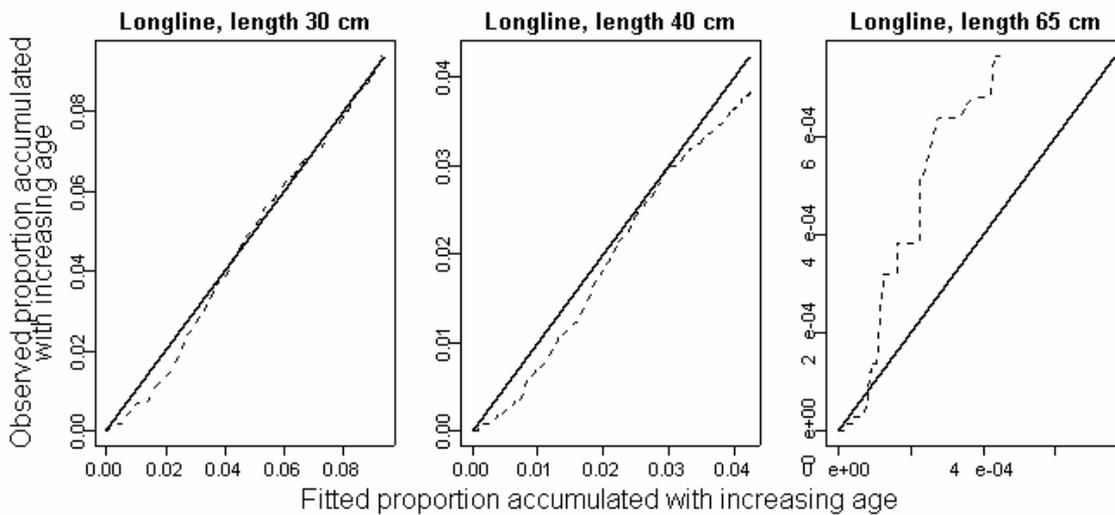


**Figure 3.3.2** Observed and fitted proportions at age and length for research trawl for 2001. For each age-class the horizontal bar shows the observed mean length and the vertical bar the 5 and 95 percentiles. The fitted lengths are shown by the mean (heavy line) and the 5 and 95 percentiles (light lines). A horizontal line at 22 cm shows the length at which a stepwise increase in variability occurs. Growth continues in the 30+ age-class, causing a stepwise increase in mean length.

P-P plots provide another overview of the quality of age-length fits. P-P plots are similar to Q-Q plots except that the axes correspond to accumulated probabilities rather than quantiles. For a given age, we plot the observed proportion against the fitted proportion. This is done by accumulating proportions from lowest to highest length class, in each age-class. This can be presented for each year's sample or for data aggregated over all samples (Figure 3.3.3). Straight lines along the 45° diagonal indicate good fits. If the last point lies on the diagonal, the fitted total proportion for that age equals that observed. Curved lines indicate that the shape of the fitted distribution differs from the observed distribution. The same can be done reversing the roles of length and age. Alternatively P-P plots can be used to check how well the model fits the age-length keys (Figure 3.3.4). For each length we aggregate all samples and scale both observed and fitted proportions to sum to one. In an age-length key the proportions in each length-class are scaled to sum to one, so that this is the proper comparison to make. In this case we are checking only whether the distribution of age-at-length matches that observed.



**Figure 3.3.3** P-P plots of accumulated observed and fitted proportions from lowest to highest length for selected ages for longline landings. All samples are aggregated.



**Figure 3.3.4** P-P plots of accumulated observed and fitted proportions from lowest to highest age for selected lengths for longline samples. All samples are aggregated. Observed and fitted proportions are each scaled to sum to one.

Another diagnostic is to plot the ratio of observed to fitted proportions, aggregated over either age or length. Values of one indicate a good model fit. Systematic deviations from a ratio of one indicate failure of the model structure. Failure in parts of the data where numbers are very small may occur because these data carry little weight in the total likelihood.

### 3.3.5 Model development

We added successively more parameters and more complex features, provided they reduced the negative log-likelihood significantly. For example, by adding the stepwise increase in growth variability we got a reduction of 243 in the negative log-likelihood for the addition of 3 parameters. This is extremely significant under the chi-squared test. By adding 17 YCS parameters we got a reduction of 107 in the negative log-likelihood.

### 3.3.6 Use of CALEN

The New Zealand Ministry of Fisheries decided not to use this model for stock assessment this year after opposition from the fishing industry. The industry scientists felt that the model required more development. There was a lack of confidence in what was an unfamiliar modelling approach. Concern was expressed at the differences between the growth factors predicted from SST and those estimated as free parameters. We consider that it is not surprising that SST cannot predict growth perfectly. The fact that the best possible minimiser was not used was another reason for concern. Bayesian posteriors have become the norm in New Zealand stock assessments and lack of them here was a further reason for criticism. A possible reason for the poor reception of the model was that the preliminary results were more pessimistic than those of previous assessments. The model was running at about 1.5 seconds per simulation, which is a bit slow to allow an adequate Monte Carlo Markov chain (MCMC) to obtain a Bayesian posterior distribution. We haven't developed code to generate a MCMC but we think it may be possible to do so.

### 3.3.7 Future developments

The model would benefit from a minimiser that is both faster and can estimate more than 50 parameters. Our age-length distributions were based mostly on annual age-length keys with length frequency samples for each gear type. It has been pointed out that it would be more statistically correct to fit directly to each age-length key and to the length frequencies (A. Punt pers. comm.). The growth variability distribution functions that we have used are slightly unsatisfactory because of the downward step in the mean caused by the necessary truncation of the distribution tails. Others have used the beta-binomial distribution (Björnsson and Sigurdsson 2003), which performs satisfactorily. A more complex selectivity curve (more than 3 parameters per gear type) might improve the fit for the oldest and largest fish. The possibility of age- and/or length-dependent natural mortality is another development that could be added to the model. We have obtained some funding for the development of the model as a simulator, to determine whether an age-structured model can approximate the age-length processes sufficiently well to be satisfactory for stock assessment. Further funding for CALEN itself has not been offered.

### **3.4 Modelling survival and growth in age- and length-structured populations dynamics models (first part of WD2)**

*Bjarte Bogstad, Institute of Marine Research, Bergen, Norway*

The first part of WD2 consists of a detailed description of the mathematical formulation of survival (mortality) and growth in age-length structured models within the multispecies, multi-area, multi-fleet framework Gadget. It is assumed that all processes depend only on the length and weight of the fish, and not on the age. This simplifies the description considerably. It is planned to extend this with a description of the other population dynamics processes included in Gadget: migration, recruitment and maturation. The extended document will be made available as part of the Gadget documentation.

#### **3.4.1 Survival (mortality)**

In Gadget, fishing and predation can be modelled as mortalities or as numbers to be subtracted, and both approaches are described here. The mortality formulation corresponds to the approach used in Fleksibest (Frøysa *et al.*, 2002), while the subtraction formulation is used for fishing and predation in BORMICON (Stefánsson and Pálsson, 1997). The Fleksibest mortality formulation is similar to the mortality model used in MSVPA, as the natural mortality  $M$  is split into three components: Residual mortality  $M_1$ , predation mortality  $M_2$  and spawning mortality  $M_S$  ( $M=M_1+M_2+M_S$ ). Predation mortality is currently only implemented for cannibalism in a single-species model. The general formulation of predation mortality is currently under development.

#### **3.4.2 Growth**

Modelling growth in length-structured models can be divided into two parts:

- modelling mean growth in length
- implementing mean growth in length by allowing fish to grow 0,1,2,3.. length groups, in such a way that mean growth is correct and the variance is appropriate. This issue is described e.g. in Björnsson and Sigurdsson (2003) and in Section 3.5 and is not discussed in WD2.

Modelling mean growth in length could be done in two ways:

- model the mean growth in length directly
- model the mean growth in weight and derive mean growth in length from the mean growth in weight

### **3.5 Some impacts of the discretisation of the growth process**

*Stéphanie Mahevas, IFREMER, Nantes, France*

#### **3.5.1 Introduction**

As with all models in discrete time which describe continuous dynamics, discretisation can lead to modelling artefacts. These artefacts can impact both the parameter estimation and simulations. In this document, we focus on the impact of the discretisation of both the length range of the population and the discretisation of the growth process in a length-structured approach. The continuous measure of fish size is decomposed into a finite number of length classes and several construction schemes can be considered. In the same way, the continuous process of growth needs to be discretised into growth increments which can be modelled using different distributions. We will describe different approaches for constructing the length classes and the usual models considered for growth increments. The impact of these choices on the growth matrix and the distribution of the population at several time steps will be presented. The purpose of this study is to identify some critical points in the discretisation of a continuous process and to give some elements to start a discussion.

#### **3.5.2 Length class definition**

In contrast to stage-structured or age-structured models, which take advantage of the natural biological divisions of the life cycle, size-structured models require a more artificial construction of a set of size classes. The discretisation of

population length is not trivial; the more length classes employed, the more parameters must be estimated in the model. Therefore the number of classes should be kept to a minimum. On the other hand, fewer classes result in more heterogeneity within each class. Moreover the choice of these categories can produce modelling artefacts and impact the parameter estimation in the model. Several ways of constructing classes can be considered:

- classes of equal width in length
- classes of equal width in staying time
- classes of unequal width defined by the user
- classes associated to biological divisions of the life cycle
- classes resulting from an optimisation of a specific criterion

The first type of length class construction is the most common in the literature (Sullivan *et al.* 1990; De Leo and Gatto 1995; DeLong *et al.* 2001; Smith and Botsford 1998; Smith *et al.* 1998; Frøysa *et al.* 2002). We have not found any application with the second or third types. The fourth method is usually employed in stage-structured models. This requires that knowledge be available about the relationship between life cycle and size in order to use a length-structured approach. Vandermeer (1978) proposed an algorithm based on the minimization of the sum of two errors, called sampling error and distribution error, which has been improved by Moloney (1986). Some details on this algorithm can be found in Mahevas *et al.* (WD1). But this approach has several drawbacks. First it requires data on individual growth (tagged fish, captive studies, good back-calculation of age at length). Classes are constructed taking into account only the departure class and not the possible arrival classes, modelling the probability of staying in the departure class. Moreover, it does not take into account the temporal variability in growth (the discrepancy is minimized to a mean value over the period) and the errors are calculated independently for each class without considering the errors of the previous classes.

### 3.5.3 Growth increments model

Many population models describe the population growth processes using a mean growth: the growth in each length class is supposed to be equal to the growth at the midpoint. Such models could produce large errors in growth rates. It is largely accepted that individual variability in growth needs to be taken into account to improve assessments. Several methods exist to estimate this variability (back-calculation of length-at-age, tagging survey, captive studies). A survey tagging young hake in the bay of Biscay has recently been initiated. Preliminary data appear promising and should give results in several years.

At this time, the lack of data constrains us to make assumptions on the variability in growth. Two approaches are classically considered to model the variability in growth, calculate growth increments for each class and then fill each row of the growth matrix. The most common model is a mean growth by length class given by the growth function and a stochastic distribution for individual variability around the mean (for instance, Sullivan 1990; DeLeo and Gatto 1995; Cruywagen 1997; DeLong *et al.* 2001; Frøysa *et al.* 2002). Another way to describe growth variability is to integrate directly individual variability in the growth function with stochastic parameters (Sainsbury 1980; Smith and Botsford 1998; Smith *et al.* 1998; Pilling *et al.* 2002). The correlation between the two parameters  $L_{\infty}$ ,  $K$  of the Von Bertalanffy function represents a major difficulty for this type of model; and a solution is proposed in this report (Section 3.6). Here, we focus on the first approach and more particularly on the uniform distribution, the beta-binomial and the gamma distribution for the stochastic distribution.

#### *Uniform distribution*

This distribution is the simplest way to describe the growth of fishes from a particular class taking into account their actual length rather than just the length of the midpoint of their class. Fishes in a given length class are supposed to be uniformly distributed within the class and their final length is larger than the final length of fish at the lower bound of the class and lower than the final length of fish at upper bound. We call this interval (i.e. the image of the departure class by the growth function) the image class. Then the accessible classes from this class are the classes between the arrival class of the lower bound and the arrival class of the upper bound. The probability of transition from a given class to an accessible class is calculated by the length of the intersection of the accessible class with the image class, divided by the width of the image class.

#### *Beta-binomial distribution*

The beta-binomial distribution is an extension of the binomial distribution whose parameter is assumed to follow a beta distribution. The traditional binomial distribution with one parameter is useful when there is only one source of

variation in the data. To describe a data set displaying overdispersion the most popular distribution is the beta-binomial (Ennis and Bi, 1998) described by two parameters.

If  $X$  denotes the random variable counting the number of choices,  $x$ , of a particular type from a maximum of  $n$

$$X \sim BB(n, \alpha, \beta)$$

$$P(X=x) \sim \binom{n}{x} \frac{\Gamma(\alpha+x)\Gamma(\beta+n-x)\Gamma(\alpha+\beta)}{\Gamma(\alpha+\beta+n)\Gamma(\beta)\Gamma(\alpha)}$$

where the gamma function is defined by  $\Gamma(x) = \int_0^{\infty} \exp(-u)u^{x-1}du$ .

When  $x$  is an integer,  $\Gamma(x) = (x-1)!$

The mean of a beta-binomial distribution is

$$E[X] \sim n \frac{\alpha}{\alpha+\beta}$$

and the variance is

$$V[X] \sim n \frac{\alpha\beta}{(\alpha+\beta)^2} \left( 1 + \frac{n-1}{1+\alpha+\beta} \right)$$

The beta-binomial distribution can be used to model the growth increments. Then, for each length class, the variable  $X$  counts the number of classes jumped during one time step,  $n$  stands for the number of accessible classes. The mean growth of a fish in this class is supposed to be the growth increment of the midpoint of the class calculated by the growth function. Parameters  $\alpha$  and  $\beta$  modify the shape and the scale of the variability around the mean growth.

Such modelling of growth assumes that the mean growth of a length class is calculated in number of classes. The method used to calculate the mean growth is described by the following algorithm for each class:

1. calculate the growth of the midpoint using the growth function during one time step
2. calculate the associated number of classes jumped by the midpoint
3. calculate the proportion of length against the width of the class reached by the midpoint
4. the mean growth is then equal to the sum of the two previous values (2. + 3.)

An application of this model is proposed in section 4.3.

#### Gamma distribution

The Gamma distribution is a two-parameter distribution, entirely defined by its two first moments. It is largely used in modelling thanks to its flexibility in describing many functional forms. More specifically, it can describe growth for small and large fish. Let  $X$  denote the random variable equal to the growth increment during a time step. If  $X$  has a gamma distribution  $G(\alpha, \beta)$ , its density function is  $f(x) = \frac{1}{\beta^\alpha} x^{\alpha-1} \exp(-x/\beta)$  and its mean and variance are

respectively equal to  $E[X] = \frac{\alpha}{\beta}$  and  $V[X] = \frac{\alpha}{\beta^2}$ .

If fishes are assumed to be at the midpoint of the departure class  $i$ , denoted  $mi$ , then the probability of transition to class  $j$  is given by the following single integral:

$$g_{ij} = \int_{\text{lowerBound } j-mi}^{\text{upperBound } j-mi} f_i(x) dx$$

If fishes are assumed to be uniformly distributed within the departure class  $i$ , then value of the following double integral is the probability of transition from class  $i$  to class  $j$ :

$$g_{ij} = \int_{lowerBound\ i}^{upperBound\ i} \int_{lowerBound\ j-y}^{upperBound\ j-y} f_i(x) dx dy$$

The use of a Gamma model with a single integral is most widely chosen to describe growth variability (Sullivan 1990; DeLong *et al.* 1998).

### 3.5.4 Simulations

The code to run the simulations has been written in C++ using ADModel Builder libraries (Otter Research Ltd., 2000). First we construct the length classes, either with an equal width in time (3 months) or with an equal width in length (5cm or 10cm). Then for each kind of length class, we observed the shape of the growth increment distribution for the uniform distribution, the beta-binomial distribution and the gamma distribution with both the single and double integral. Finally we simulate the growth of the first class of a population growing according to the Von Bertalanffy function described above without any mortality, for each combination of length class construction and growth increment model (Table 3.5.1). The beta parameter of the beta-binomial distribution was set such that the variance of the beta-binomial distribution is equal to the variance of a gamma distribution with a beta parameter equal to 1. The alpha parameter of both distributions is set according to the mean growth.

	Delta t = 3months	Delta l = 5cm	Delta l = 10cm
<b>Uniform</b>	(Figure 3.5.1 up and left)	(Figure 3.5.2 up and left)	(Figure 3.5.3 up and left)
<b>BetaBin</b>	(Figure 3.5.1 up and right)	(Figure 3.5.2 up and right)	(Figure 3.5.3 up and right)
<b>Gamma 1</b>	(Figure 3.5.1 down and left)	(Figure 3.5.2 down and left)	(Figure 3.5.3 down and left)
<b>Gamma 2</b>	(Figure 3.5.1 down and right)	(Figure 3.5.2 down and right)	(Figure 3.5.3 down and right)

**Table 3.5.1:** For each scheme of length class construction (columns) and each growth increment distribution (rows) the list of the figures illustrating the growth matrix and the simulation of the first class of the population is given.

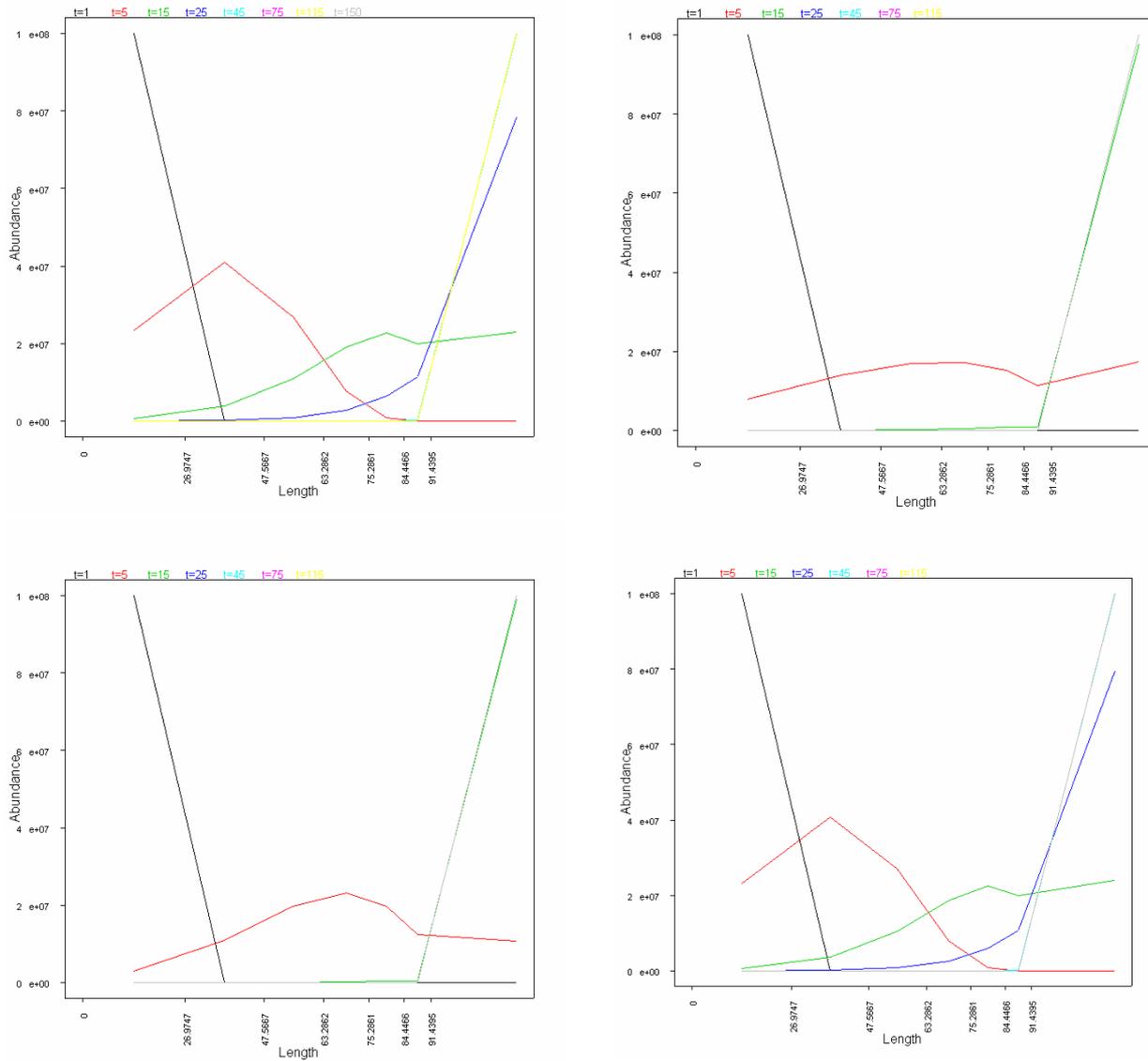
Differences in the length classes can be observed (X axis in Figures 3.5.1, 3.5.2 and 3.5.3). Whatever the growth increment model is, length classes of width equal in time seem to induce a larger number of reachable classes (probability of transition not null) than other length class types spread distribution. Given the quick growth at the beginning of the life, this scheme of length-class construction results in larger first few classes which thus are more heterogeneous in length than the last ones. For instance fishes of initial size between 0cm and ~26cm can grow up to a size of ~84.4cm during one time step (Figure 3.5.2 up and left). At this stage of the analysis, it would be interesting to measure sampling and distribution errors (Vandermeer, 1978) induced by the choice of the scheme of construction to have quantitative criteria of selection among these choices. However such an analysis has not yet been carried out.

Regarding the growth increment distribution, Figures 3.5.1, 3.5.2 and 3.5.3 show differences for each scheme of length-class construction. The uniform distribution and the gamma distribution with the double integral are very similar. These two distributions make the same assumption on the position of fishes in the departure class. The beta-binomial distribution has a more widely spread distribution as expected given its overdispersion characteristic. The choice of a gamma distribution with a single integral results in a slower arrival in the last class.

It would be useful to find a metric to quantify the differences between the different models of growth increment variability. One approach may be to use a Chi<sup>2</sup>.

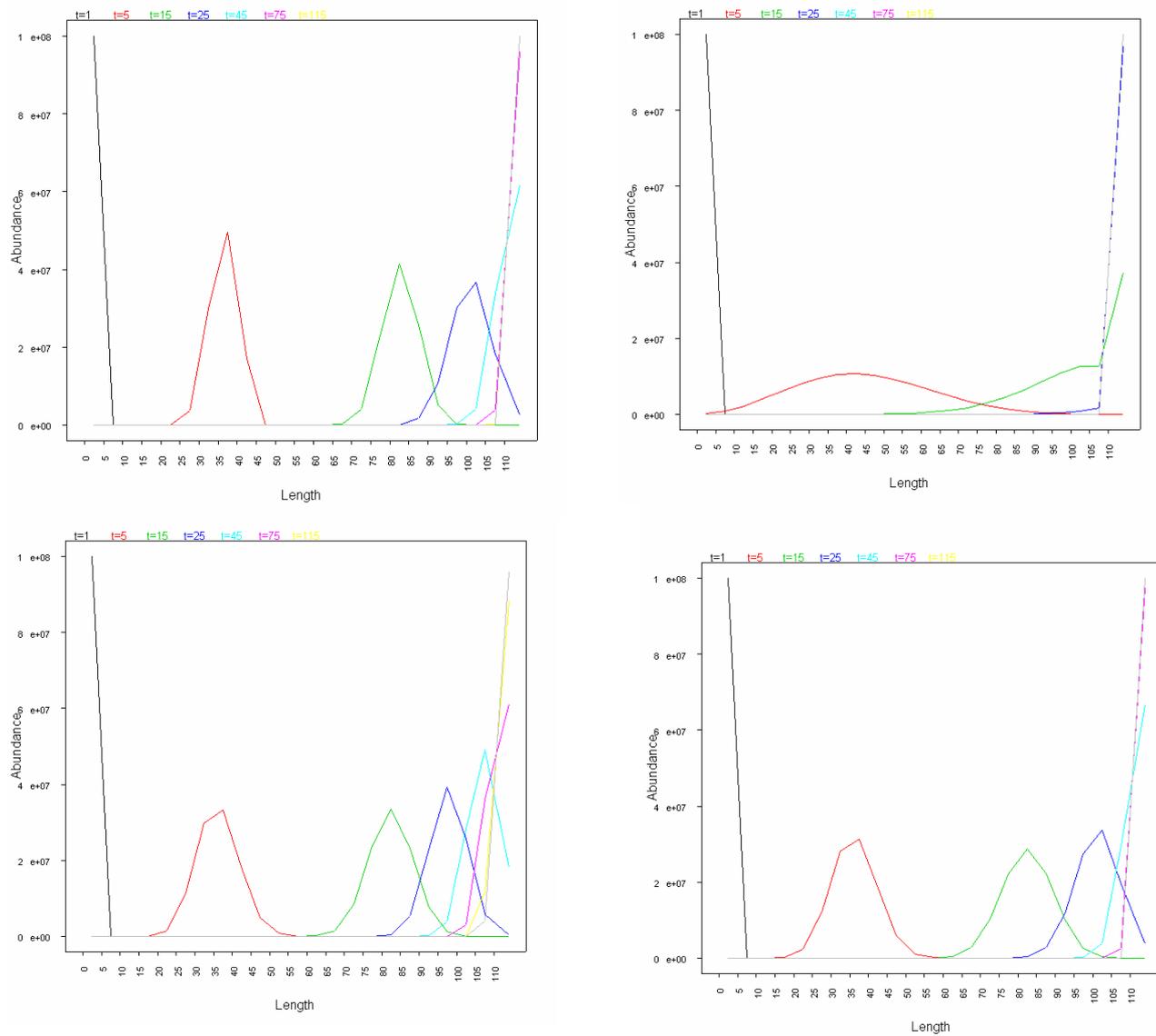
Finally, after these preliminary simulations, it should be noted that great caution needs to be taken not only in the choice of the scheme of length class construction but also in the model of growth increments.

The program is sufficiently generic that different schemes of length-class construction can be simulated. The next step will be the simulation of the construction of length classes using the algorithm of Vandermeer, and also the simulation of a stochastic Von Bertalanffy growth function where the parameter  $L_{\infty}$  has a normal distribution and the parameter  $K$  has a gamma distribution. Finally, we would like to quantify the impact of these choices of discretisation on the parameter estimation using a simulated data set.

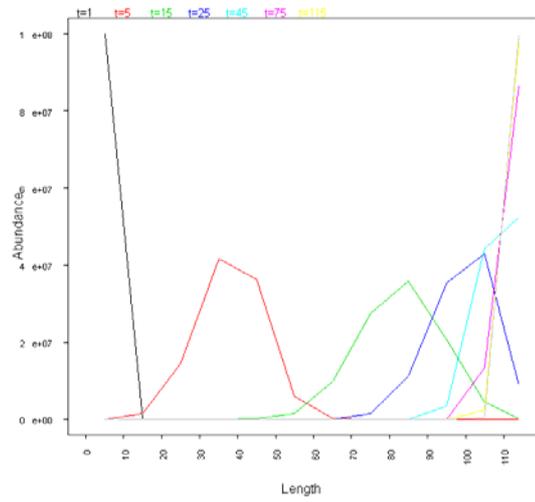
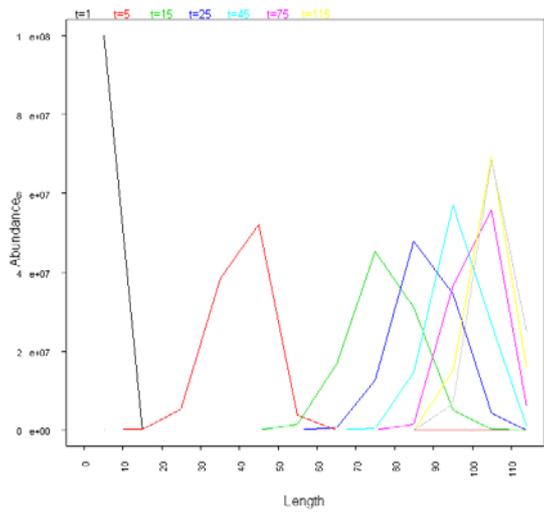
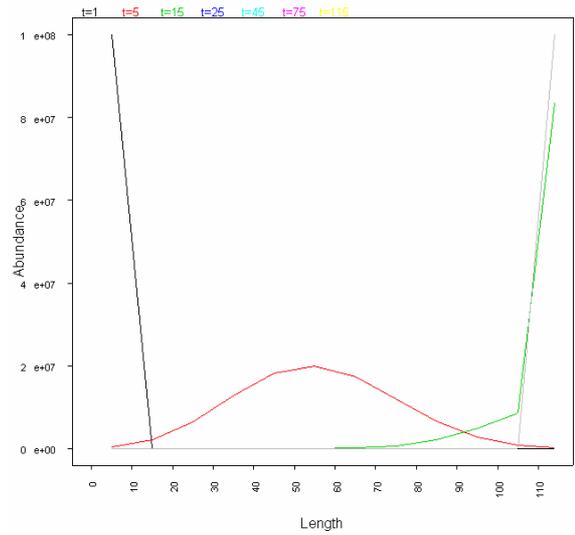
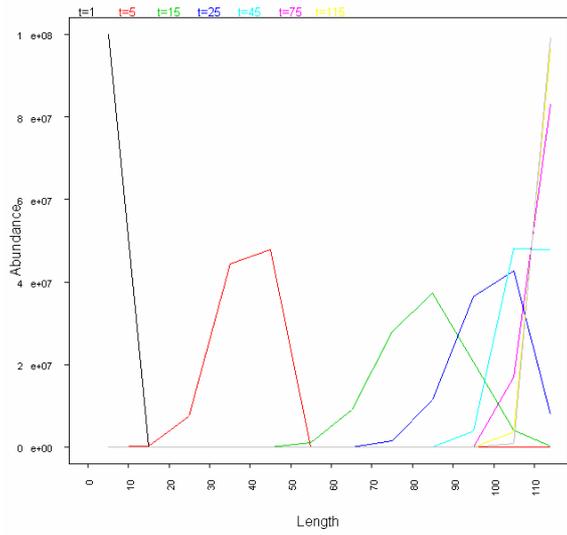


**Figure 3.5.1**

Each graph represents the distribution of the first class of population over length classes after a simulation of growth without any mortality at  $t=1$ ,  $t=5$ ,  $t=15$ ,  $t=25$ ,  $t=50$ ,  $t=75$ ,  $t=115$  (in months), when classes have a width equal to three months according to different hypotheses of growth variability, from left to right and up to down, a uniform distribution, a beta-binomial distribution, a gamma with single integral and a gamma with double integral. The X-axis represents the length decomposed into length classes. The Y-axis displays the number of fishes.



**Figure 3.5.2** Identical to Figure 3.5.1 when classes have a width equal to 5cm



**Figure 3.5.3** Identical to Figure 3.5.1 when classes have a width equal to 10cm

## 3.6 Importance of growth variability in stock assessment models

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### 3.6.1 Introduction

The importance of including length-based processes and annual variability in growth in population models may be demonstrated, and considerable bias may be incurred in conventional age-structured population models that ignore these features. A conventional age-structured model (AMOD) is currently used to assess New Zealand snapper *Pagrus auratus*, (Sparidae), (Paul 1976, Gilbert *et al.* 2000). This is similar to the well-known stock-synthesis model of Methot (1990). Length and age data from commercial catches collected since 1989 revealed an interesting pattern in snapper growth. The observed average weight-at-age was variable, and for most years after 1991 was lower than the published estimates assumed in AMOD for calculating population size. Approximations are made in AMOD for what are essentially length-based processes, e.g., constant weight-at-age and selectivity at age, and these are most likely not constant between years. Also, Millar *et al.* (1999) showed snapper growth to be significantly correlated to sea surface temperature. This discrepancy between assumed and observed weight-at-age and the approximations made in AMOD had implications for the accuracy of current stock size estimates and the advice made regarding the sustainability of current catches. Therefore, we made a comparison between estimates from AMOD and an age-length structured model (CALEN, described in section 3.3) fitted to the same set of observations, and attempted to evaluate the implications of the age-specific approximations made in AMOD using a simulation method.

### 3.6.2 Age-structured model

AMOD is discrete with respect to year; has age classes 4 to 20+ years. The model assumes: both sexes have the same dynamics; constant natural mortality; a single stock with no spatial stratification; no age-specific fecundity; and annual variability in year class strength (YCS) correlated to sea surface temperatures (SST); and no stock-recruit relationship. Annual age-specific fishing mortalities are calculated for five methods: longline, single trawl, Danish seine, other commercial (combined), and recreational. Constant weight-at-age was derived from von Bertalanffy, and length-weight parameters, thus the implicit assumption is that all fish of a given age have the same length and weight. This is a common assumption made in age-structured models.

The population was modelled from exploited equilibrium in 1970 and projected to 2021. Parameters estimated (37) were 17 YCS from 1980-96, mean recruitment, and a relationship between YCS and SST. Fishing method selectivity-at-age was parameterized using double-normal distributions and estimated for the longline, single trawl, and Danish seine methods. Constant selectivity-at-age was assumed for the other commercial and recreational methods. Annual gear-specific fishing mortality was determined from the observed landings and distributed according to the year- and gear-specific selectivity-at-age functions. Parameters were estimated by maximum likelihood with terms for CPUE abundance indices, catch-at-age, research trawl survey relative recruitment indices, and tag-recapture absolute biomass estimates.

The latest AMOD stock assessment results indicate that the stock is over-fished with a current stock size of about 50-70% of the target biomass which supports maximum sustainable yield ( $B_{MSY}$ ). Following a decline from 1970 to the mid-1980's stock size has remained relatively stable and an increase towards  $B_{MSY}$  is predicted.

### 3.6.3 Structural and statistical differences between AMOD and CALEN

There are structural differences between the models, as well as statistical differences in how they are fitted to observations. The main structural difference is the length dimension of CALEN in the population state variable (matrix of numbers-at-age and length). The maximum age class in CALEN is 30 years, while that in AMOD is 20 years. Growth in CALEN is length-based with age-length dependence that approximates phenotypic plasticity, and includes between-year variability that is either SST-dependent or scaled by independently estimated annual growth factors. Growth in AMOD is age-specific and assumes constant weight-at-age. Fishing mortality in CALEN is length-specific while in AMOD it is age-specific. In CALEN the proportion of fish in each age class that exceed the minimum legal size is a function of the estimated fishing method-specific selectivity-at-length and annual growth. In AMOD constant proportions for the partial recruitments of the 4 and 5 year-old fish are assumed. For some recent years empirical estimates were used. Statistical differences between the models relate to the way the models were fitted to the observations and the assumed observation error distributions. In CALEN, the output was a matrix of catch-at-age and length, and a multinomial distribution was assumed. The AMOD output for commercial catches was the vector of catch-at-age proportions, while that for research trawl catches was a time-series of relative recruitment indices and log-normal

observation error was assumed. In CALEN, predicted numbers-at-length were fitted directly to the mark-recapture estimates of absolute numbers-at-length (Gilbert *et al.* 2000). In AMOD the output was absolute biomass.

### 3.6.4 Comparison of model fits to observations

CALEN biomass estimates were considerably lower than AMOD, apart from a short period in the early 1990's where the two model estimates coincided. The models deviated widely after 1993, with AMOD biomass increasing while CALEN biomass was relatively flat. There was only a small difference between the estimates of  $B_{MSY}$  but a large difference in current stock size relative to  $B_{MSY}$ . Overall, the AMOD estimates of biomass and current stock status were more optimistic than CALEN.

The CALEN estimates of annual mean-weight-at-age differ considerably from the constant mean weights-at-age assumed in AMOD. This was due to the estimated variation in annual growth resulting in CALEN mean weight-at-age having a wide range for any given age class. Mean weight-at-age is consistently higher in AMOD than CALEN for the ages between 7 and 20 years. These differences in growth were reflected in the model estimates of mean weight-at-age in catches. This has generally declined in commercial and research trawl catches from 1985 to 2001, with a steep decline occurring from 1990 to 1995. The CALEN estimates were broadly consistent with this trend. Compared to both the observed and CALEN estimates, the constant mean weights-at-age assumed in AMOD are lower for young age classes during the mid- and late-1980's, and are consistently and substantially higher during the 1990's.

CALEN estimates of annual biomass from 1993 to 2001 were considerably lower than AMOD and this was largely due to the combined effects of SST-dependence and annual variability in growth and YCS. CALEN predicts long-term effects on cohort mean weight-at-age due to growth variability in the juvenile life stages. This creates "inertia" in the trend of mean fish weight in the population in subsequent years that affects population biomass, because relatively slight fluctuations in annual length increments throughout the population, translate to large fluctuations in mean weight, and hence population biomass. This is compounded by the impacts of YCS variation on recruited biomass that occur after a time lag caused by the time period required for individuals in a cohort to attain the minimum legal size. Consequently, CALEN predicts that sustained cold periods, such as were experienced during the El Nino event in the early- to mid-1990's, result in the delayed recruitment of smaller cohorts that have below-average weight. AMOD assumed a higher constant weight-at-age during these periods, and therefore short-term predictions of recruited biomass were higher than for CALEN.

### 3.6.5 Sensitivity tests

The structural difference in growth between the models was clearly a factor in the differences between the model estimates. The sensitivity of CALEN was tested for a structure similar to AMOD, i.e., fixing growth at a constant mean; using a von Bertalanffy function to define growth; a temporal change in the selectivity-at-length (SEL86-87), and also altering the relative weights between terms in the likelihood. We also tested the sensitivity of AMOD using observed mean weight-at-age for the biomass and catch weight calculations. CALEN biomass from 1970 to 2001 was sensitive to the structural assumptions tested and gave trends in recent biomass similar that of AMOD, i.e., an upward trend since the early 1990's, and CALEN biomass in 2001 became considerably higher. The AMOD biomass trajectory was more similar to CALEN estimates when observed estimates of mean weight-at-age were used.

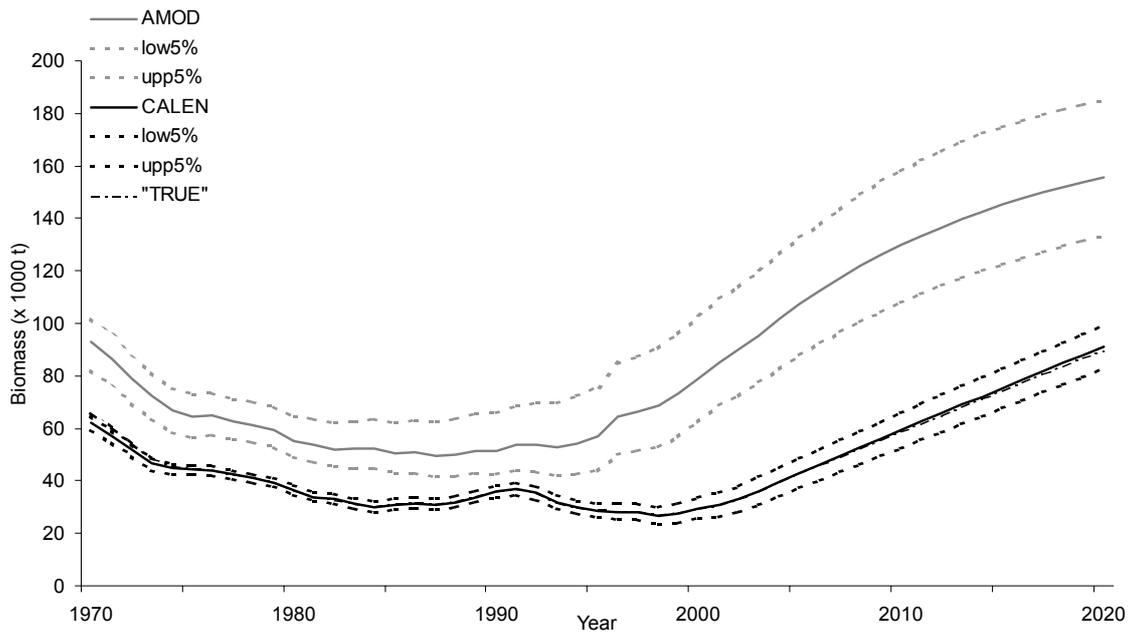
### 3.6.6 Simulation comparisons

AMOD was tested by fitting it to data generated from a hypothetical "true" population specified using the CALEN maximum likelihood estimate from the fit to the observed data. "Observed" data were simulated from the operating model and summarised for input to AMOD. Proportions caught-at-age and -length data were summed by length to produce proportions caught-at-age. Relative abundance indices of 2 year-old fish were derived from the research trawl catch-at-age and length data. Tag-recapture absolute length frequencies were converted to absolute biomass using a length-weight relationship.

Operating model and AMOD estimates of annual biomass from 1970 to 2001 were compared. Both deterministic and stochastic comparisons were made. In the deterministic simulation AMOD consistently overestimated the "true" population biomass, especially through the period immediately following the El Niño event in the early 1990's, despite the two models having similar YCS estimates.

The mean of the stochastic simulation estimates of AMOD annual biomass and stock status in 2001 and 2006 were between 116% and 175% positively biased relative to the CALEN "true" population (Figure 3.6.1). The AMOD bootstrap confidence intervals considerably overestimated the "true" population annual biomass and stock status.

### 3.6.7 Conclusions



Population estimates derived from AMOD and CALEN fits to snapper data differ considerably, and this is mostly due to the variable and temperature-dependent growth estimated in CALEN that predicts annual variability in mean weight-at-age. The simulation results indicate the importance of accounting for growth variability in model structure. They show the magnitude of positive bias (over 100%) in short-term predictions of biomass possible by assuming constant mean weight and selectivity at age, in instances of sustained and below average growth. CALEN is recommended as the better approach for estimating snapper populations given its flexibility to accommodate the complex features of snapper growth. It will also be more accurate for evaluating the relative performance of length-based management strategies such as minimum legal landing size.

**Figure 3.6.1** Comparison of stochastic simulation estimates of biomass from a conventional age-structured population model (AMOD) and “true” biomass from an age-length structured operating model (CALEN).

### 3.7 Maturation process

*Mikko Heino, IMR, Bergen, Norway and IIASA, Laxenburg, Austria*

The results summarized here are based on work conducted together with a large number of international collaborators; much of this activity has been coordinated through the Adaptive Dynamics Network at the International Institute for Applied Systems Analysis (IIASA; Austria). The work has focused on changes in maturation in exploited fish stocks, and relies heavily on so-called probabilistic reaction norms for age and size at maturation (see Heino *et al.* 2002a). These can be defined as probabilities for an immature fish to mature during a given time interval and at a certain age and size; extensions to account for other state variables are straightforward. These probabilities can also be used to parameterise process-oriented maturation models in the context of stock assessment models. In addition, such probabilities are valuable in their own right for describing the maturation process and in disentangling environmental and genetic effects in maturation.

Maturation is an irreversible ontogenetic transition that refers to the process in which maturity status of an individual changes from immature to mature state. Although in reality this process involves several physiological changes that span a period of time (as discussed in SGGROMAT report; ICES C. M. 2003/D:01), in population models maturation process can usually be treated as an instantaneous transition. Thus, at the individual level maturity can be treated as a binary state variable. Maturity at stock level is customarily described by so-called maturity ogives, which give proportions of mature fish as functions of age and/or some other state variables.

There are a number of reasons why a population's structure with respect to maturity may warrant consideration in stock assessment models:

- 1) Maturation may have strong effects both on growth and on survival. In many fishes growth considerably decelerates at maturation. Changes in maturation will then be manifested as changes in weight and length-at-age. Changes in survival are particularly important for stocks that suffer from high mortality after spawning, such as capelin (Barents Sea capelin are essentially semelparous) and many salmonids.
- 2) Maturation may influence the availability of fish to harvesting. Thus, catchability may depend on maturity status. In particular, some fisheries may target only the mature or immature component of a stock.
- 3) Spawning stock biomass (and reproductive potential) depends on maturity. Spawning stock biomass is perhaps the single most important metric used to summarize temporal changes in fish stocks; SSB is also frequently used to determine reference points for stock management. Having a decent estimate of SSB becomes critical when recruitment is modelled using a spawning stock-recruitment relationship. This is common in stock projections.

The importance of these factors will obviously vary from one stock to another, and an approach that does explicitly consider maturity may be sufficient for certain assessment purposes. For example, immature fish are essentially "invisible" for assessment models if maturation occurs before fish become vulnerable to harvesting and survey gear. Even when the harvest consists of both immature and mature fish, it may be possible to ignore that structure if maturity (with respect to salient variables such as age and size) remains constant over time. In that case, stock parameters will be average values over immature and mature individuals. However, maturation dynamics (and maturity) often change considerably over time reflecting demographic, environmental, and possibly genetic changes. This needs to be taken into account in population models.

In population models, one is ultimately interested in the state of maturity. Depending on the model, maturity structure could be established in one of three ways:

- 1) Directly estimated from data as a function of state variables in the model. For stock projections or periods without appropriate data, one needs to assume that, e.g., maturity-at-length remains unchanged.
- 2) Estimated from data using a regression model that relates maturity to chosen explanatory variables, e.g. temperature. This method allows somewhat more robust projections or patching of missing observations.
- 3) Inferred with a help of a process-based model that has been estimated from the data. If the process model can be estimated with a reasonable confidence, this method provides the most robust way of predicting maturity for stock projections or periods with missing data.

For population models in discrete time, the natural way of formulating a process model for maturation is to express it as a transition probability from the state of being immature to mature, dependent on the state variables of the model. Process-oriented maturation models have been used in a number of fish-population models, e.g. by Parma and Deriso (1990), De Leo and Gatto (1995), Anon. (2002), Frøysa *et al.* (2002), and Ernande *et al.* (2002). Of these, only the Gadget family (Anon. 2002; Frøysa *et al.* 2002) represents models developed for stock assessment purposes.

Three kinds of datasets, representative of the population in question, could be used to estimate the age- and size-dependent probability that a juvenile fish matures during one time step:

- 1) A sample of fish, measured for age and size and classified as being juvenile, first-time spawner or repeat spawner; the last class is not needed in the analysis.
- 2) Two consecutive samples of fish, measured for age and size and classified as either juveniles or adults (or as immature and mature). In the case of sampling with replacement, no individual identification is required.
- 3) Data on individual growth and maturation histories, originating from a mark-recapture study (or any other study where individually identified fish are followed).

Of the types of data listed above, the first two have been used in practice, and are described in more detail by Heino *et al.* (2002a,b) and Barot *et al.* (2002a,b); a brief summary is available as a working document to SGGROMAT (Heino 2002). However, use of data on individual growth and maturation histories to estimate age- and size-dependent maturation probabilities seem not to have been attempted. The use of such data appears both powerful and straightforward — mark-recapture studies are often used to gain fishery-independent estimates of mortality, and maturation is an irreversible event similar to death. Therefore, the suite of methods developed for the analysis of mark-recapture and survival data are available (e.g. Diggle *et al.* 1994). Table 3.7.1 summarizes the key results of the case studies where age- and size-specific maturation probabilities have recently been estimated (others probably exist).

Stock	Time span	Age effect?	Temporal change?	Sex	Source
Northeast Arctic cod	1932–1998	Yes (–)	Yes	Mixed	Heino <i>et al.</i> 2002a-c
Georges Bank cod	1970–1998	Yes (+)	Yes	Separate	Barot <i>et al.</i> 2002b
Gulf of Maine cod	1970–1998	Yes (+)	Yes	Separate	Barot <i>et al.</i> 2002b
Northern cod	1977–2002	Yes (+)	Yes	Separate	Olsen <i>et al.</i> in prep
Norwegian spring-spawning herring	1935–2000	Yes (+)	Yes, but weak	Mixed	G. Engelhard in prep.
North Sea plaice	1955–1995	Yes (+)	Yes	Females	Grift <i>et al.</i> 2003
Newfoundland American plaice	1969–2000	Yes (+)	Yes	Separate	S. Barot <i>et al.</i> in prep.
European grayling	†	Yes (+–)	Yes	Mixed	T. Haugen in prep.

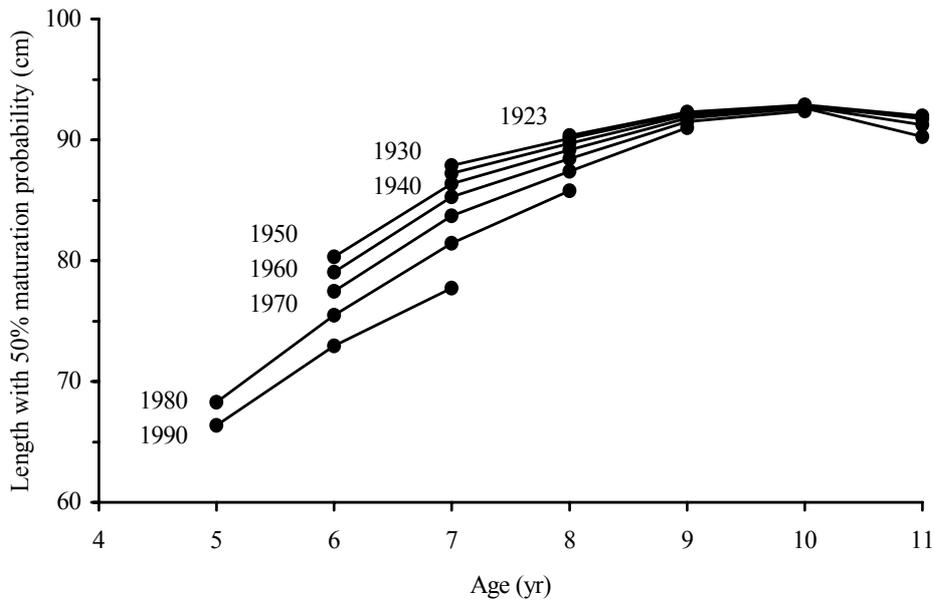
† Comparison of four artificially stocked populations that have a common ancestry some 80 years ago.

**Table 3.7.1** Key results of some case studies where age- and size-specific maturation probabilities have recently been estimated.

Table 3.7.1 bears two important messages. First, in all the stocks analysed, age has a significant influence on maturation (even though the magnitude of this effect greatly varies). In most of the cases, maturation probability at a certain length increases with age (denoted with “+” in the above table). However, the pattern is opposite for Northeast Arctic cod (denoted with “–”) and non-monotonic for grayling.

Second, maturation probabilities can evolve significantly within a time scale of less than ten generations. There has typically been a trend towards increasing maturation probabilities at a certain age and size. In other words, there is a tendency towards maturation at an earlier age. Norwegian spring-spawning herring is an exception, showing only very weak trends that vary by age. Divergence among the grayling populations show that temporal changes have occurred but the trends in the individual stocks cannot be known.

Figure 3.7.1 shows age- and length-dependent maturation probabilities estimated for the Northeast arctic cod (Heino *et al.* 2002c). The figure clearly shows that maturation probabilities are age-dependent and that maturation probabilities have changed drastically over the time.



**Figure 3.7.1** Age- and length-dependent maturation probabilities estimated for Northeast arctic cod of cohorts from 1923 to 1990 (Heino *et al.* 2002c). For the purpose of the illustration, only age-specific lengths at which probability of maturing is 50% are shown.

The main conclusions arising from the work on maturation probabilities are the following:

- 1) Estimation of conditional maturation probabilities is feasible with various kinds of data collected for fisheries assessments purposes, thus providing necessary input for process-oriented maturation models
- 2) Although maturation may as a first approximation be described as only length-dependent, it also depends on age, condition etc.
- 3) Maturation may evolve over a time scale of a few generations, i.e. at a decadal scale for typical exploited stocks. Thus the parameters of maturation sub-models cannot necessarily be assumed to remain constant in the long-term. This has implications both for stock projections and for stock assessments based on lengthy time-series.

### 3.8 Diagnostics with Gadget

*Morten Nygaard Åsnes, IMR, Bergen, Norway*

#### 3.8.1 Introduction

Gadget (Anon 2002) is a powerful tool for building age-length-structured models. Because the Gadget framework allows a lot of freedom in specifying a model, there are many pitfalls that need to be avoided. Having diagnostics for a model is critical, both when it is being set up, and when it is being used. The Gadget program itself does not provide much diagnostic output. A complete printout of the modelled population and the optimisation process is produced by Gadget, and external programs must then be used to produce plots or tables.

The Fleksibest model (Frøysa *et al.* 2002) implemented using Gadget has been used as an alternative to XSA for assessing Northeast Arctic cod at the Arctic Fisheries Working Group (ICES C.M. 2003/ACFM:22). Some of the diagnostic tools that have been used with Fleksibest are presented here. This Fleksibest model is a single-species model, but the immature and mature parts of the stock are modelled separately. It runs over 73 quarterly time steps, has 10 age groups, and 120 length groups. Two fishing fleets are modelled, and 11 likelihood components are used to fit 133 parameters to catch, survey, and stomach data.

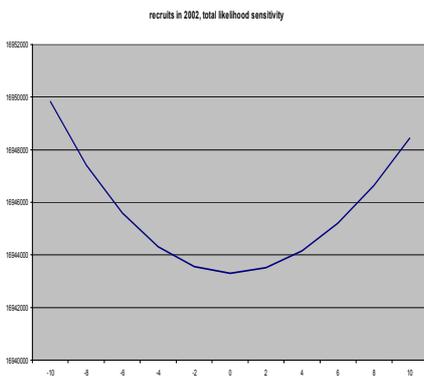
Most of the plots presented here have been produced by custom scripts (using Perl and Awk), specifically written for the Fleksibest model. For most some work is needed before they can be used for all Gadget models. A script for making sensitivity plots that already works for all Gadget models is included with the Gadget distribution.

### 3.8.2 Sensitivity diagnostics

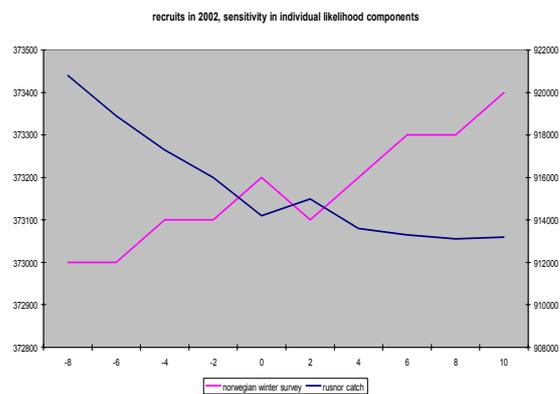
After a Gadget optimisation run, a set of sensitivity plots can be produced. Each of these plots show the total likelihood score resulting from changing a single parameter in steps, and keeping the other parameters fixed at the optimum. An example is shown in Figure 3.8.1. It can also be useful to see how a parameter influences one or more likelihood components individually. This will show how much information is contained in different data sources, and whether data sources are conflicting. Figure 3.8.2 shows such a plot of two of the individual likelihood components that are pulling a parameter in different directions.

A sensitivity plot involves changing each parameter in steps, and evaluating the likelihood function at each step. When a single simulation run takes several seconds, a complete sensitivity analysis will usually be quite time consuming to produce, if all parameters are to be sampled. Table 3.8.1 shows another way of getting an overview of the likelihood sensitivity. Each parameter has been changed in turn by  $-5\%$  and  $+5\%$  of its starting value, and the resulting change in likelihood score is listed. To produce this table only two evaluations of the likelihood function for each parameter are necessary. It will not show as much detail about the likelihood surface as a detailed sensitivity plot, but it is much faster to produce. It can also give a quick overview of the relative importance of each parameter.

To verify that a solution found by the optimiser is sensible, it can be useful to look at the model formulations with the final parameter values entered. For instance, Figure 3.8.3 shows the selection functions for two modelled fleets. The dome shaped selection is from a different run where a different selection function was used for the gillnet fleet. The similarity between the two gillnet curves over most of the range of the data indicates that despite using a different model formulation, there is little difference in the effective selection pattern between the two runs.



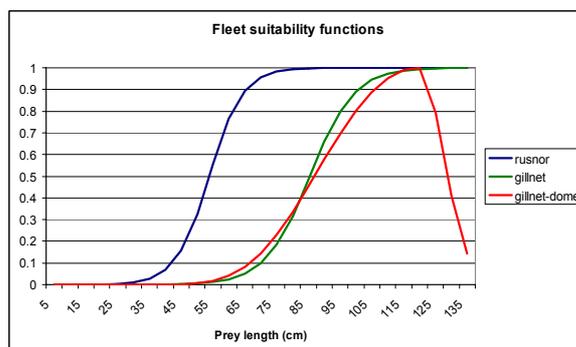
**Figure 3.8.1:** Total likelihood sensitivity to recruitment parameter for 2002.



**Figure 3.8.2:** Partial likelihood sensitivities to recruitment parameter for 2002.

Parameter	Value	-5%	+5%
n_minage.1986	117.512	16.68	16.84
n_minage.1987	36.2056	5.53	5.67
n_minage.1988	29.059	7.30	7.56
n_minage.1989	20.4847	4.84	4.99
n_minage.1990	30.4749	5.96	6.13
n_minage.1991	49.0125	8.19	8.35
n_minage.1992	76.257	2.84	2.93
n_minage.1993	97.2025	0.35	0.36
n_minage.1994	89.904	0.10	0.09
n_minage.1995	57.8611	0.06	0.06
n_minage.1996	35.8281	0.05	0.05
n_minage.1997	59.9047	0.10	0.08
n_minage.1998	73.4807	0.11	0.10
n_minage.1999	51.6259	0.06	0.06
n_minage.2000	58.5576	0.05	0.04
n_minage.2001	38.6685	0.02	0.02
n_minage.2002	33.9831	0.01	0.01
n_minage.2003	90.6698	0.01	0.01

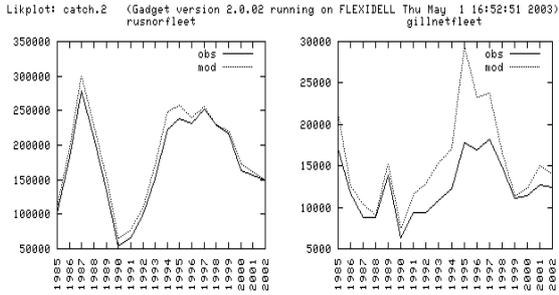
**Table 3.8.1:** Parameter name, value, and percentage change in total likelihood score resulting from changing each parameter by + or  $-5\%$ .



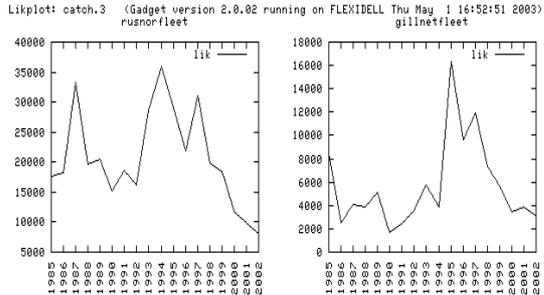
**Figure 3.8.3:** Fleet suitability functions.

### 3.8.3 Fitting the model to data

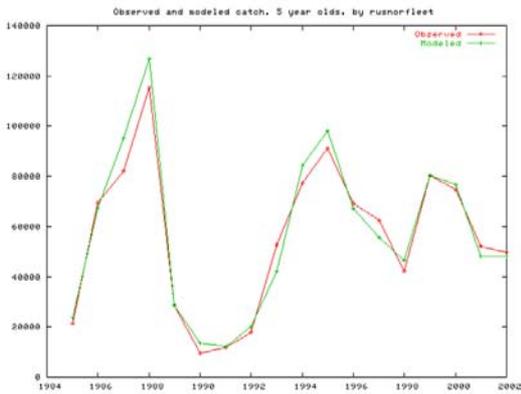
A Gadget model run will try to fit a population model to many different data sources, by finding the set of model parameters that gives the optimum likelihood score. In doing so it will usually have to be a compromise between how well it can fit to the individual components. Figure 3.8.4 shows a plot of modelled and observed catch by year, for two fleets. This can be used to compare how well the various components are fitted, and if particular years are problematic for the optimiser. The actual (un-weighted) likelihood contribution from each of these is shown in Figure 3.8.5. More detailed plots, showing individual years, ages, and length groups, can also be produced. The modelled and observed is plotted by year for a single age in Figure 3.8.6, and for a single length group in Figure 3.8.7. Catch in a single year can be plotted by age (Figure 3.8.8), or by length group (Figure 3.8.9).



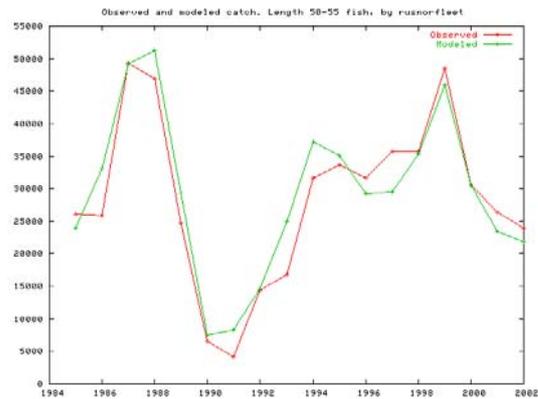
**Figure 3.8.4:** Observed and modelled catch in number.



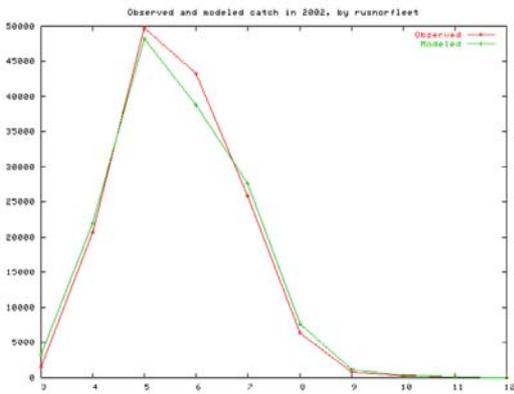
**Figure 3.8.5:** Likelihood score by year, for catch likelihood.



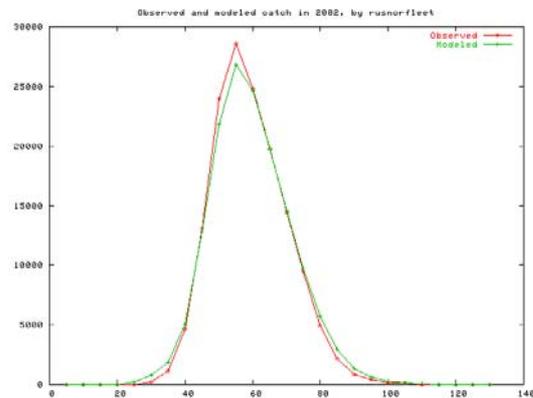
**Figure 3.8.6:** Observed and modelled catch of 5 year olds.



**Figure 3.8.7:** Observed and modelled catch of 50-55 cm fish.



**Figure 3.8.8:** Observed and modelled catch by age in 2002 by a single model-fleet.



**Figure 3.8.9:** Observed and modelled catch by length-group in 2002 by a single model-fleet.

### 3.8.4 Model results

After Gadget has found a solution, output of the modelled populations, and fleets, can be printed to text files by the program. For the Fleksibest model, a script is available that will summarise this information by age and year. Some of these tables can also be plotted. Figure 3.8.10 shows a plot of SSB, produced from this file. Results from other models can be added to these plots, for comparison. Results from an XSA run are added to the plot of recruitment in Figure 3.8.11. More than one run of the Fleksibest model can also be plotted together. In Figure 3.8.12 the stock biomass is plotted, for two different runs. One is the reference run, and the other is a run where the Norwegian winter survey has had its weight increased by a factor of 10 during the optimisation. Retrospective plots can also be produced for various properties of the modelled stock. Figure 3.8.13 shows the retrospective pattern in  $F_{5-10}$ , which may indicate some overestimation in the final year.

Because the Fleksibest model has been used as an alternative to XSA, several plots for comparing the two models have been made. A comparison of observed and modelled weight-at-age is shown in Figure 3.8.14, and in Figure 3.8.15 the proportion mature at age in Fleksibest is compared with observed maturity ogives. For checking mean length-at-age in the model, survey data has been used for comparison. Mean length of a single age group in the immature sub-stock is compared with survey data in Figure 3.8.16. The same information can also be plotted by cohort, as in Figure 3.8.17.

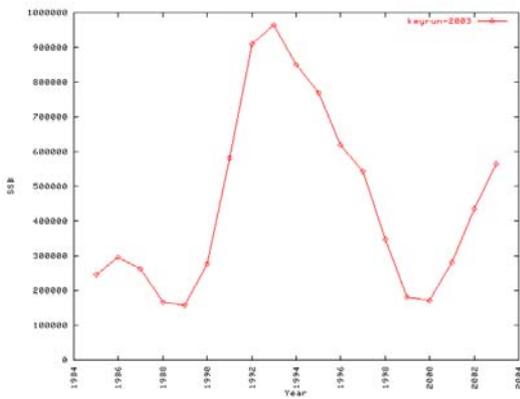


Figure 3.8.10: Modelled spawning stock biomass

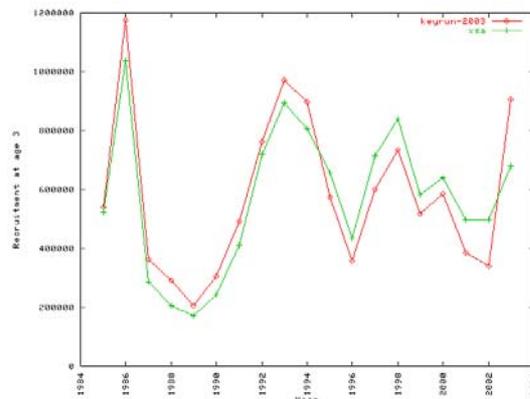


Figure 3.8.11: Modelled recruitment in Fleksibest and XSA.

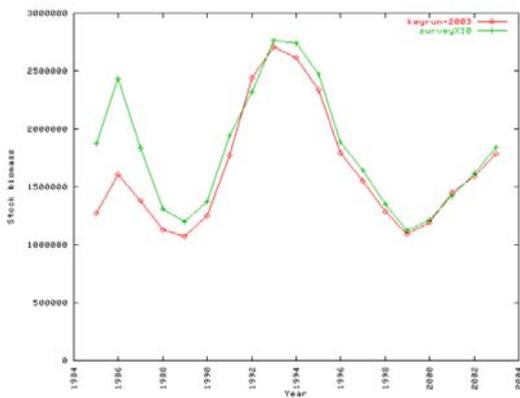


Figure 3.8.12: Modelled stock biomass for two different Fleksibest runs.

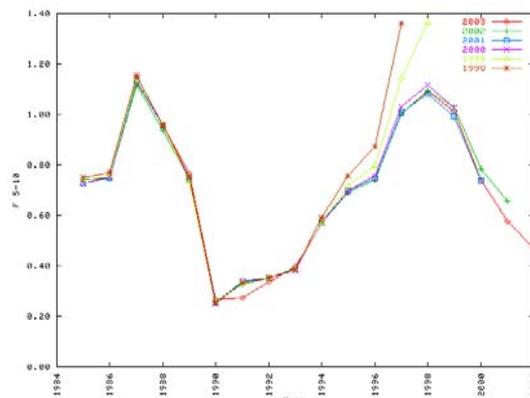
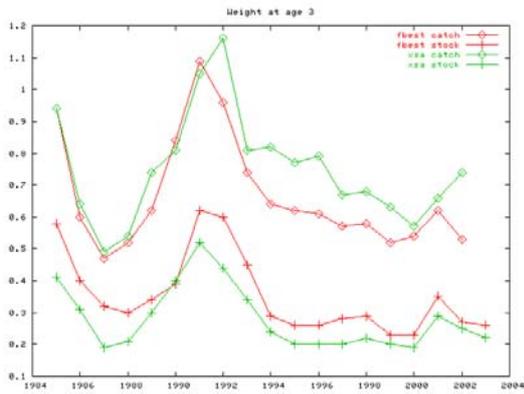
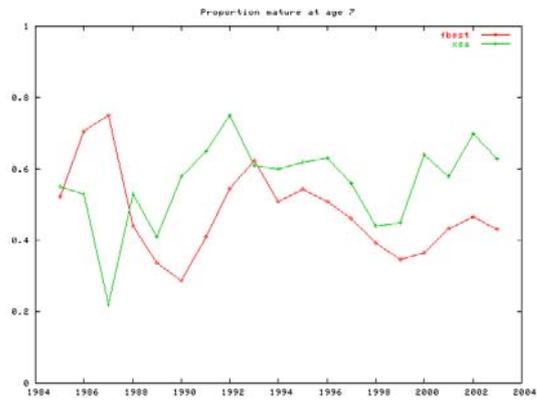


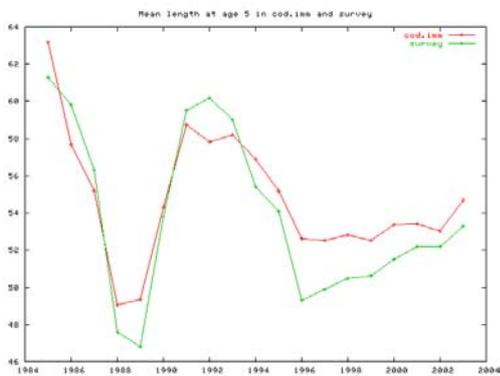
Figure 3.8.13: Retrospective pattern in  $F_{5-10}$  when changing the final year from 1998 to 2003



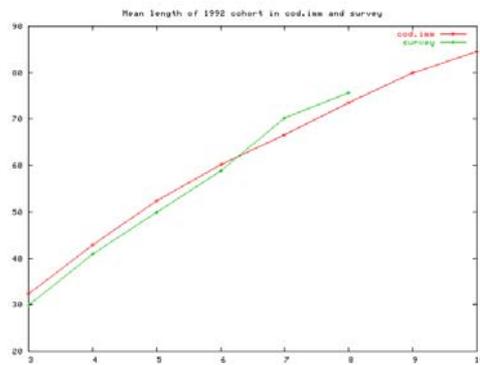
**Figure 3.8.14:** Observed and modelled weight in stock and catch-at-age 3.



**Figure 3.8.15:** Observed and modelled proportion mature at age 7.



**Figure 3.8.16:** Mean length-at-age for immature 5 year olds, in Fleksibest and in one of the surveys.



**Figure 3.8.17:** Mean length-at-age for the immature part of the 1992 cohort, in Fleksibest and in one of the surveys.

## 4 CASE STUDIES

### 4.1 Challenges for assessment of shellfish

*Mike Smith, CEFAS, Lowestoft, UK*

A variety of taxa fall within the term shellfish, primarily three classes of molluscs (gastropods, bivalves and cephalopods) and the decapod crustaceans, but other groups such as echinoderms may be included and are important in certain countries and regions. Even within the two major groups (molluscs and crustaceans) a wide range of specialised life-cycles and adaptations are exhibited, which may pose particular problems for the stock assessment biologist. However, there are also some characteristics that are common to many shellfish and fisheries and it may be that satisfactorily accounting for these in assessment models provides the greater challenge.

Perhaps the most widespread feature of shellfish is spatial structure in the distribution of the population, which generally leads to spatially distributed fishing effort. Spatial structure may take a wide variety of forms from mobile pelagic aggregations of squids to static patches of bivalves within which individuals may clump tightly (mussels) or tend to spread more uniformly (razorshells). Aggregations may form for spawning purposes or as a result of settlement dynamics, seabed topography or other environmental influences.

Several important species (e.g. cockles, mussels) inhabit tidal flats and occur in fairly distinct beds where it may be possible to estimate abundance directly. Transects can be surveyed and abundance can be raised by area to give estimates for standing stock using geostatistical methods (e.g. kriging; Conan, 1985). In clear water dive transects extend such methods to shallow water and are particularly popular in warmer waters. If reliable estimates of standing

stock can be collected with relative ease then 'rule of thumb' management can proceed without the application of population dynamics models for stock assessment. This is the situation for a number of littoral stocks.

Area-raised methods are also applied to survey data collected from deeper waters, but low and variable gear efficiencies (dredges, traps) may introduce high levels of uncertainty. In such cases stock assessment will usually also include the use of stock and fishery dynamics models. For assessment purposes data must be analysed at a spatial scale where relevant assumptions (e.g. equal availability for capture of all fish) are not violated. Comparison of aggregated per-recruit analyses with individual (Hart, 2001) and spatially disaggregated (Myers *et al.*, 2000) per-recruit models have shown that results may differ substantially.

A number of models have been developed in which the population is spatially compartmentalised (Caddy, 1975; Seijo *et al.*, 1993; Caddy and Seijo, 1998). Modern computing power facilitates the use of complex models of this type. Such models provide useful insights into likely responses to management options, particularly those involving spatial measures such as closed areas and rotational harvesting policies. In theory these methods can be used for assessment by adjusting the parameters of interest to minimise differences between modelled and observed data. However, in practice it remains difficult to estimate all the parameters required for each spatial cell of such models, and their main use is for evaluation of management strategies.

Shellfish species are often high value products and many of the landings are from artisanal fisheries that also have a high socio-economic value. Reductions in whitefish stocks have further increased the importance of shellfish fisheries, both in terms of alternative resources for displaced fishing effort and proportion of the landings. However, for many important shellfish species insufficient data exist for satisfactory assessment to take place. Key processes in life-histories and behaviour patterns may not be adequately quantified, catch and effort data may be unreliable or only available for short time periods particularly in artisanal fisheries. Furthermore, size distributions may not necessarily correspond to exploitation rate, and environmental drivers may be poorly understood and are difficult to predict.

Crustaceans, which include a number of high value species, have a discontinuous growth pattern and as no hard parts are retained during the moult process they cannot be routinely aged. Research into using lipofuscin pigments to estimate age for crustaceans has been carried out (Sheehy *et al.*, 1995; 1998; 1999), but the process requires biochemical extractions and analyses and cannot be carried out routinely on large numbers of animals. Assessment of Crustacea is therefore generally limited to length-based approaches. Historically, equilibrium length-based methods (e.g. Length Cohort Analysis (LCA); Jones, 1981; 1984) have been widely applied and, in conjunction with length based yield-per-recruit analyses, can provide a useful framework for analysing the potential effects of size limits. However, if, as has been suggested, length distributions are influenced by topographical features they will not necessarily reflect the level of exploitation (Addison, 1986). Age-structured methods may be applied following transformation of data from length to age as is the case for ICES assessments of *Nephrops*. In general length-slicing reduces contrast in the catch-at-age which may result in under-estimation of fishing mortality and poor discrimination of year class strength.

Improving understanding of stock recruitment relationships remains a major challenge for shellfish stock management. As noted above, length-based methods may be inefficient in detecting recruitment signals, a problem compounded in some species (e.g. crab, lobster) by a long time period between hatching and recruitment to the fishery. Many mollusc species, particularly those found in littoral and estuarine environments, are subject to severe environmental drivers which further complicates stock and recruitment relationships. This problem is not limited to shallow water species as recruitment and/or growth of scallop stocks may be influenced by environmental forces (Caputi *et al.*, 1998).

Stock identity is not clear for many shellfish populations; metapopulations are thought to exist in both molluscan and crustacean species. Species with extended pelagic larval phases are most likely to exist as metapopulations, and environmental forcing may result in metapopulation dynamics that vary from year to year.

A feature which is common to those shellfish fisheries using dredges and traps is the relatively low and variable efficiency of these fishing gears. Catchability of traps may vary due to both inter- and intra- specific behavioural factors where densities of animals are high (Addison and Bell, 1997; Addison and Bannister, 1998). Trap catchability is also influenced by environmental conditions and bait properties which can affect the area of attraction (McQuinn *et al.*, 1988; Bell *et al.*, 2001). Dredges may cause damage to the benthos and introduce additional mortalities on both target and non-target species not taken by the gear. Traps are more benign environmentally, although concerns have occasionally been raised regarding 'ghost fishing' by lost gear and the destruction of cuttlefish eggs laid on traps.

In addition to the general features discussed above shellfish and their fisheries display a range of specialist features that challenge standard assessment techniques. A non-exhaustive list includes: semelparous life cycles, simultaneous and sequential hermaphroditism, discontinuous growth, terminal moults, ephemeral populations and catastrophic environmental events, seasonal migrations, aggregation/bulk landing of catch and subtle shifts in target species.

Key challenges for shellfish and fisheries are accounting for spatial structure and the difficulties in ageing crustacea. A wide range of methods for estimation of stock level and status exists which do not require age-structured data including biomass dynamics models, depletion models, length-structured methods, stage-structured models, traffic light approaches. It is important that development of such methods continues in order to provide alternative methods for use where age-structured data are not available. Models are also available or being developed which can explicitly account for spatial structure and improvements in computing power have enabled increased complexity to be considered without prohibitive increases in run-times.

Highly complex models tend to be 'data hungry' and this may limit their use for assessment of shellfish in data poor circumstances. However, they play an important part as simulation frameworks for the evaluation of both simpler assessment techniques (including length-structured only) as well as management strategies under plausible assumptions regarding stock and fishery dynamics.

Another challenge common to all fisheries may lie in developing an integrated approach to sampling, monitoring, assessment and modelling, taking account of the requirements for management and advice, the value (socio-economic and ecosystem) of the resource and allowing some flexibility to account for contingencies.

## **4.2 Length-based assessment of Northern Shelf anglerfish**

*Helen Dobby, FRS, Aberdeen, UK*

### **4.2.1 Introduction**

Anglerfish (*Lophius spp.*) occur in a wide range of depths, from shallow inshore waters down to at least 1000 m. Small anglerfish occur over most of the northern North Sea and Division VIa, but large fish, the potential spawners, are more rarely caught. Little is known about when and where anglerfishes spawn in northern European waters and consequently stock structure is unclear. This lack of knowledge is due mainly to the unusual spawning behaviour – although the eggs and larvae are pelagic, unlike most marine fish, the eggs are spawned in a long gelatinous ribbon which may contain more than a million eggs. This rather clumped distribution of eggs (and subsequent larvae) means that conventional plankton surveys provide little information about the spawning behaviour.

A recent EU-funded project entitled 'Distribution and biology of anglerfish and megrim in the waters to the West of Scotland' (Anon., 2001) has however, improved our understanding. A particle tracking model was used to predict the origins of young fish and has indicated that post-larval anglerfish may be transported over considerable distances before settling to the seabed (Hislop *et al.*, 2001). Anglerfish in deeper waters to the west of Scotland and at Rockall could therefore be supplying recruits to the western shelf and the North Sea. Furthermore, results of microsatellite DNA analysis carried out as part of this project have shown no structuring of the anglerfish stock into multiple genetic populations within or among samples from Divisions IVa (northern North Sea), Division VIa (West of Scotland), Rockall and Subarea VII. For the purpose of the assessment presented here, the Northern Shelf is considered to comprise Division IIIa, Subarea IV and Subarea VI; anglerfish in Subarea VII are assessed by the Southern Shelf WG.

Historically, anglerfish were regarded as a by-catch species of mixed demersal fisheries targeting cod and haddock. As TACs for these other demersal stocks became more restrictive, increased targeting of anglerfish began to occur. A rapid increase in landings during the early 1990s, followed by an equally rapid decline provoked increased interest in stock assessment of this species. At the 2000 ICES Northern Shelf Working Group, an exploratory length-based approach was presented for this stock (ICES C.M. 2001/ACFM:01) and this was compared to the separable catch-at-age analysis (Cook *et al.*, 1991) which had previously been considered. This alternative length-based approach was considered following concerns raised by the WG about i) uncertainties in the anglerfish age readings and ii) that the possibility that the age-based separability assumption may be violated in a rapidly developing fishery such as this.

The assessment uses a size-transition matrix approach based on the catch-at-size analysis (CASA) of Sullivan *et al* (1990). Following a number of years of exploratory work (Dobby, 2000, 2001, 2002, ICES C.M. 2001/ACFM:01, ICES C.M. 2002/ACFM:02, ICES C.M. 2003/ACFM:04), this assessment was accepted by ICES in 2002 and used as the basis for advice. The population is described by a vector of numbers-at-length, which is projected forwards in time using a size transition matrix obtained from a stochastic growth model with externally estimated parameters. All population dynamics processes (e.g. recruitment, fishing mortality) are assumed to be dependent on length rather than age. Parameter estimates (yearly recruitment, mean and standard deviation of recruitment distribution, selectivity parameters and temporal component of fishing mortality) are then obtained by fitting the annual catch-at-length predicted by the model to the observed data. These parameters can then be used (together with estimates of maturity and individual weight) to obtain short-term predictions of catch and biomass and in yield-per-recruit analysis. An outline of the available data and the anglerfish specific implementation of this general model is given below.

#### 4.2.2 Data availability

Reported total international landings of Northern Shelf anglerfish are available for a relatively long period (since 1970s), however, regular market sampling of this species did not begin until much more recently. Therefore annual catch-at-length distribution data are available only for the years 1993-2002. No discard information is incorporated into the catch-at-length distributions. However, there is no minimum landing size for this species and discard rates are very low. Scottish March West Coast survey data is available from the 1980s onwards. Effort data is available from the Scottish Light Trawl fleet (SCOLTR), the offshore component of which is associated with this fishery. This fleet is considered to be one of the most important in terms of catches.

#### 4.2.3 Assumptions and Exploratory analysis

Due to inconsistencies in the ageing of Northern Shelf anglerfish, initial exploratory investigations using this model used growth parameters taken from a Southern shelf stock of anglerfish and assumed no differences between males and females (Dobby 2000, ICES C.M. 2001/ACFM:01). Age reading now appears to be more internally consistent and preliminary analysis of data collected on a recent (2000) Scottish anglerfish survey of Division VIa appear to indicate a somewhat faster growth rate and also large differences between males and females. Furthermore, new information which has become available from the EU-funded project indicates very different maturity ogives for males and females with male 50% maturity at approximately 57 cm and females at over 90 cm. Populations of males and females are therefore modelled separately with growth differentiated by sex, but with the assumptions that equal numbers of males and females recruit to the fishery and that both sexes are subject to the same fishing mortality at length. Model estimates of male and female catch-at-length therefore have to be summed before comparison with the total international catch-at-length distribution which is not disaggregated by sex.

Mean growth is calculated from a von Bertalanffy growth equation with the parameters estimated externally (from the above survey data). The variability in growth in length-based population models has been modelled using a variety of distribution functions and a further discussion of the appropriateness of these is given elsewhere in this report. Initial investigations (Dobby, 2002) indicate that using a beta distribution to model growth increment variability in anglerfish gives a good fit to the data. The mean of this growth model is consistent with that of the externally estimated von Bertalanffy mean growth.

Both fishing and natural mortality are assumed to be continuous throughout the year. Natural mortality may depend on either size or sex, but here it is assumed to be a constant of  $0.15 \text{ yr}^{-1}$ .

Fishing mortality is assumed to be separable into a year specific fishing mortality and a single time-independent length-based selectivity function. In initial exploratory runs of this model the selectivity was assumed to take the form of the function suggested by Cook and Reeves (1996). This function was chosen because of its ability to model a range of exploitation patterns from logistic to dome-shaped. However, due to the lack of large fish in the available catch-at-length data (Figure 4.2.1), the fitted exploitation parameters consistently indicated a dome shaped exploitation pattern with much reduced fishing mortalities at greater lengths. The resulting estimated spawning stock biomass therefore appeared to be relatively high due to the low mortality of the spawning fish, indicating an apparent refuge for these larger individuals. However, targeted research vessel surveys of this area and of deeper water further west conducted in 1999 and 2000 have caught very few of these fish, and similarly, observers on commercial vessels in the same period have seen very few large anglerfish. It is therefore unclear as to whether such a refuge exists or whether the stock contains very few of these large individuals. If, instead, selectivity is assumed to follow a logistic function, spawning stock biomass is estimated to be much lower, as in this scenario fishing mortality is high on large individuals. Thus it seems more prudent to adopt a logistic exploitation pattern until such times when evidence for a refuge becomes available. (Model runs comparing a logistic and a Cook and Reeves type function show insignificant differences in fit to the catch-at-length data.)

Recruitment to the fishery is assumed to occur at the beginning of the year and over a range of length classes, the distribution of which is fixed from year to year. In this implementation, the distribution is assumed to be Gaussian with estimated mean length at recruitment and standard deviation. This distribution function is then multiplied by total annual recruitment (also estimated) to give the number of individuals recruiting to each length class.

Population numbers at length at the beginning of the time-series (1993) can be estimated by assuming that prior to this, the population was in equilibrium with constant fishing mortality and recruitment estimated in the model.

#### 4.2.4 Implementation and parameter estimation

Assuming that survivorship and recruitment operate deterministically, then the only errors are those in the catch-at-length observations. Making the further assumption that the errors between predicted and observed catch-at-length are

independent and identically distributed, then the model parameters can be estimated using a combination of grid-search and non-linear optimisation to minimise a suitable objective function which consists of the residuals between predicted and observed catches at length.

Uncertainty in the parameter estimates can be reduced by the incorporation of auxiliary data. Due to the historical relative commercial unimportance of Northern Shelf anglerfish, research vessels surveys have not been designed to catch anglerfish or at least do not sufficiently cover the spatial distribution of the population to provide good indices of relative abundance. Research vessel surveys generally cover only relatively shallow areas and therefore only catch small anglerfish in significant numbers. Data from one such Scottish survey (March West Coast) are used as a recruitment index which is used to constrain the model estimates of total annual recruitment. Removal of this index results in large retrospective patterns – huge overestimation of recruitment and underestimation of fishing mortality in the most recent years (Dobby, 2001).

A further constraint on parameter estimates can be made by assuming that the temporal component of the fishing mortality is related in some way to fishing effort. Fishing effort most associated with the fishery for Northern Shelf anglerfish is assumed to be the offshore component of the Scottish Light Trawl fleet. It is assumed that the trend (over the full time-series) in the temporal component of the fishing mortality estimates is equal to the trend in the SCOLTR effort data over the corresponding years. It is not assumed that fishing mortality is directly proportional to this effort as the effort has not been corrected for the proportion of the fleet actively targeting anglerfish.

The equilibrium fishing mortality which is assumed for the period before 1993 is constrained by assuming that equilibrium catch was equal to the mean of the reported landings of the previous 10 years.

#### 4.2.5 Results

A summary of the stock trends and estimated parameters (from the Northern Shelf WG 2003) are illustrated in Figure 4.2.2. Catches as estimated by the model follow the reported landings relatively well. Landings and fishing mortality show a strong downward trend in recent years. The model estimate of spawning stock biomass in 2002 is below 7,000 t, although there is some indication of a levelling off in the decline which is apparent in previous years. Total biomass is estimated to have declined rapidly during the mid- 1990s followed by a period of relative stability – these fluctuations are reflected in those of the estimated number of recruits. If the model estimates of spawning stock biomass are broken down by sex, a huge imbalance is observed with over 6,000 t of mature males and less than 1,000 t of mature females. This difference is due to the differences in size at maturity for males and females. The fact that mature female anglerfish are rarely observed either on scientific surveys supports a very low estimate of biomass, yet there is little evidence of a marked reduction in the spatial distribution of young fish. It has been hypothesized that females may become pelagic when spawning as they produce buoyant eggs (Hislop *et al.*, 2000) and would therefore not appear in the catch of trawlers. This would imply different exploitation patterns for males and females which is not incorporated in the model. It is also not known whether anglerfish are an iteroparous or semelparous species. The latter would also account for the almost complete absence of spawning females in commercial catches or research vessel surveys.

Despite the short time-series of data, the sensitivity of the results to the addition of an extra year of data can be tested. Like so many stock assessment models, the addition of an extra year of data appears to result in an upward revision of fishing mortality and a corresponding downward revision of estimated spawning stock biomass. Estimates of total annual recruitment appear to show less retrospective bias.

#### 4.2.6 Forecasts and management

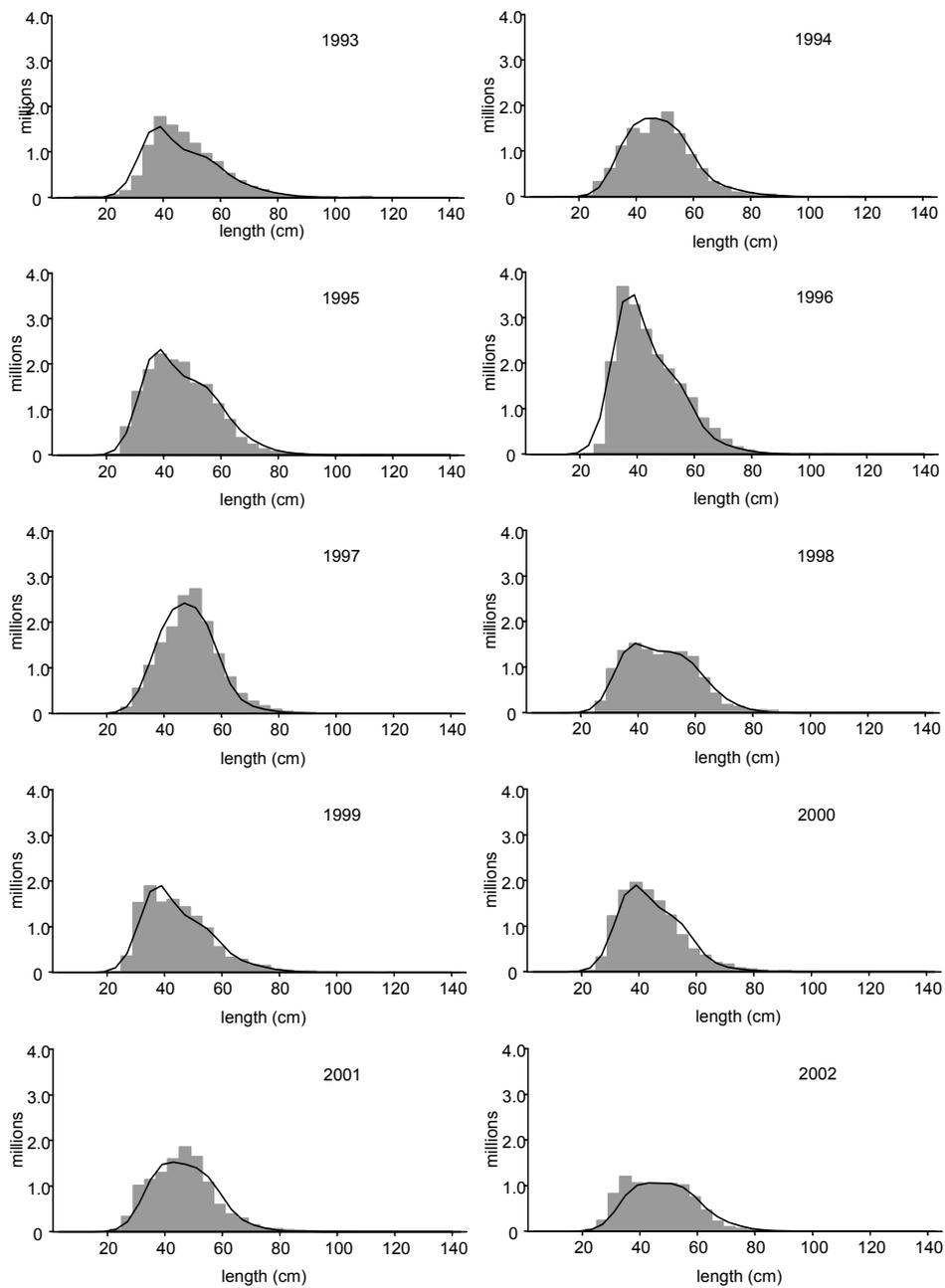
Short-term predictions can be run assuming geometric mean recruitment and *status quo* fishing mortality. The catch-at-length analysis is run forwards in time to produce predictions of landings, biomass and spawning stock biomass, applying various multipliers to the *status quo* fishing mortality.

For this stock ICES has proposed that the precautionary level for fishing mortality ( $F_{pa}$ ) should be 0.3, based on a fishing mortality at 35 % pristine SSB/R calculated at the Study Group on Biological Reference Points (ICES C.M. 2001/ACFM:11). No other reference points are proposed. Based on the short-term predictions from the 2002 Northern Shelf WG, a reduction of fishing mortality to below this level implies a reduction in TAC of around 60 % for the current year.

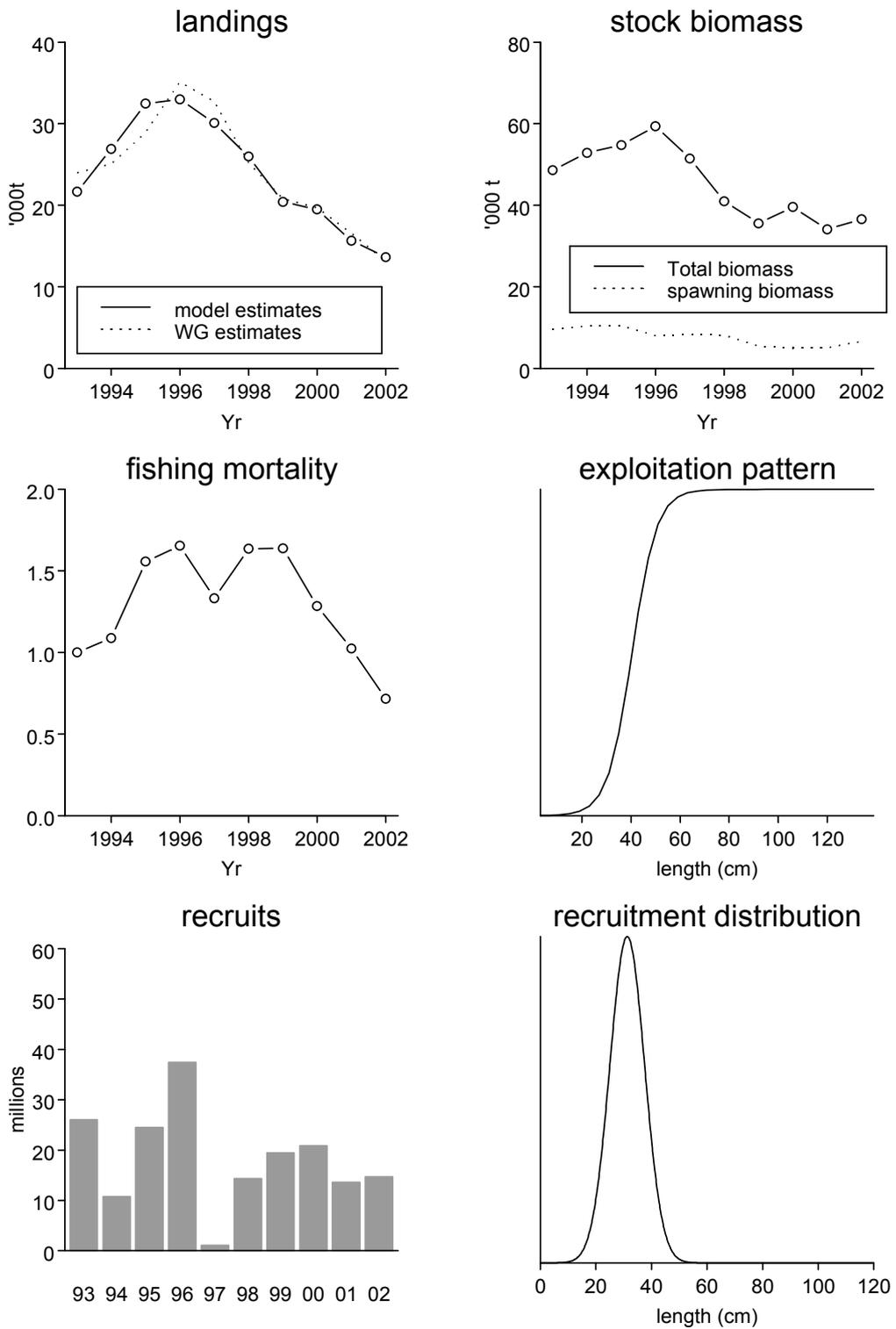
No medium-term predictions are carried out for this stock as it is considered that the time-series of data is too short to provide an adequate stock-recruitment relationship.

#### **4.2.7 Assessment considerations**

The Northern Shelf WG has previously attempted assessment of the anglerfish stock(s) within its remit using a number of different approaches. As yet, none have proved entirely satisfactory. The catch-at-length analysis presented here appears to address a number of the suspected problems with the data due to the rapid expansion of the fishery and previous inconsistencies in age readings. It also provides a satisfactory fit to the existing data.



**Figure 4.2.1** Anglerfish on the Northern Shelf (Subarea VI, the North Sea & Division IIIa). Raised catch-at-length frequency distributions (bars) compared to model estimates (lines).



**Figure 4.2.2**

Anglerfish on the Northern Shelf (Subarea VI, the North Sea & Division IIIa). Final run summary outputs from the catch-at-length analysis.

### 4.3 Gadget Haddock Model

Daniel Howell, IMR, Bergen, Norway

#### Abstract

Gadget is a flexible tool for running and optimising multispecies, multi-area age&length-structured model developed from the BORMICON and Fleksibest models (Stefánsson and Pálsson, 1997; Anon, 2002; Frøysa et. al. 2002). Included in the distribution of Gadget is a relatively simple single-species single-area annotated model for Icelandic haddock (*Melanogrammus aeglefinus*). This is intended both as a model in its own right, and as an introduction to Gadget and a template for creating new models (e.g. Section 3.2; 3.4; 4.4).

#### *Icelandic Haddock*

The haddock example is the most accessible of the various models currently available for Gadget. The model itself is relatively simple, with a single-species, one commercial fleet and one survey fleet, and running on a single area. The model does not contain any spawning-stock recruitment relationship, maturation, cannibalism, predation, or migration. All of these components can be included in a Gadget model, and may well result in a more realistic model and a better fit to the data. In the case of the haddock model they have been excluded in order to keep the model as simple as possible to serve as an introductory model to Gadget. In particular adding maturation and possibly weight loss at spawning would improve the modelling of growth, however this would require the stock to be split into mature and immature components, and this would increase the model complexity.

The model runs from 1978-1999 with data, and extends to 2006 as a prediction model. The 1978 start date allows for a long lead-in period before the 1990s, ensuring that the population structure during this period is entirely due to internal model dynamics.

This model is by far the best documented of the models available to run in Gadget. The model files have extensive comments within them describing the different entries, making them suitable for use in learning Gadget or as a template for generating new models. Further documentation is available on the Gadget web site at <http://www.hafro.is/gadget>, describing the file set-up and the equations used within the model. A mathematical description of model formulation is given in this report (Bogstad *et al.*, WD2).

Key features of the simulation model for Icelandic Haddock:

- Age&length structured
- 1978-1999 (2006)
- Quarterly time step
- Age 1-10+ (with ages 10 and older as a plus group)
- 1cm length classes
- Single-species, single-area model
- Von Bertalanffy mean growth, fitted beta-binomial for actual growth around this mean
- Fishing as direct subtraction from stock, not as a fishing mortality
- Recruits directly estimated each year

Data used to constrain the haddock model:

A single commercial fleet, and a single survey

- Mean length with variance: survey & catch
- Length distribution: survey & catch
- Age-length distribution: survey & catch
- Survey index: abundance by length

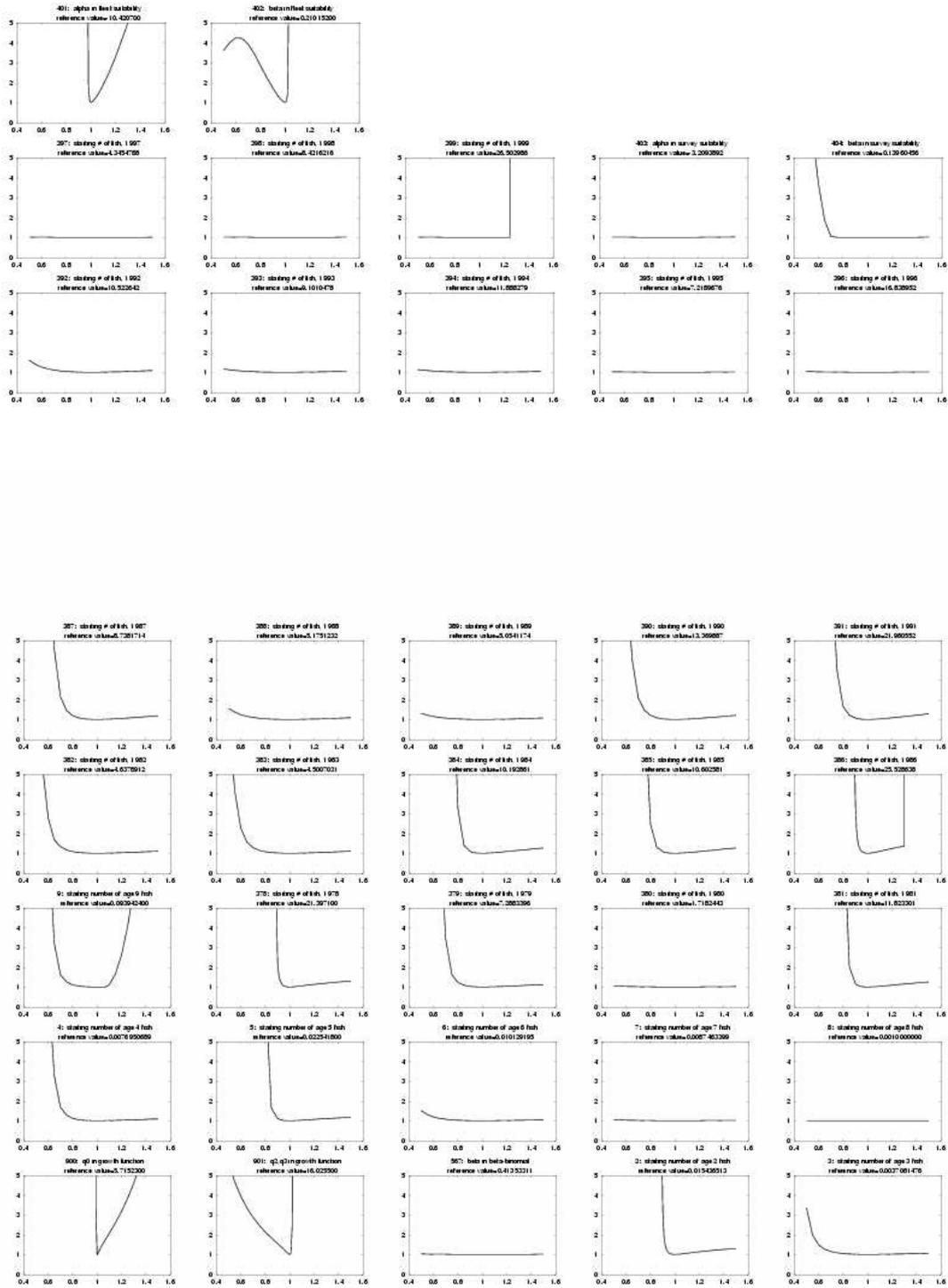
The default version of the haddock model is specified with a set of 37 input parameters (8 for initial population, 22 for annual recruitment, 3 for growth, 2 each for survey and fleet) already optimised to a 'good' solution. Scripts for running sensitivity analyses are included with the Gadget program. Results from a sensitivity analysis of the haddock model are presented in Figure 4.3.1. From this it can be seen that the model is highly sensitive to the mean growth parameters and the selectivity in the commercial fleet. The model is also sensitive to the number of recruits in large year classes.

Recruits in small year classes are poorly constrained within the model as they have little impact on the population. The number of recruits in the last few years of the model is also poorly constrained, as these individuals have not entered the fisheries by the end of the data series, creating uncertainty when trying to extend the model into the future. This also impacts on the stock biomass in the last year(s) making this unreliable unless the youngest fish are excluded from the output. Therefore spawning stock biomass is not affected by this uncertainty.

The distribution of sensitive and poorly-constrained parameters seen in the haddock example is a feature of all Gadget models. The same distribution is probably common to all age&length-structured models, as it is driven by the data and biological-processes rather than the model structure. The sensitivity analysis also indicates that a genuine optimum has been attained.

Gadget is capable of producing extensive output on the population dynamics. The haddock example is set to produce a range of output files on the age&length structure of the population, and give data on the modelled fishery. These are all explained in the on-line documentation and can be used as a template for other similar Gadget models. Examples of such Gadget outputs can be seen in Section 3.8.

Further information is available from <http://www.hafro.is/gadget> or from [gadgethelp@hafro.is](mailto:gadgethelp@hafro.is).



**Figure 4.3.1**

Sensitivity analysis of the Gadget haddock example. Each variable in turn has been varied stepwise by up to  $\pm 50\%$  from the calculated optimum, with all other variables being kept constant. The response of the likelihood function has been plotted for each variable. The value of the examined parameter at the optimum is shown above each graph. Vertical lines indicate cases where a pre-set bound has been reached during the sensitivity analysis.

## 4.4 An example of a multispecies Gadget model for the Celtic Sea

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### 4.4.1 Introduction

Gadget, the Globally applicable Area Dis-aggregated General Ecosystem Toolbox, has evolved from two existing age-length based modelling approaches, **Bormicon** and **Fleksibest**. Bormicon was originally developed by the Marine Research Institute, Iceland (Stefánsson and Pálsson, 1997), whilst Fleksibest was developed by the Institute of Marine Research, Norway (Frøysa *et al.*, 2002).

A major aim of the EU Framework V project DST<sup>2</sup>, is to develop models for the Celtic Sea, an area of continental shelf situated between France, Ireland and then UK. Until work began on the 'Celtic Sea case study', multispecies Gadget models had only been created for fish stocks around Iceland. The single-species version of Gadget (in the guise of Bormicon or Fleksibest) by contrast has been more widely applied and has proven particularly useful for species where it is difficult to obtain reliable age estimates, (e.g. *Sebastes marinus*, Björnsson and Sigurdsson 2003) or where there are large inter-annual variations in growth and thus size at age, (e.g. Northeast Arctic cod, Frøysa *et al.*, 2002).

It was hoped that a Celtic Sea model would provide a considerably different case study with which to test the multispecies Gadget formulation. The model itself could include more species and complex technical interactions and the available data is considerably different in comparison with the Icelandic or Norwegian situation. Fisheries in the Celtic Sea are international in nature, and consequently no one country possesses all of the data which would be necessary for a full and thorough assessment. ICES working groups frequently draw on data submitted by four or five countries.

DST2 has brought together scientists from France and the UK; fishery, survey, biological and habitat data have all been combined into a single 'data warehouse' with the aim that, in the future, Gadget input files will be automatically extracted in the required format.

Originally, it was hoped that a model might be developed which included nine stocks: cod, hake, haddock, whiting, monkfish, megrim, sole, plaice and *Nephrops*, chosen largely on the basis of their commercial importance. These species together represent around 49% of the total value of all Celtic Sea landings yet they account for only 17% of the tonnage landed and less than 3% of fish biomass in the system. Preliminary analyses of published stomach content data (in particular the studies of Du Buit 1982, 1992, 1995, 1996), revealed that biological interactions between the proposed species would be relatively weak and consequently that a multispecies formulation would prove of very limited value. 98% of predation by cod for example, focussed on species that would be outside of the proposed model. It was suggested (Anon. 2002) that the addition of pelagic fish species might introduce more interesting dynamics into the model, notably, 58% of all predation pressure on blue whiting *Micromesistius poutassou* was thought to be exerted by the nine 'selected species' and consequently the original short-list was broadened to include blue whiting, horse mackerel (54% of all landings) and mackerel (56% of fish biomass).

In the first instance it was decided that three single-species models would be developed in parallel (cod, whiting, blue whiting), and that these would be combined into a single multispecies model at a later stage. The models would cover the period 1984-1998, since French commercial data became somewhat problematical from 1999 onwards. Most of the commercial and fleet data used in the model covered the period 1991-1998, whilst UK survey data would extend over a 'lead-in' period (1984-1989), added to ensure that modelled populations between 1991-1998 reflected internal model dynamics and not the inputted initial population variables. The model would operate on a quarterly (seasonal) time-scale and cover ICES areas VIIe-k, the geographical unit used in most demersal stock assessments for the region.

### 4.4.2 Single-species Gadget models

All three single-species models were based heavily upon the 'haddock example' as described in Section 4.3. Two fleets were specified for each species, a commercial fleet and a survey fleet. For the cod and whiting models data included age-length keys for each fleet, length-distribution data for each fleet and mean length-at-age (and variance) data for each fleet. One major problem which became apparent was related to the lack of temporal detail in commercial catch data from each country operating in the Celtic Sea. ICES collate data for all counties on an annual basis. These annual international catches were distributed in proportion to the quarterly (seasonal) distribution of catches in the combined

French and UK database. A survey index based on UK spring-survey catches (for the period 1984-1998) was also utilised. Only survey stations in the central Celtic Sea were selected (see Trenkel *et al.*, submitted).

For cod and whiting models the following variables were estimated:

- Growth parameters (3) [2 controlling the mean, 1 controlling the beta binomial].
- Fleet selectivity parameters (4) [2 fleets, 2 parameters each]
- Initial population parameters (9) [ages 1-9]
- Recruitment estimates (15) [years 1984-1998]

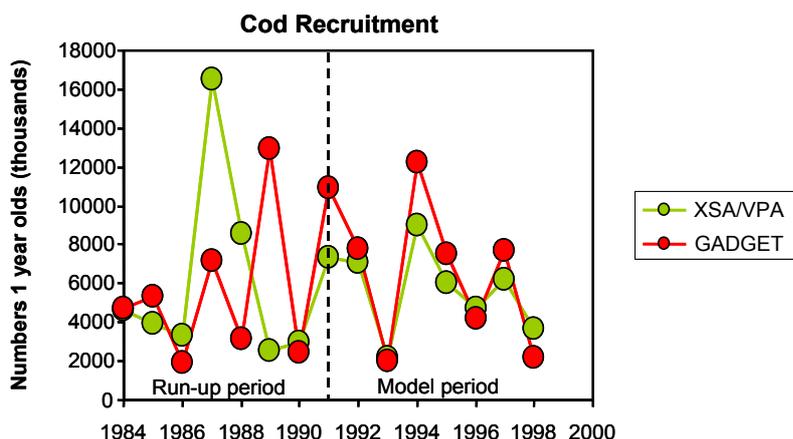
= 31 estimated parameters in each single-species model. Nine likelihood components were evaluated within each of the cod and whiting models.

The North Atlantic blue whiting *Micromesistius poutassou* stock is assessed by ICES over an enormous geographic range (ICES areas II, III, IV, V, VI, VII, VIIIc, IX). For the Celtic Sea model, we are only interested in the southernmost extremity of this stock, for which very limited data are available. Neither France nor the UK regularly collect age data for blue-whiting in the Celtic Sea, and thus in modelling this stock we were reliant upon data provided by Spain and Portugal.

For the blue-whiting model growth parameters were fixed at  $W_{\infty}=0.326$ ,  $K=0.151$ , since age-length keys were only available for the period 1994–1998. Length-distribution data were available (by quarter) in ICES working-group reports from 1989 onwards and from the UK spring survey (1984-1998). A survey index based on the UK spring trawl survey was also utilised, hence 6 likelihood components were implemented in this model.

#### 4.4.3 Results

Sensitivity analyses were performed on each single-species model (see section 4.3) to confirm that an optimum solution had been found. In some cases it was necessary to re-examine model settings, bounds or to re-optimize the model using more sensible starting values, before arriving at a final solution. Population estimates were then compared and contrasted with values reported by ICES working groups based on age-based methods (ICES working groups WGSSDS and WGNPBW). In general, age-based and Gadget estimates of recruitment and numbers-at-age coincided surprisingly well for cod and whiting (e.g. Fig. 4.4.1). For blue whiting, trends indicated by the two approaches coincided but there were no data which would allow us to ascertain if blue whiting numbers for the Celtic Sea sub-stock were sensible or not.



**Figure 4.4.1** Numbers of 1 year old cod in the Celtic Sea (ICES area VIIe-k) as estimated by age-length- (Gadget) and age-based (XSA/VPA) methods.

#### 4.4.4 Towards a multispecies Gadget model

In order to link single-species models together in terms of predators and prey it was necessary to establish the availability of stomach content data for the region. French data on 7 species were available spanning 1977-1988, sampled from commercial trawlers. UK stomach data were available for 66 predator species, spanning 1990-1994, collected during annual research cruises. A total of 26,539 prey items were recorded from 18,129 predator stomachs

(Pinnegar *et al.* submitted), although of these, only 1691 records related to cod and 1749 related to whiting as predators. Additional data were available relating predator length to prey length, and these plots (see Pinnegar *et al.* submitted) were used to establish length-based suitability patterns. A logistic suitability function was chosen (Stefánsson and Pálsson, 1997) and the required parameters were established externally, according to the fit with observed data.

The function which describes a predator's consumption in Gadget has been outlined by Bogstad *et al.* (WD2), and closely follows the way that predation by cod was characterised in MULTSPEC for the Barents Sea (Bogstad *et al.* 1997). In cod the maximum consumption as a function of predator length ( $C_{\max}$ ) was based on the values reported by Bogstad *et al.* (1997) but originally taken from the laboratory studies of Jobling (1988). It was assumed that cod can eat a maximum of 5 times their own body weight in a given year, i.e. 1.25 times their own body weight in any given quarter.

To date only the cod and whiting models have been joined by predation linkages. In this first tentative attempt at a multispecies model the 'half-value' (the food abundance at which cod eats half of maximum consumption) was set at zero, hence food consumption by cod was treated as being independent of food availability in the environment (Bogstad *et al.*, WD2). Sufficient 'other-food' in the current model is always available, and thus the predator can always obtain the food it needs (i.e.  $\Psi = 1$ ).

It was assumed on the basis of stomach content data, that approximately 5% of cod diet consists of whiting. In order to establish a density estimate for 'other food' we examined biomass estimates from a preliminary run of the single-species whiting model (as well as values reported in the ICES Southern Shelf Working Group report, ICES C. M. 2003/ACFM:03). We then assumed that 'otherfood' would be about 20 times more abundant (i.e. whiting is 5% of the diet), and hence the abundance of 'otherfood' was set at  $\sim 1 \times 10^8$  kg. No relative preference was assumed between 'otherfood' and whiting.

It is hoped that with the forthcoming addition of the blue whiting model, more complex predation dynamics will be investigated since both cod and whiting consume considerable amounts of this prey species. Similarly hake *Merluccius merluccius* eat large quantities of blue whiting in the Celtic Sea (Du Buit, 1996), and hence this species would be a logical candidate for inclusion should the model be expanded further in the future.

#### 4.4.5 Conclusions and summary

- Single-species models for cod, whiting and blue whiting are giving 'sensible' values and seem to be at an 'optimum'.
- Cod and whiting models have been joined together (in terms of predation but not technical interactions), but blue whiting has not yet been added.
- This is the first documented attempt at a fully multispecies Gadget model outside of Icelandic waters.
- All necessary data from France and the UK has been entered into a DST<sup>2</sup> data warehouse with the aim of using automatic extraction processes to create new single-species Gadget models, e.g. for hake and/or megrim (*Lepidorhombus whiffiagonis*).

## 5 CONCLUSIONS AND RECOMMENDATIONS

### 5.1 Conclusions

#### 5.1.1 Work in progress

There is a considerable amount of modelling work currently in progress throughout the world, using either age-length models or processes relevant to age-length models. At present communication between different modellers is limited. Scientists working in different working groups within ICES do not always collaborate as well as they should, and links between ICES countries and non-ICES countries are not well developed. As a result effort can be duplicated, and uptake of potential advances can be hindered because they do not have a sufficiently high profile.

Age-length models provide a flexible structure that can be used to investigate new process sub-models. For many processes there is no other model structure which can provide the detailed dynamics required by the process sub-model (e.g. the maturation process, Section 3.7). Conversely, new process sub-models may easily be incorporated into age-length models, and can provide a valuable improvement in the overall model performance. Furthermore, many other extensions in complexity (e.g. multi-area, technical interactions, length-dependent predation) may require age-length models.

Age-length models provide a different class of models to purely age- or length-based models, with different underlying assumptions. Age-length models can therefore be used to provide an independent tool to model real-world data, and thus a comparison to existing alternative models. In comparisons, age-length-based models may identify process error in the simpler models. As a result lessons derived from age-length based modelling exercises may be of use in improving the simpler models, or it may become apparent that it is necessary to switch to the more complex formulation.

### **5.1.2 Opposition to age-length-structured models**

There is often considerable inertia to accepting new assessment methods, both by individual scientists and by bodies such as ICES. This is partially due to the inherent complexity of more sophisticated models. However it can be exacerbated by a lack of documentation, difficulty in constructing, running and interpreting the model, and a possible over-confidence in existing, familiar, models. Where there is no current accepted assessment methodology there may be a greater acceptance of new models than in situations with a long history of using conventional tools.

A good case for the implementation of age-length based models can be made in cases where existing methods are known to have problems (such as where length-dependent selectivity cannot be adequately modelled as a function of age). It would therefore be sensible to identify a number of such stocks and implement existing age-length models in these cases. Where an age- or length-based model is replaced with an age-length-based model it would be valuable to conduct a comparison between the two different approaches. As well as simply comparing the final fit to the data of both models a more thorough investigation could be attempted to identify the relative improvements gained from each component of the age-length-structured model.

One reason for not employing age-length models is a lack of knowledge of the amount of work that such a process would entail. It would therefore be valuable to conduct a study to identify the cost (in time and/or money) involved in this transition. This could be coupled with comparison between different model types to produce an indication of the costs and benefits involved in this transition.

### **5.1.3 Artefacts in the modelled population**

There is a need to produce models which, as far as possible, avoid introducing any modelling artefacts into the modelled population. Artefacts can arise from the choice of discretisation scheme within the model, and from a failure to reach the true, optimal, solution. In order to model continuous processes (e.g. length and time) it is necessary to split them into discrete intervals. This discretisation process will inevitably introduce errors into the model. It is therefore vital to ensure that these errors are understood and kept to a minimum, and do not significantly impact on the validity of the modelled population structure.

An important part of any modelling process is selecting parameter values which produce the closest fit to the available data. This is typically automated using one or more optimisation routines. For complex models with a large number of parameters (such as age-length models) this optimisation process can become difficult. It is therefore important to select an appropriate optimiser which can arrive at an optimal solution accurately and rapidly. It is also important to ensure that the selected optimiser is used appropriately in any given situation. Once the optimiser has arrived at a 'solution' it is important to verify that a genuine and realistic solution has been reached. This can be approached in several ways. A sensitivity analysis can indicate that an optimum solution may have been reached, while examination of the realism of the resulting modelled population is also important. It would also be worthwhile to investigate numerical techniques for establishing if the selected point is actually an optimum.

### **5.1.4 Statistical issues**

More complex models require more complex description of error structures in the data. Variance-covariance estimation techniques require further development. These are limited by the run-time of the models and optimisation process, which limit the number of replications that can be conducted. Nevertheless techniques such as bootstrapping, estimation of the Hessian matrix or Bayesian analysis can be applied.

Weighting of different data sources is a problem for all models, not just age-length models. It is thus an issue that requires a more general approach. At present *ad hoc* methods are often used to produce relative weightings between different data sets, however a more rigorous statistical approach may well prove beneficial.

### 5.1.5 Data

Complex models (e.g. age-length, multispecies, multi-area) require large quantities of high quality dis-aggregated data. Even when these data are available they are rarely in an easily accessible form, and unnecessary time is spent on data collation and formatting from existing databases. Data quality is vital to all modelling studies, thus effort needs to be spent to ensure that data are collected and made available in the quantity and quality required. It is also the case that modelling studies can sometimes be limited by the difficulty in sharing data across national boundaries, even where multiple countries are fishing the same stocks.

### 5.1.6 Software issues and diagnostics

In order to be widely used and accepted, complex models must be presented in the most accessible and comprehensible form possible. This includes the ease of constructing and running the model and obtaining diagnostics and model output. The quality of the underlying documentation and support for the modelling tool (e.g. Gadget) is also of critical importance.

Age-length models can be quite computationally intensive, which combined with current computer technologies, constrains the possible uses of these models. Certain statistical approaches (e.g. those involving iteration or re-sampling) become extremely time-consuming, and even simple optimisations can become problematic in the context of a working group. Although this will be resolved to some extent as computation power increases, it is worth placing emphasis on increasing the speed of the model code, and possibly using multiple processors or machines to speed up run time.

An important part of any modelling exercise is to observe the model output, and compare model results to real-world data. Because of the inherent complexity of age-length-based models it is important to provide tools capable of doing this in the most comprehensive and user-friendly manner possible. This is especially important for models intended for use in a working group context.

Differences between Operating Systems have proved to be a significant, if unexpected, obstacle to the uptake of certain models. In addition to the problems encountered of trying to run a program written for one OS on another, there is a cultural difference between users of different systems. In particular the command line format of many traditional UNIX programs has proved to be unpopular with PC users. Implementation of a graphical user interface would alleviate this cultural problem, by hiding many of the differences from the researcher. Such an interface would also greatly increase the ease of use of the model, and diagnostic tools.

## 5.2 Recommendations

### *General Recommendations*

- Investigate work being carried out on length- and age-length-based models globally, including common problems encountered and useful solutions.
- Develop user-friendly interfaces for running models, producing diagnostics, analysing model results and handling/preparing data. Provide detailed documentation (mathematical description and user instructions) and support for existing models. Ensure that a standard version of the tool is available.
- Identify through literature studies, stocks where an age-length based model is likely to be more appropriate than existing methods, and develop a test case.
- Increase the number of ICES stocks for which age-based and age-length-based assessments are conducted in parallel and compared. Investigate the additional time and resources required to move to an age-length based assessment.

### *Specific Recommendations*

- For different optimisers, examine the mathematical description and compare performance.
- Investigate methodologies for assigning appropriate weights to different data sources.
- For existing age-length models improve diagnostics. These need to be useful, informative, easy to use, easy to interpret, and include output comparable to existing diagnostics for standard assessment methods.
- Artefacts (modelling and computational): identify and examine the errors introduced, for example by the discretisation (in time and size) of continuous processes.
- Develop and promote a commonly accessible repository for fine-scale (time and space) quality-controlled data, in a standard format.

Existing age-length structured models could easily be extended to include process-based formulations where growth, maturity and fecundity depend on fish age, length and weight. The utility of such models for projection should be considered by SGGROMAT at its January 2004 meeting.

### 5.3 Second Study Group Meeting

It remains valuable to have a forum for studying length- and age-length structured models outside the ICES Working Group on Methods on Fish Stock Assessment (WGMG), because there are several modelling issues for such methods, which do not apply to age-structured models.

The SGASAM recommends that the Resource Management Committee makes the following recommendation:

The Study Group on Age-Length Structured Assessment Models (SGASAM) (Chair: ) should meet again at a location to be decided for 5 days in late 2004 to:

- Review developments in methodologies and applications of length- and age-length structured population models in ICES areas and elsewhere, and provide a forum for dissemination of information regarding these methods
- Investigate the feasibility of incorporating process-based growth, maturity, condition and fecundity models into existing model frameworks [ref. ToR b) for the January 2004 SGGROMAT meeting]
- Evaluate the utility of age-length structured modelling frameworks for investigating the performance of models with different levels of complexity
- Identify stocks where an age-length based model is likely to be more appropriate than existing methods, and develop test cases.

### 5.4 Acknowledgements

The work on Fleksibest has been partly funded by the Research Council of Norway (Project No. 130197/130).

Current funding for the development of Gadget and Fleksibest has come from the EU project "Development of Structurally Detailed Statistically Testable Models of Marine Populations" (known as DST<sup>2</sup>, QLK5-CT1999-01609).

The work described by Davies *et al.* and Gilbert *et al.* in section 3.3 and 3.6 was funded by the New Zealand Ministry of Fisheries contract SNA2000/01.

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## APPENDIX 1

Working document 1.SGASAM

3-6 June 2003 Bergen

Not to be cited without prior reference to the authors

### A preliminary analysis of the impact of the growth process discretisation

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#### Introduction

Age-structured models have shown their limits in stock assessment and predictions of population abundance. Several reasons for this have been pointed out. The most common is the deficiencies in the data required to fit the model. For instance, the difficulties in determining the age at length result in uncertainty in catches-at-age. Moreover the aging techniques are very expensive and so few fishes can be aged, increasing even more the sampling error and variability in the age-length key. Another source of uncertainty is the size-dependant selectivity function which is not explicitly taken into account in this kind of model. The large variations in size within an age class could thus result in incorrect estimates of fishing mortality by age. Consequently, length-structured models have undergone considerable development in recent years. The required catch data to fit this kind of model are catches at length. The selectivity can be explicitly modelled as a function of size. Hake (*Merluccius merluccius*) is a typical species for which an age-structured model appears to be inappropriate for estimating inter-annual variations of abundance. It is also a species which needs rapid and efficient management measures to limit the over-exploitation. Marine protected areas may be a possible solution, but this requires that the spatial characteristics of the population dynamics are known. We are therefore developing a spatial and length-structured population model for hake in the Celtic sea and the bay of Biscay, using a maximum likelihood method. This model is fitted to commercial data (landings, effort, discards,...) and to scientific data (index of abundance, marking-recapture, ...). The maximum likelihood method estimates jointly all the parameters given an assumption of the error distribution. Consequently, confidence intervals on the fitted variables can be estimated. The method of estimation allows us to test the relevance of a more complex model using statistical criteria to compare the fit of the models. For instance, the value of adding the spatial dimension or the suitability of the spatial or temporal dimension of the model can be analysed. Nevertheless, great caution needs to be taken in the choice of the maximisation algorithm and the starting values to be sure that the optimum estimated is a feasible solution. In developing our model we used ADMModel Builder, a generic and efficient tool for constructing and optimising non-linear models.

As with all models in discrete time which describe continuous dynamics, the discretisation can lead to modelling artefacts. These artifacts can impact both the parameter estimation and the simulations. In this document, we focus on the impact of the discretisation of both the length range of the population and the discretisation of the growth process in a length-structured approach. The continuous measure of the fish size is decomposed into a finite number of length classes and several construction schemes can be considered. In the same way, the continuous process of growth needs to be discretised into growth increments which can be modelled using different distributions. We will describe different approaches for constructing the length classes and the usual models considered for growth increments. The impact of these choices on the growth matrix and the distribution of the population at several time steps will be presented. The purpose of this study is to identify some critical points in the discretisation of a continuous process and to give some elements to start a discussion.

#### A spatial length-structured population model

A matrix formulation of a model in discrete time has been derived to describe the population dynamics of hake. The sequence of events in the population life cycle imposed at each time step is as follows: first each length class of the population can grow, then migrate, then recruit, and finally undergo fishing and natural mortality. The abundance in number at time  $t+1$  is given by the following equation:

$$N(t+1) = Sr(t)[R(t) + M(t)G(t)N(t)]$$

**N(t)** : vector of abundance per class and per area at time  $t$ ,

**Sr(t)** : survival rate at time  $t$ ,

**M(t)** : matrix of migration coefficients between areas,

## G(t) : matrix of probabilities of transition between length classes

The survival rate is calculated using a fishing mortality rate per fleet characterized by a selectivity factor:  $F(\text{fleet},t)=s(\text{fleet})q(t)E(\text{fleet},t)$ .

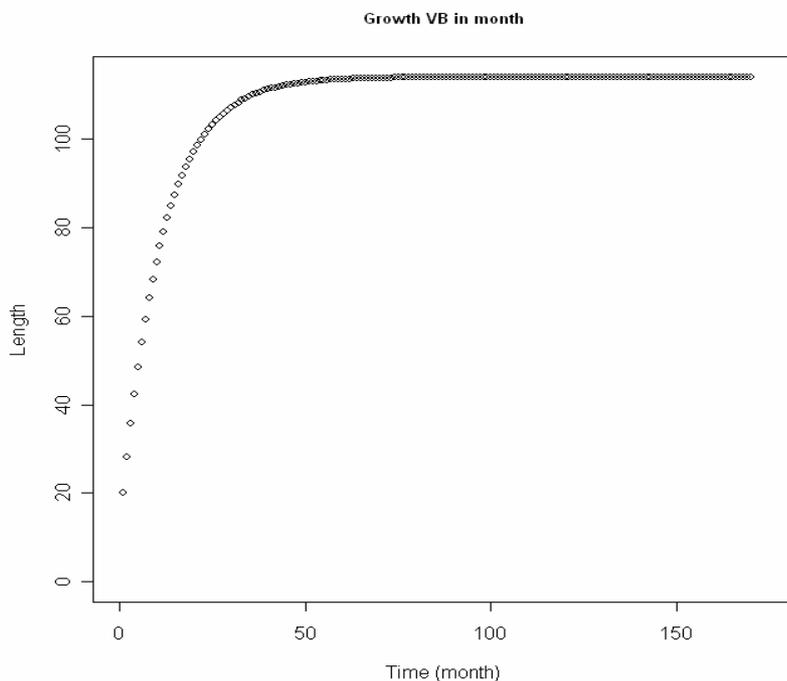
### Growth function

For the specific case of hake, we used a Von Bertalanffy growth function, but more general growth functions can be considered as polynomial, Gompertz, Verhulst, Richards, Schnute,...(Schnute, 1981).

The Von Bertalanffy function is parameterized by the three parameters  $L_\infty$ ,  $K$  and  $T_0$ ,  $l=L_\infty(1-\exp(-K(t-T_0)))$ .

The growth increment for a fish of size  $l$  during  $\Delta t$  is given by the following equation  $\overline{\Delta l}=(L_\infty-l)(1-\exp(-K\Delta t))$ .

Figure1 shows the Von Bertalanffy growth function used in this study ( $L_\infty=114$ ,  $K=0.09$  and  $T_0=-1.16$ ).



**Figure 1:** The shape of the von Bertalanffy function is defined by the following parameters ( $L_\infty=114$ ,  $K=0.09$  and  $T_0=-1.16$ ). The time is in month and the length is in cm.

### Length class definition

In contrast to stage-structured models, which take advantage of the natural biological divisions of the life cycle, size-structured models require a more artificial construction of a set of size classes. The discretisation of population length is not trivial; The more length classes employed, the more parameters that must be estimated. Therefore the number of classes should be kept to a minimum. But on the other hand, fewer classes result in more heterogeneity within each class. Moreover the choice of these categories can produce modelling artefacts and impact the parameter estimation in the model. Several ways of constructing classes can be considered:

- classes of equal width in length
- classes of equal width in staying time
- classes of unequal width defined by the user
- classes associated to biological divisions of the life cycle
- classes resulting from an optimisation of a specific criteria

The first type of length class construction is the most common in the literature (Sullivan 1990; DeLeo *et al* 1995; DeLong *et al* 1998; Smith *et al.* 1998; Frøysa *et al* 2002). We have not found any application with the second or third types. The fourth method is usually employed in stage-structured models. This requires that knowledge about the relationship between life cycle and size be available in order to use a length-structured approach. Vandermeer (1978) proposed an algorithm based on the minimization of the sum of two errors, called sampling error and distribution error, which has been improved by Moloney (1986). Some details on this algorithm are given in the annex. But this approach has several drawbacks. First it requires data on individual growth (tagged fish, captive studies, good backcalculation of age at length). Classes are constructed taking into account only the departure class and not the possible arrival classes, modelling the probability of staying in the departure class. Moreover, it does not take into account the temporal variability in growth (the discrepancy is minimized to a mean value over the period) and the errors are calculated independently for each class without considering the errors of the previous classes.

### **Growth increment model**

Many population models describe the population growth processes using a mean growth: the growth in each length class is supposed to be equal to the growth at the midpoint. Such models could produce large errors in growth rates. It is largely accepted that individual variability in growth needs to be taken into account to improve assessments. Several methods exist to estimate this variability. The most popular is the back-calculation of length-at-age using information contained in fish hard parts. The main drawback of this approach is the imprecise results due to difficulties in detecting the increment in this part. The second way is the tagging survey. This approach is very expensive and many fishes have to be tagged in order to be successful. A survey for tagging young hake in the bay of Biscay has recently been initiated. Preliminary data appear promising and should give results in several years. Finally captive studies can be used. However their results could be questioned given the differences in life conditions between captivity and the ocean.

At this time, the lack of data constrains us to make assumptions on the variability in growth. Two approaches are classically considered to model the variability in growth, calculate growth increments for each class and then fill each row of the growth matrix. The most common model is a mean growth by length class given by the growth function and a stochastic distribution for individual variability around the mean (Sullivan 1990; DeLeo *et al* 1995; Cruywagen 1997; DeLong *et al* 1998; Frøysa *et al* 2002 ). Another way to describe growth variability is to integrate directly individual variability in the growth function with stochastic parameters (Sainsbury 1980; Smith *et al* 1998a; Smith *et al* 1998b; Pilling *et al* 2002). The correlation between the two parameters  $L_{\infty}$ ,  $K$  of the Von Bertalanffy function represents a major difficulty for this type of model; and no general solution has yet been proposed. In this document we focus on the first approach and more particularly on the uniform distribution, the beta-binomial and the gamma distribution for the stochastic distribution

### **Uniform Distribution**

This distribution is the simplest way to describe the growth of fishes from a particular class taking into account their actual length rather than just the length of the midpoint of their class. Fishes in a given length class are supposed to be uniformly distributed within the class and their final length is larger than the final length of fish at the lower bound of the class and lower than the final length of fish at upper bound. We call this interval (i.e. the image of the departure class by the growth function) the image class. Then the accessible classes from this class are the classes between the arrival class of the lower bound and the arrival class of the upper bound. The probability of transition from a given class to an accessible class is calculated by the length of the intersection of the accessible class with the image class, divided by the width of the image class.

### **Beta-binomial distribution**

The beta-binomial is an extension of the binomial distribution whose parameter is assumed to follow a beta distribution. The traditional binomial distribution with one parameter is useful when only one source of variation is in the data. To describe a multivariate data set, known as overdispersion, the most popular distribution is the beta-binomial (Ennis *et al.* 1998) described by two parameters. If  $X$  denotes the random variable counting the number of choices,  $x$ , of a particular type from a maximum of  $n$

$$X \sim BB(n, \alpha, \beta)$$

$$P(X=x) \sim \binom{n}{x} \frac{\Gamma(\alpha+x)\Gamma(\beta+n-x)\Gamma(\alpha+\beta)}{\Gamma(\alpha+\beta+n)\Gamma(\beta)\Gamma(\alpha)}$$

where the gamma function is defined by  $\Gamma(x) = \int_0^{\infty} \exp(-u)u^{x-1}du$ .

When  $x$  is an integer,  $\Gamma(x) = (x-1)!$

The mean of a beta-binomial distribution is

$$E[X] \sim n \frac{\alpha}{\alpha + \beta}$$

and the variance is

$$V[X] \sim n \frac{\alpha\beta}{(\alpha + \beta)^2} \left( 1 + \frac{n-1}{1 + \alpha + \beta} \right)$$

The beta-binomial distribution can be used to model the growth increments. Then, for each length class, the variable  $X$  counts the number of classes jumped during one time step,  $n$  stands for the number of accessible classes. The mean growth of a fish in this class is supposed to be the growth increment of the midpoint of the class calculated by the growth function. Parameters  $\alpha$  and  $\beta$  modify the shape and the scale of the variability around the mean growth.

Such modelling of growth assumes that the mean growth of a length class is calculated in number of classes. The method used to calculate the mean growth is described by the following algorithm for each class:

1. calculate the growth of the midpoint using the growth function during one time step
2. calculate the associated number of classes jumped by the midpoint
3. calculate the proportion of length against the width of the class reached by the midpoint
4. the mean growth is then equal to the sum of the two previous values (2. + 3.)

### Gamma

The Gamma distribution is a two-parameter distribution, entirely defined by its two first moments. It is largely used in modelling thanks to its flexibility in describing many function forms. More specifically, it can describe growth for small and large fish. Let  $X$  denote the random variable equal to the growth increment during a time step. If  $X$  has a gamma distribution  $G(\alpha, \beta)$ , its density function is  $f(x) = \frac{1}{\beta^\alpha} x^{\alpha-1} \exp(-x/\beta)$  and its mean and variance are respectively

equal to  $E[X] = \frac{\alpha}{\beta}$  and  $V[X] = \frac{\alpha}{\beta^2}$ .

If fishes are assumed to be at the midpoint of the departure class  $i$ , denoted  $m_i$ , then the probability of transition to class  $j$  is given by the following single integral:

$$g_{ij} = \int_{\text{lowerBound } j-m_i}^{\text{upperBound } j-m_i} f_i(x) dx$$

If fishes are assumed to be uniformly distributed within the departure class  $i$ , then value of the following double integral is the probability of transition from class  $i$  to class  $j$ :

$$g_{ij} = \int_{\text{lowerBound } i}^{\text{upperBound } i} \int_{\text{lowerBound } j-y}^{\text{upperBound } j-y} f_i(x) dx dy$$

The use of a Gamma model with a single integral is the most widely choice to describe growth variability (Sullivan 1990; DeLong *et al* 1998).

## Simulations

The code to run the simulations has been written in C++ using ADModel Builder libraries (Otter Research Ltd. 2000). First we construct the length classes, either with an equal width in time (3 months) or with an equal width in length (5cm or 10cm). Then for each kind of length class, we observed the shape of the growth increment distribution for the uniform distribution, the beta-binomial distribution and the gamma distribution with both the single and double integral. Finally we simulate the growth of the first class of a population growing according to the Von Bertalanffy function described above without any mortality, for each cell of the Table 1. The beta parameter of the beta-binomial distribution was set such that the variance of the beta-binomial distribution is equal to the variance of a gamma distribution with a beta parameter equal to 1. The alpha parameter of both distributions is set according to the mean growth.

	Delta t = 3months	Delta l = 5cm	Delta l = 10cm
Uniform	(Figure 2 column 1) (Figure 6 up and left)	(Figure 2 column 2) (Figure 7 up and left)	(Figure 2 column 3) (Figure 8 up and left)
BetaBin	(Figure 3 column 1) (Figure 6 up and right)	(Figure 3 column 2) (Figure 7 up and right)	(Figure 3 column 3) (Figure 8 up and right)
Gamma 1	(Figure 4 column 1) (Figure 6 down and left)	(Figure 4 column 2) (Figure 7 down and left)	(Figure 4 column 3) (Figure 8 down and left)
Gamma 2	(Figure 5 column 1) (Figure 6 down and right)	(Figure 5 column 2) (Figure 7down and right)	(Figure 5 column 3) (Figure 8 down and right)

**Table 1:** For each scheme of length class construction (columns) and each growth increment distribution (rows) the list of the figures illustrating the growth matrix and the simulation of the first class of the population is given.

Differences in the length classes can be observed in Figures 2, 3, 4 and 5. Whatever the growth increment model is, length classes of width equal in time seem to induce a larger number of reachable classes (probability of transition not null) than other length class types. Given the quick growth at the beginning of the life, this scheme of length-class construction results larger the first classes and so more heterogeneous in length than the last ones. For instance fishes of initial size between 0cm and ~26cm can grow up to (Vandermeer, 1978) a size of ~84.4cm during one time step (Figure 3 column 1). At this stage of the analysis, it would be interesting to measure sampling and distribution errors induced by the choice of the scheme of construction to have a quantitative criteria of selection among these choice. However such an analysis has not yet been carried out.

Regarding the growth increment distribution, Figures 6, 7 and 8 show differences for each scheme of length-class construction. The uniform distribution and the gamma distribution with the double integral are very similar. These two distributions make the same assumption on the position of fishes in the departure class. The beta-binomial distribution has a more widely spread distribution as expected given its overdispersion characteristic. The choice of a gamma distribution with a single integral results a slower arrival in the last class.

It would be useful to find a metric to quantify the differences between the different models of growth increment variability. One approach may be to use a  $\text{Chi}^2$ .

Finally, after these preliminary simulations, it should be noted that great caution needs to be taken not only in the choice of the scheme of length class construction but also in the model of growth increments.

The program is sufficiently generic that different schemes of length-class construction can be simulated. The next step will be the simulation of the construction of length classes using the algorithm of Vandermeer, and also the simulation of a stochastic Von Bertalanffy growth function where the parameter  $L_{\infty}$  has a normal distribution and the parameter  $K$  has a gamma distribution. Finally, we would like to quantify the impact of these choices of discretisation on the parameter estimation using a simulated data set.

### Annex : more details on the Algorithm of Vandermeer.

- Criteria= minimize the sum of two kinds of error
- Sampling error (i.e. not enough fishes to estimate the heterogeneity within a class)
- Distribution error (i.e. classes are considered homogeneous despite their heterogeneity in length and growth)

## Notations

I fishes measured at  $t=1, \dots, T$  and length classe  $C = [C_{min}, C_{max}]$

$m_i(t)$  : length of the  $i$ th fish at  $t$

$d_i(t) = m_i(t+1) - m_i(t)$  : growth increment

If the  $i$ th fish starts from  $C$

$S_i(t) = 1$  if  $m_i(t)$  is in  $C$  and  $0$  otherwise

If the  $i$ th fish stays in  $C$

$R_i(t) = 1$  if  $m_i(t)$  is in  $C$  and  $m_i(t+1)$  is in  $C$  and  $0$  otherwise

The average probability of staying in  $C$  during the time interval  $[1, T]$  is :

$$P = \frac{\sum_t \sum_i R_i(t)}{\sum_t \sum_i S_i(t)}$$

Calculus of the Distribution Error (ED) :

If there is no distribution error,  $P$  is independent of the size of the fishes in  $C$  at  $t$ . Assuming all the fishes have a size equal to the middle length of the class,  $m_i(t) = (C_{max} - C_{min})/2$  for each  $i$  and so a size at  $t+1$  equal to  $m_i(t+1) = (C_{max} - C_{min})/2 + d_i(t)$ , the probability of staying in  $C$  at time  $t$  is

$$P^*(t) = \frac{\sum_i R_i(t)}{\sum_i S_i(t)}$$

The Distribution error is defined by the mean sum of square of the discrepancy between  $P^*(t)$  and  $P$  and also between  $(1 - P^*(t))$  and  $(1 - P)$

$$ED = \frac{1}{T-1} \sum_t \frac{1}{2} \left( \left( \frac{P^*(t) - P}{P} \right)^2 + \left( \frac{P^*(t) - P}{1 - P} \right)^2 \right)$$

Calculus of the sampling Error (EE)

Let us consider the fishes in  $C$  at  $t$  ( $S_i(t) = 1$ ).  $K$  samples of size  $N$  are constructed by drawing with replacements among these fishes. Keeping the same notations as above, for each individual (denoted  $i$ ) in  $C$  at  $t$ ,  $R_i^k(t)$  is equal to  $1$  if the  $i$ th individual is still in  $C$  at  $t+1$ . Then the probability of staying in  $C$  at  $t$  for the  $k$ th sample is:

$$P^k(t) = \frac{\sum_i R_i^k(t)}{K}$$

The sampling error is defined by the mean sum of square of the discrepancy between  $P^k(t)$  and  $P$  and between  $(1 - P^k(t))$  and  $(1 - P)$

$$EE = \frac{1}{K(T-1)} \sum_t \sum_k \frac{1}{2} \left( \left( \frac{P^k(t) - P}{P} \right)^2 + \left( \frac{P^k(t) - P}{1 - P} \right)^2 \right)$$

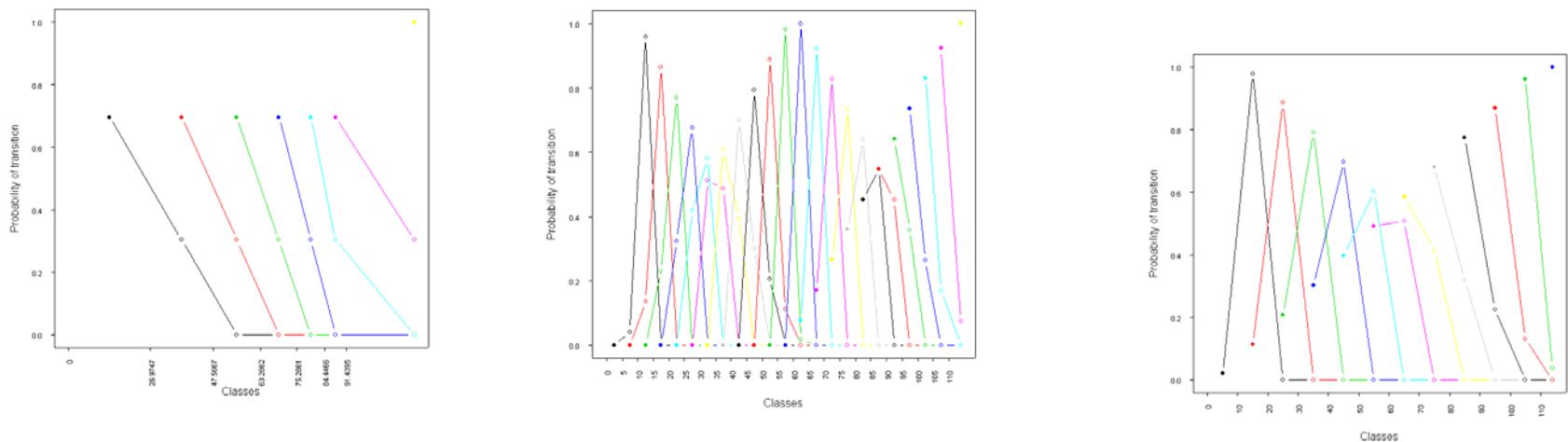
**Algorithm**

$j=0$ . The lower bound of the first class is set to  $C_{\min}(0) = C_{\min}$  and  $C_{\max}(0)$  is calculated such that  $EE+ED$  is minimized;

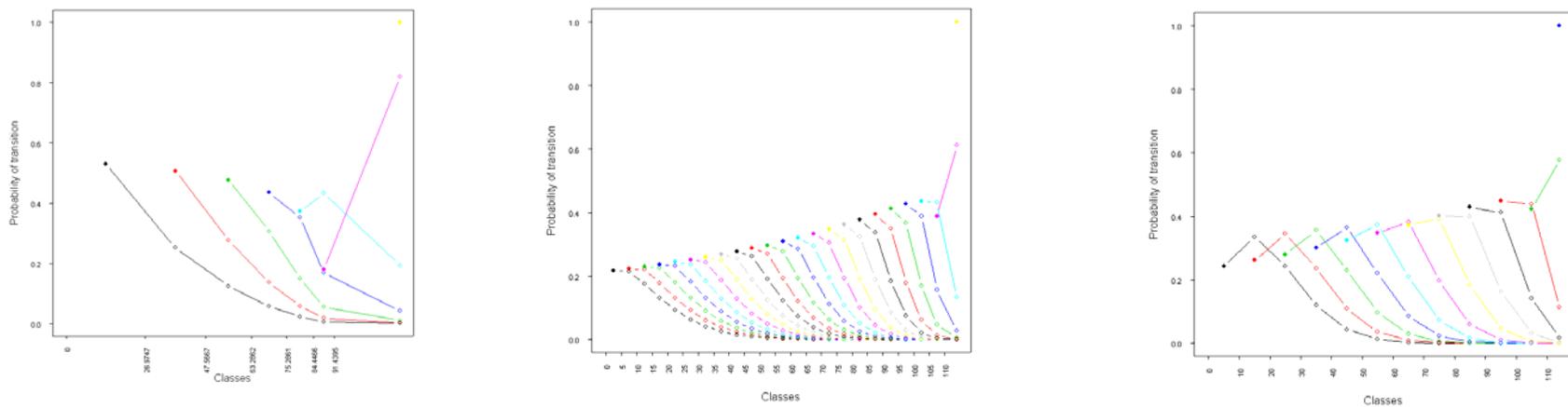
while  $C_{\max}(j) < C_{\max}$

$C_{\min}(j+1)=C_{\max}(j)$  and  $C_{\max}(j+1)$  is obtained by minimizing  $EE+ED$  ;

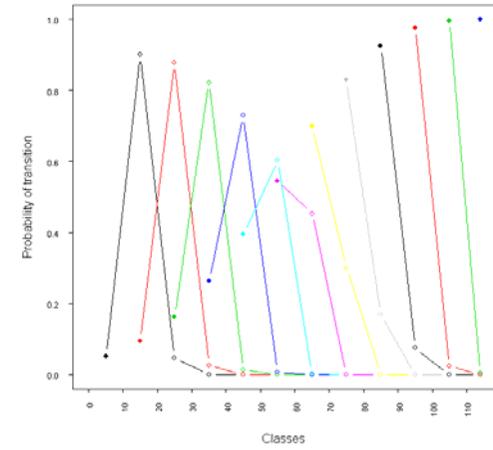
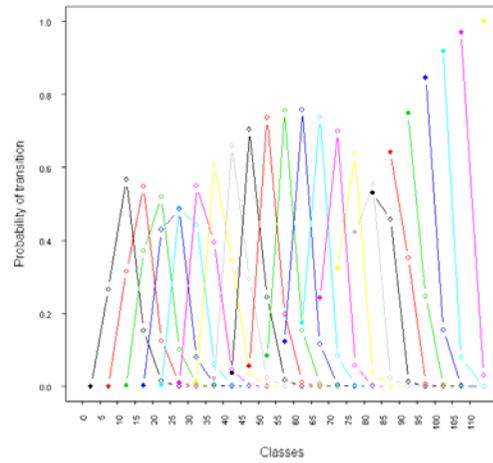
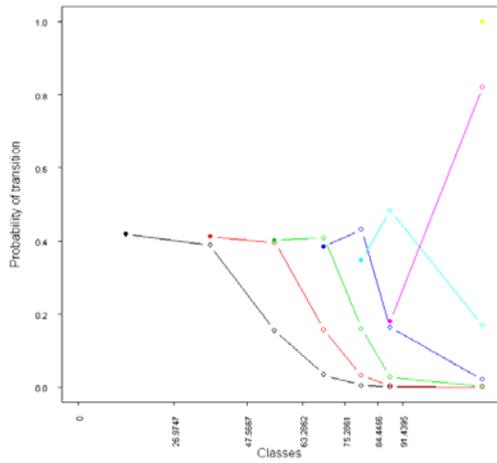
$j=j+1$  ;



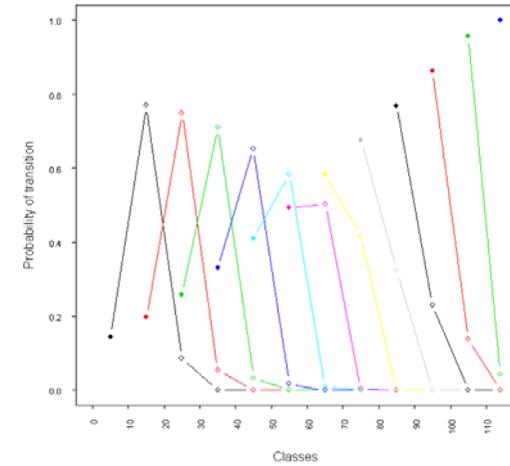
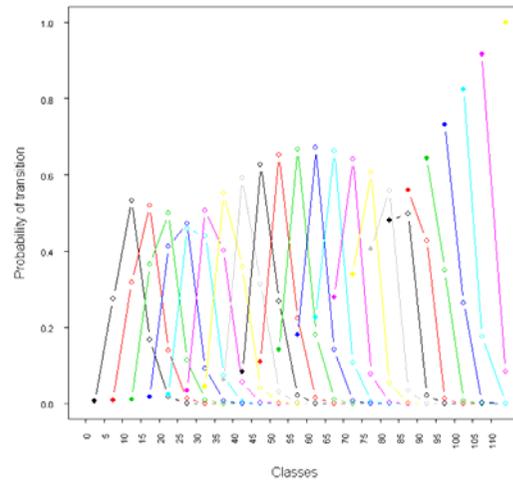
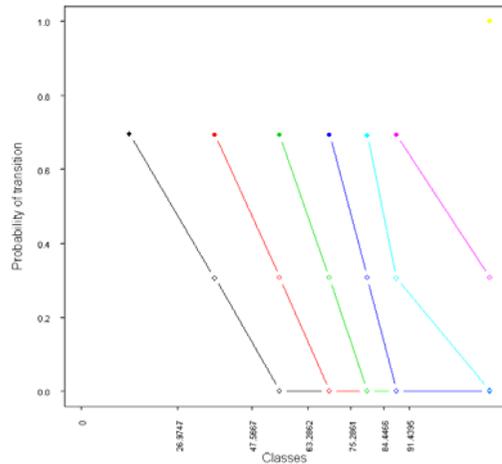
**Figure 2** The three growth matrices for the three schemes of length classes construction are plotted. These graphs have been constructed using a uniform distribution to describe the growth variability. The X-axis represents the length decomposed into length classes. The Y-axis allow to read the probability of transition. Each graph contains as many curves as many classes there are, and each curve gives the probabilities of transition from a class to another (a curve correspond to a row in the growth matrix).



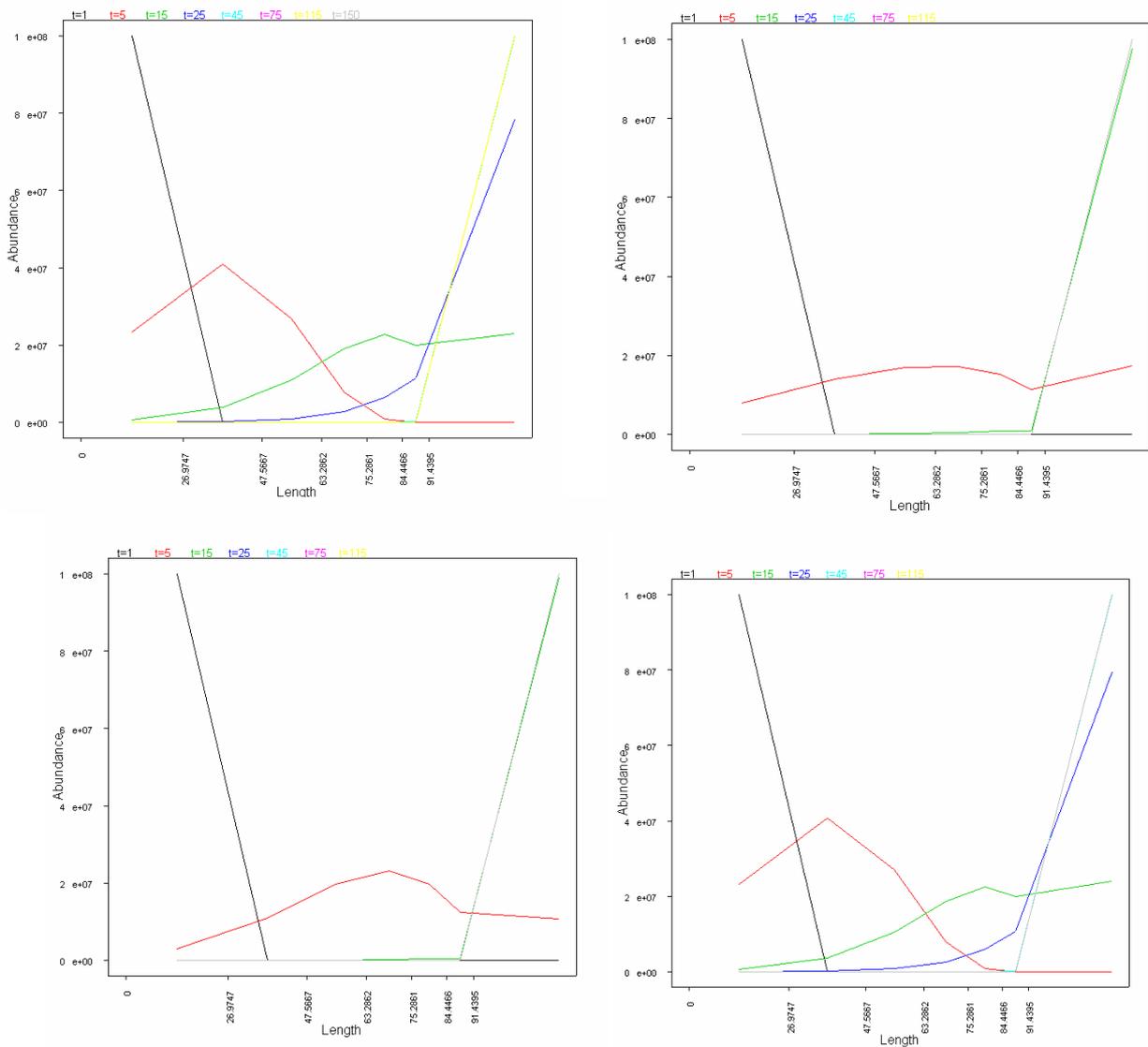
**Figure 3** Identical to Figure 2 with a beta-binomial distribution



**Figure 4 .** Identical to Figure 2 with a gamma distribution with a double integral (beta=1)

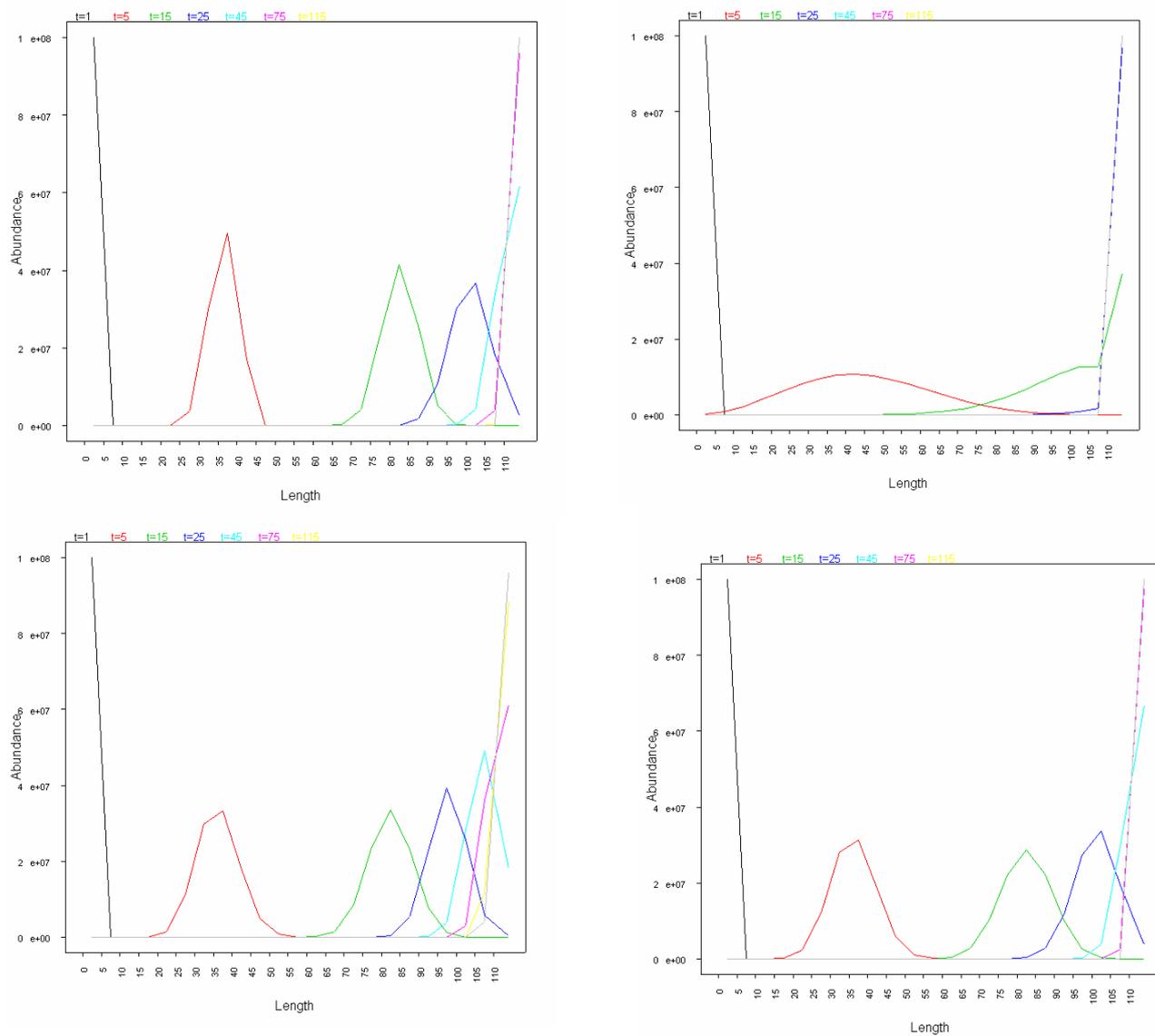


**Figure 5:** Identical to Figure 2 with a gamma distribution with a double integral (beta=1)

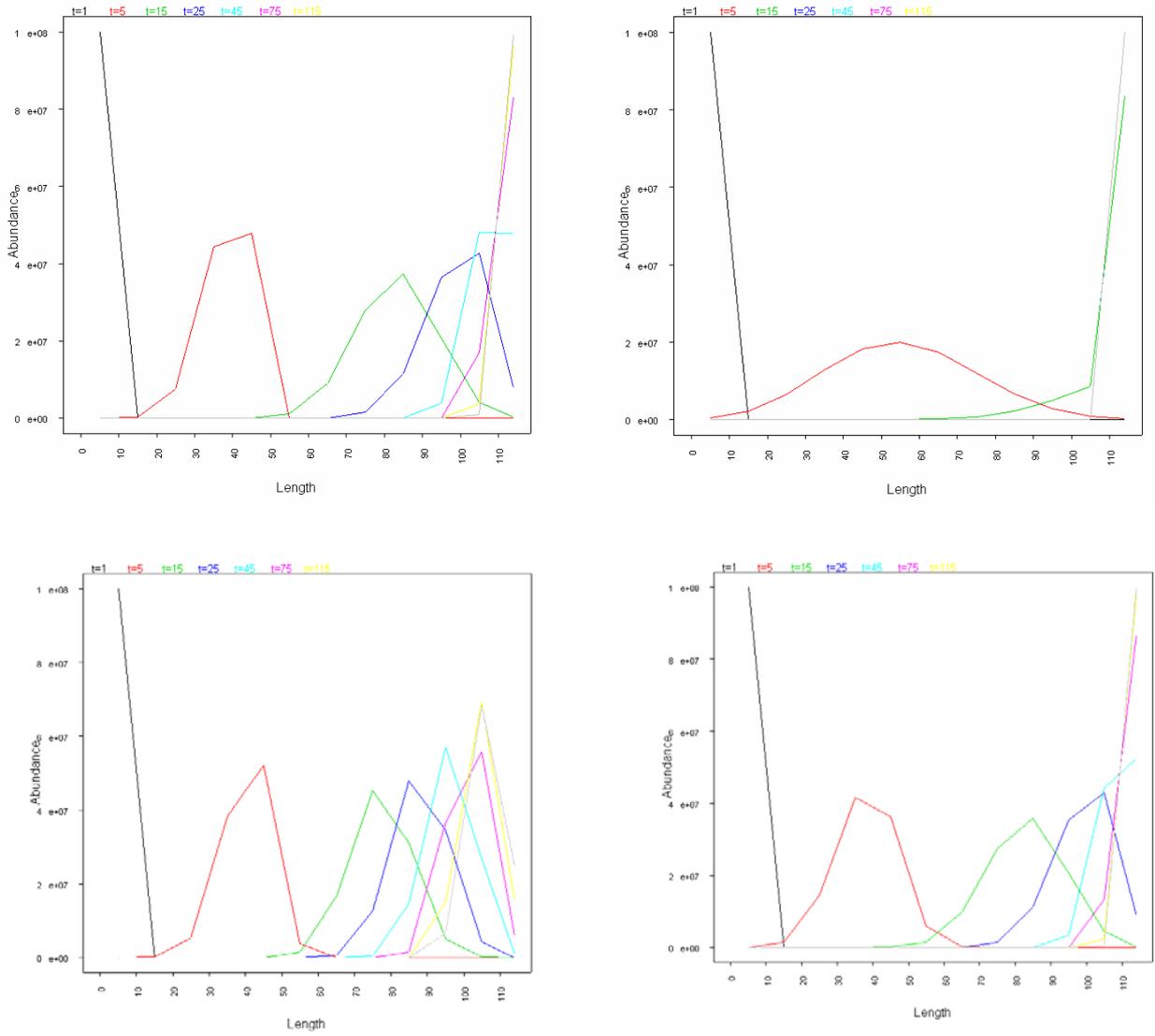


**Figure 6**

Each graph represents the distribution of the first class of population over length classes after a simulation of growth without any mortality at  $t=1$ ,  $t=5$ ,  $t=15$ ,  $t=25$ ,  $t=50$ ,  $t=75$ ,  $t=115$  (in months), when classes have a width equal to three months according to different hypotheses of growth variability, from left to right and up to down, a uniform distribution, a beta-binomial distribution, a gamma with single integral and a gamma with double integral. The X-axis represents the length decomposed into length classes. The Y-axis displays the number of fishes.



**Figure 7** Identical to Figure 6 when classes have a width equal to 5cm



**Figure 8** Identical to Figure 6 when classes have a width equal to 10cm

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# Modeling survival and growth in age- and length-structured population dynamics models, and relating model variables to observations in such models

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Working Document, ICES Study Group on Age-Length Structured Assessment Models (SGASAM), Bergen, Norway June 3-6, 2003.

Not to be cited without prior reference to the authors

## 1 Introduction

Gadget (Anon., 2002) is an extension of the Icelandic multi-species, multi-area, multi-fleet model BORMICON (Stefánsson and Pálsson, 1997). Gadget is a statistically based, parametric model framework for modeling population dynamics. It is written in C++, and can handle e.g. multi-species, multi-area, multi-fleet, age and length structured models. During the work on Gadget, it was found necessary to describe the mathematical foundation of the model framework in more detail. The present paper is a first attempt at making such a description.

In this paper a mathematical description of survival and growth in a multi-species, multi-area and multi-fleet age and length-structured population dynamics model is given. Examples of functional forms for these processes are also given.

The relation between observations and model variables is also described, but likelihood functions for use when fitting a model to observations are not given.

It is noted whether a formulation actually is implemented in Gadget. In some cases, the present Gadget code has more options than presented in this paper, while in other cases, the present paper outlines how Gadget should be extended.

Frøysa et al. (2002) give a mathematical description of a single-species age- and length-structured population dynamics model where the stock is divided into a mature and an immature part. In the present paper, we will extend the description in Frøysa et al. (2002) to a multi-area and multi-species model where growth and two different formulations of mortality are described. We will assume that all processes are dependent on length, some are also dependent on individual weight, but they are not dependent on age. We will also for most of

the descriptions assume that a stock is not divided into population groups such as a mature and an immature part.

A justification for choosing a Gadget-type modeling approach for modeling species interactions in boreal systems is given by Stefánsson and Pálsson (1998), and a discussion of the usefulness of multi-species and ecosystem models in a management context is given by Stefánsson (2002).

## 2 Basic population model

### 2.1 Basic processes

The basic biological processes in Gadget-type models are:

- aging
- survival
- length growth
- transition between biological stages (e.g. between maturation stages)
- recruitment
- migration

In this paper we only consider the mathematical formulation of mortality and growth.

### 2.2 Symbols and definitions

The symbols and definitions used are given below:

- $N$  - number of fish
- $W$  - individual weight of fish
- $k$  - area index
- $s, x$  - species indices
- $a$  - age index
- $l$  - (continuous) length

- $i, j$  - length group indices
- $l_{s,i}$  - discrete length, mid point in length group no.  $i$  for species  $s$
- $l_{s,min}$  - minimum fish length for species  $s$
- $l_{s,max}$  - maximum fish length for species  $s$
- $K$  - number of areas
- $A(k)$  - size of area  $k$
- $L_s$  - the number of length groups for species  $s$
- $A_s$  - the number of age groups for species  $s$
- $NS$  - number of model species
- $t_m$  - time step.
- $m_{max}$  - the number of time steps in a run
- $y$  - year
- $f$  - fleet index
- $NF$  - number of fleets
- $d$  - survey index
- $q_{d,s}$  - the catchability of species  $s$  by survey  $d$
- $\Xi_{x,s}(l_{x,j}, l_{s,i})$  the suitability of prey species  $s$ , length class  $i$  for predator  $x$ , length class  $j$ .
- $T(k, t)$  - temperature in area  $k$  at time  $t$
- $Cons(x, j, s, i, k, t)$  - consumption per predator  $x, j$  of prey  $s, i$  in area  $k$  during time step  $t$  (numbers)
- $BCons(x, j, s, i, k, t)$  - consumption per predator  $x, j$  of prey  $s, i$  in area  $k$  during time step  $t$  (biomass)
- $PredCons(x, j, k, t)$  - total consumption per predator  $x, j$  in area  $k$  during time step  $t$  (biomass)
- $PreyCons(s, i, k, t)$  - total consumption of prey  $s, i$  in area  $k$  during time step  $t$  (numbers)
- $BPreyCons(x, j, k, t)$  - total consumption by predator  $x, j$  in area  $k$  during time step  $t$  (biomass)
- $Z(s, i, k, t)$  - total mortality of prey  $s, i$  in area  $k$  during time step  $t$

- $F(f, s, i, k, t)$  - fishing mortality by fleet  $f$  of prey  $s, i$  in area  $k$  during time step  $t$
- $M(s, i, k, t)$  - total natural mortality of prey  $s, i$  in area  $k$  during time step  $t$
- $M1(s, i, k, t)$  - residual natural mortality of prey  $s, i$  in area  $k$  during time step  $t$
- $M2(s, i, k, t)$  - natural mortality due to predation of prey  $s, i$  in area  $k$  during time step  $t$
- $MS(s, i, k, t)$  - spawning mortality of prey  $s, i$  in area  $k$  during time step  $t$
- $S(s, i, k, t)$  - survival probability of prey  $s, i$  in area  $k$  during time step  $t$
- $C(f, k, t)$  - catch in biomass by fleet  $f$  in area  $k$  during time step  $t$
- $Catch(f, s, i, k, t)$  - catch in numbers by fleet  $f$  of prey  $s, i$  in area  $k$  during time step  $t$
- $BCatch(f, s, i, k, t)$  - catch in biomass by fleet  $f$  of prey  $s, i$  in area  $k$  during time step  $t$

$steps$  is the number of (equally long) time intervals within a year, and the time step  $\Delta t$  is then given by

$$\Delta t = \frac{12}{steps} \quad (1)$$

$$t_m = y_0 + m\Delta t, m = 1, 2, \dots, m_{max} \quad (2)$$

$$y = y_0 + \left[ \frac{m}{steps} \right], m = 1, 2, \dots, m_{max} \quad (3)$$

where  $[ ]$  denotes the integer part of the argument.

The width of the length groups is then given by

$$\Delta l_s = \frac{l_{s,max} - l_{s,min}}{L_s} \quad (4)$$

and the mean point of the length groups by

$$l_{s,i} = l_{s,min} + \left(i - \frac{1}{2}\right)\Delta l_s \quad (5)$$

For convenience, we assume that the model is started in the first step of the first year.

### 3 Functional forms of mortality and growth

In this section the functional forms for mortality and growth are described.

For each area and species, the stock number in an age-length structured model can be represented by a matrix  $N(\text{age}, \text{length})$ . For simplicity, we consider a model where survival/mortality/growth only depends on the length or weight of the fish, not on the age. Thus, the index for age can be omitted in the description, and the state variable will be described by a vector  $N(\text{length})$  for each species and area. The stock number can then be represented by  $N(s, i, k, t)$ , where  $s$  denotes species,  $k$  area and  $t$  time.

We also assume that the species in consideration are not divided into population groups (e.g. immature/mature fish).

#### 3.1 Survival/mortality

Two approaches to modeling mortality (and hence survival) are implemented in the Gadget code at present: The BORMICON approach (Stefánsson and Pálsson, 1997) and the Fleksibest approach (Frøysa et al., 2002). The Fleksibest approach has so far only been used for a single-species case where cannibalism is included. The BORMICON approach implements mortality due to catch and predation by *subtracting* a number of individuals from a stock, while the Fleksibest approach implements this mortality by applying a *mortality rate* to a stock.

The BORMICON approach corresponds to the *totalfleet/linearfleet* formulation in Gadget, while the Fleksibest approach corresponds to the *mortalityfleet* formulation. In the BORMICON approach, the *totalfleet* formulation is always used for predation, while for fishing either the *totalfleet* or the *linearfleet* formulation may be used. For both formulations spawning mortality may also be included. This is important for species like capelin (*Mallotus villosus*) where most of the fish die after spawning. Spawning mortality is at present included as a proportion of the stock which is removed in the time step after spawning occurs.

The abundance  $N^*(s, i, k, t)$  after mortality has taken place is given by

$$N^*(s, i, k, t) = N(s, i, k, t)S(s, i, k, t) \quad (6)$$

where  $S(s, i, k, t)$  is the survival probability. Note that  $N^*(s, i, k, t)$  is not equal to  $N(s, i, k, t + 1)$  because the other processes (growth, maturation, migration) will also influence the change from  $N(s, i, k, t)$  to  $N(s, i, k, t + 1)$ . The calculation of the survival probability differs between the BORMICON and the Fleksibest approach:

**The BORMICON approach** The calculation of the survival probability using the BORMICON approach is a hybrid between subtraction of a number of fish from the stock and application of a mortality. The abundance  $N^*(s, i, k, t)$  of fish after mortality has taken place at time  $t$  is calculated from the abundance at time  $t$  in the following way:

First, the number of fish which die due to predation and catch are subtracted, and then the (residual) natural mortality  $M1(s, i, k, t)$  and spawning mortality  $MS(s, i, k, t)$  are applied as mortality rates:

$$N^*(s, i, k, t) = (N(s, i, k, t) - PreyCons(s, i, k, t) - Catch(s, i, k, t))e^{-M1(s, i, k, t) - MS(s, i, k, t)} \quad (7)$$

$M1$  is the (residual) natural mortality and  $MS$  the spawning mortality.

The consumption  $PreyCons(s, i, k, t)$  is a sum of the consumption by all the predators, see equation 24. Similarly, the catch  $Catch(s, i, k, t)$  is a sum of the catch by all fleets, see equation 32.

It may happen in a simulation run that the abundance of a stock in an area is not high enough to account for the catch and predation. This can be due to an incorrect migration pattern, too slow growth or other incorrect assumptions in the model. This phenomenon is known as understocking (Stefánsson and Pálsson, 1997), and given a penalty weight during optimisation. In the Gadget implementation, a minimum fraction of the stock ( $\gamma$ , a value of 0.05 is often used) which will remain after predation and catch is included to prevent negative stock abundance.

The survival probability is then given by

$$S_{s, i, k, t} = \max\left(\frac{N(s, i, k, t) - PreyCons(s, i, k, t) - Catch(s, i, k, t)}{N(s, i, k, t)}, \gamma\right)e^{-M1(s, i, k, t) - MS(s, i, k, t)} \quad (8)$$

**The Fleksibest approach** This is obtained by extending the approach given in Frøysa et al. (2002) to a multi-area and multi-species case.

The survival probabilities  $S(s, i, k, t)$  are given by:

$$S(s, i, k, t) = e^{-Z(s, i, k, t)} \quad (9)$$

The total mortality is given as

$$Z(s, i, k, t) = F(s, i, k, t) + M(s, i, k, t) \quad (10)$$

where  $F(s, i, k, t)$  is the fishing mortality and  $M(s, i, k, t)$  is the natural mortality.

The natural mortality  $M(s, i, k, t)$  can be divided into predation mortality  $M2$  and residual natural mortality  $M1$ , as in multispecies VPA (Helgason and Gislason, 1979; Pope, 1979). In addition, spawning mortality  $MS$  may occur.

The total natural mortality can then be written as

$$M(s, i, k, t) = M1(s, i, k, t) + M2(s, i, k, t) + MS(s, i, k, t) \quad (11)$$

### 3.1.1 Predation/consumption

We first define the suitability  $\Xi_{x,s}(l_{x,j}, l_{s,i})$  of prey species  $s$ , length class  $i$  for predator  $x$ , length class  $j$ . The suitability can be any positive number but it is convenient in practice to keep it between 0 and 1. It is convenient to write it in a separable way:

$$\Xi_{x,s}(l_{x,j}, l_{s,i}) = \alpha_1(x, s)\alpha_2(x, s)\alpha_3(l_x, l_s) \quad (12)$$

where

- $\alpha_1(x, s)$  describes the preference of predator  $x$  for prey  $s$  due to factors like mobility, colour, pelagic vs. demersal distribution etc.
- $\alpha_2(x, s)$  describes the geographical overlap between predator and prey
- $\alpha_3(l_x, l_s)$  describes the size preference of predator  $x$  for prey  $s$

Let  $\alpha_1(x, s)$  be a number between 0 and 1 which describes the preference coefficient of a predator for a given prey, such that  $\alpha_1(x, s) = 1$  for the most preferred prey species for this predator.

If we assume that the area division in the model takes care of the geographical overlap,  $\alpha_2(x, s)$  can be omitted from equation 12.

In the MSVPA, the function describing the size preference of the predator is given by

$$\alpha_3(l_x, l_s) = e^{-\frac{(\ln(\frac{W_{x,j}}{W_{s,i}}) - \eta)^2}{2\sigma^2}} \quad (13)$$

(Gislason and Sparre, 1987). Several suitability functions are available in Gadget. In one of the suitability functions available in Gadget weight is replaced by length in equation 13, and the function is allowed to be skew-symmetric.

Equation 12 can then be written as:

$$\Xi_{x,s}(l_{x,j}, l_{s,i}) = \begin{cases} p2_{x,s} e^{-\frac{(\ln(\frac{l_{x,j}}{l_{s,i}}) - p1_{x,s})^2}{p3_{x,s}}} & \text{if } \ln(\frac{l_{x,j}}{l_{s,i}}) \leq p1_{x,s} \\ p2_{x,s} e^{-\frac{(\ln(\frac{l_{x,j}}{l_{s,i}}) - p1_{x,s})^2}{p4_{x,s}}} & \text{if } \ln(\frac{l_{x,j}}{l_{s,i}}) > p1_{x,s} \end{cases} \quad (14)$$

where  $p1_{x,s}$ ,  $p2_{x,s}$ ,  $p3_{x,s}$ ,  $p4_{x,s}$  are constants.  $p1_{x,s}$  is the logarithm of the preferred predator size/prey size ratio for predator  $x$  and prey  $s$ , while  $p2_{x,s}$  is the preference of prey  $s$  for predator  $x$ . We assume that  $0 \leq p2_{x,s} \leq 1$ .

In order to give a biological interpretation of  $p3_{x,s}$  and  $p4_{x,s}$ , they can be related to the two values of  $\frac{l_{x,j}}{l_{s,i}}$  for which the suitability function is equal to  $p2_{x,s}/2$ , i.e. half of its maximum value. Denote these values by  $r_{50}$ . The values of  $r_{50}$  can be found by solving the equations

$$\frac{(r_{50} - p1_{x,s})^2}{p3_{x,s}} = \ln 2 \quad (15)$$

for  $r_{50} \leq p1_{x,s}$

and

$$\frac{(r_{50} - p1_{x,s})^2}{p4_{x,s}} = \ln 2 \quad (16)$$

for  $r_{50} > p1_{x,s}$

with respect to  $r_{50}$ .

**BORMICON** In this formulation, predation is modeled from the predators' point of view. First the consumption in biomass per predator and time step is calculated. The total consumption per time step is then calculated by multiplying by the number of predators and summing over all predator groups. The consumption per predator in a given time step is thus independent of the predator abundance during that time step, except when understocking occurs.

Consumption *PredCons* (biomass consumed per predator and time unit) is a function of the abundance of all prey species  $s$ . It is calculated in the same way as in Bogstad et al. (1997):

Let  $H_x(W, T)$  be the maximum consumption per time step by individual predator  $x$  with weight  $W$  when the temperature is  $T$ . The consumption per predator per time step is given by the maximum consumption

multiplied by a fraction:

$$PredCons(x, j, k, t) = H_x(W(x, j, k, t), T(k, t))\Psi(x, j, k, t) \quad (17)$$

where the feeding level,  $\Psi(x, j, k, t)$  denotes the ratio between the actual consumption and the maximum consumption per predator.

Define the amount of prey species  $s$ , length class  $i$  suitable for predator  $x$ , length class  $j$  as

$$\Phi(x, j, s, i, k, t) = \Xi_{x,s}(l_{x,j}, l_{s,i})N(s, i, k, t)W(s, i, k, t) \quad (18)$$

The feeding level  $\Psi$  is modeled as a number in the interval  $[0,1]$  defined by

$$\Psi(x, j, k, t) = \frac{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(x, j, s, i, k, t) + other\ food(x, k, t)\Xi_{x,other}(l_{x,j})A(k)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(x, j, s, i, k, t) + other\ food(x, k, t)A(k) + \Phi_{1/2}(x, j)A(k)} \quad (19)$$

Here

- $A(k)$ : the size of area  $k$ ,
- $other\ food(x, k, t)$ : the density of other food available.
- $\Phi_{1/2}(x, j)$ : the value of the food density for which the predator eats half of maximum consumption, i.e.  $\Psi = 1/2$ . It should be noted that  $\Phi_{1/2}(x, j)$  is NOT half of the predator's maximum consumption!

If modeling food shortage is not of interest, the half value  $\Phi_{1/2}$  is set to 0. Then  $\Psi = 1$  and the consumption is independent of the food abundance.

The consumption per predator of a given prey species and size group (in biomass) is given by the consumption per predator from equation 17, multiplied by the suitable biomass of this prey group and divided by the total suitable biomass of prey. This gives the following equations:

$$BCons(x, j, s, i, k, t) = \frac{H_x(W(x, j, k, t), T(k, t))\Psi(x, j, k, t)\Phi(x, j, s, i, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(x, j, s, i, k, t) + other\ food(x, k, t)\Xi_{x,other}(l_{x,j})A(k)} \quad (20)$$

for the consumption per predator of a given prey (in biomass) and

$$Cons(x, j, s, i, k, t) = \frac{H_x(W(x, j, k, t), T(k, t))\Psi(x, j, k, t)\Phi(x, j, s, i, k, t)}{W(s, i, k, t)(\sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(x, j, s, i, k, t) + other\ food(x, k, t)\Xi_{x,other}(l_{x,j})A(k))} \quad (21)$$

for the consumption per predator of a given prey (in numbers).

The consumption of other food (in biomass) is given by

$$c_{other}(x, j, k, t) = \frac{H_x(W(x, j, k, t), T(k, t))\Psi(x, j, k, t)other\ food(x, j, t)\Xi_{x,other}(l_{x,j})A(k)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(x, j, s, i, k, t) + other\ food(x, k, t)\Xi_{x,other}(l_{x,j})A(k)} \quad (22)$$

The total consumption in biomass of a given prey is then given by

$$BPreyCons(s, i, k, t) = \sum_{x=1}^{NS} \sum_{j=1}^{L_j} BCons(x, j, s, i, k, t)N(x, j, k, t) \quad (23)$$

and the consumption in numbers of that prey is given by

$$PreyCons(s, i, k, t) = \sum_{x=1}^{NS} \sum_{j=1}^{L_j} Cons(x, j, s, i, k, t)N(x, j, k, t) \quad (24)$$

**Fleksibest** This formulation has not yet been developed for a multi-species case.

In the present single-species implementation for NEA cod, the only predation mortality accounted for in the Fleksibest formulation is cannibalism, which is assumed to be proportional to the 'suitable predator' biomass and inversely proportional to the biomass of the preferred prey, capelin. The existing implementation is a slight modification of the equation given in Frøysa et al. (2002):

$$M2(s, i, k, t) = \frac{\alpha_s \sum_{j=1}^{L_s} N(s, j, k, t)W(s, j, k, t)\Xi_{s,s}(l_{s,j}, l_{s,i})}{(Capelin(k, t))^\beta} \quad (25)$$

A generalisation of this formulation should allow the predation mortality to depend on the biomass of 'suitable predators' as well as on prey abundance.

It is possible to apply the Fleksibest formulation for the fishing mortality and the BORMICON formulation for the predation, but this is at present not supported in the code.

### 3.1.2 Catch

Let  $\Xi_{f,s}(l_{s,i})$  be the fleet selectivity.

A typical logistic selectivity curve for commercial fleets would be

$$\Xi_{f,s}(l_{s,i}) = \frac{\beta_{f,s}}{1 + e^{4\alpha_{f,s}(l_{50f,s} - l_{s,i})}} \quad (26)$$

where  $l50_{f,s}$  is the length at which half of the fish of species  $s$  is available to fleet  $f$ , and  $\alpha_{f,s}$  is the slope of  $\Xi_{f,s}(l_{s,i})$  when  $l50_{f,s} = l_{s,i}$ .  $\beta_{f,s}$  (at present fixed to 1 in Gadget) describes the maximum preference for prey  $s$  by fleet  $f$  ( $0 \leq \beta_{f,s} \leq 1$ ).

**BORMICON** The catch is modelled in a similar way as the predation. However, there are two approaches, denoted as *totalfleet* and *linearfleet*. In the *totalfleet* approach, the catch in biomass is given, and this catch is then distributed on the various prey groups. In the *linearfleet* approach, the fishing effort is given, and the catch of each prey group is calculated based on the effort.

Define the biomass of prey species  $s$ , length class  $i$  available for fleet  $f$  as

$$\Phi(f, s, i, k, t) = \Xi_{f,s}(l_{s,i})N(s, i, k, t)W(s, i, k, t) \quad (27)$$

In the *totalfleet* approach,  $C_{f,k,t}$  is the total catch in biomass by fleet  $f$  in area  $k$  during time step  $t$ , which is supplied as a (possibly estimated) parameter to the model. The proportion which species  $s$  and length group  $i$  constitutes of the biomass of fish available for fleet  $f$  is multiplied by the total catch,  $C_{f,k,t}$  to give the catch in biomass of that prey group.

The catch in biomass is then given by

$$BCatch(f, s, i, k, t) = \frac{C_{f,k,t}\Phi(f, s, i, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(f, s, i, k, t)} \quad (28)$$

Further dividing by the mean weight of the prey group gives the catch in numbers:

$$Catch(f, s, i, k, t) = \frac{C_{f,k,t}\Phi(f, s, i, k, t)}{W(s, i, k, t) \sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(f, s, i, k, t)} \quad (29)$$

When using the *linearfleet* approach, the catch is set to be proportional to the abundance of prey. The effort is then supplied as parameters  $E_{f,k,t}$  and the catch in biomass is calculated as

$$BCatch(f, s, i, k, t) = \nu_f E_{f,k,t} \Phi(f, s, i, k, t) \quad (30)$$

where  $\nu_f$  are constants.

The catch in numbers is then given by

$$Catch(f, s, i, k, t) = \frac{\nu_f E_{f,k,t} \Phi(f, s, i, k, t)}{W(s, i, k, t)} \quad (31)$$

In both cases the total catch in numbers by all fleets is given by:

$$Catch(s, i, k, t) = \sum_{f=1}^{NF} Catch(f, s, i, k, t) \quad (32)$$

**Fleksibest** The total fishing mortality in area  $k$ ,  $F(s, i, k, t)$  is the sum over the partial fishing mortalities  $F(f, s, i, k, t)$ :

$$F(s, i, k, t) = \sum_{f=1}^{NF} F(f, s, i, k, t) \quad (33)$$

Each partial fishing mortality  $F(f, s, i, k, t)$  is a product of a time- and area dependent fishing level  $\xi_{f,k,t}$  and a selection curve, both fleet specific:

$$F(f, s, i, k, t) = \xi_{f,k,t} \Xi_{f,s}(l_{s,i}) \quad (34)$$

The catch in numbers by fleet  $f$  is then given by the usual catch equation:

$$Catch(f, s, i, k, t) = \frac{F(f, s, i, k, t)N(s, i, k, t)(1 - e^{-Z(s,i,k,t)})}{Z(s, i, k, t)} \quad (35)$$

and the catch in biomass is given by

$$BCatch(f, s, i, k, t) = \frac{F(f, s, i, k, t)N(s, i, k, t)W(s, i, k, t)(1 - e^{-Z(s,i,k,t)})}{Z(s, i, k, t)} \quad (36)$$

### 3.1.3 Residual natural mortality

Currently, the BORMICON formulation only allows for an age-dependent residual natural mortality (a given number for each species and age group,  $M1(s, a)$ ). This should be extended to allow for size, area- and time-dependent residual natural mortality.

In the Fleksibest formulation, we have chosen a function describing the residual natural mortality which allows for higher natural mortality of small and large fish than of fish of intermediate lengths. Tretyak (1984) suggested the following formulation, where the residual natural mortality is dependent on age:

$$M1(a) = \alpha_1(-a + (a_e - a_s)\ln(a_e - a)) + \alpha_2 \quad (37)$$

which has a minimum at  $a = a_s$ .

In the Fleksibest formulation in Gadget, we have currently implemented a length-dependent mortality which is similar, but also allows for a constant natural mortality:

$$M1(s, i, k, t) = M1^*(l_{s,i}) = \begin{cases} \frac{a_1(s)}{b_1(s)+l'} & l_{s,min} \leq l_{s,i} < l_1(s) \\ c(s) & l_1(s) \leq l_{s,i} \leq l_2(s) \\ \frac{a_2(s)}{b_2(s)+l'} & l_2(s) < l_{s,i} \leq l_{s,max} \end{cases} \quad (38)$$

$$l'(s) = l_{s,i} * (M1^*(s, l_{s,max}) - M1^*(s, l_{s,min})) \quad (39)$$

Note that  $a_1(s)$ ,  $a_2(s)$ ,  $b_1(s)$ ,  $b_2(s)$ ,  $c(s)$  must be chosen so that  $M1^*(s, l_{s,i})$  is continuous at  $l_{s,i} = l_1(s)$  and  $l_{s,i} = l_2(s)$ .

This should be reformulated.

### 3.1.4 Spawning mortality

This is an instantaneous mortality  $MS(s, i, k, t)$  which is applied to the mature fish in the time step(s) when spawning occur, and is zero otherwise. Assume that the stock is divided into immature fish (index  $im$ ) and a mature fish (index  $ma$ ). We thus have  $MS(s, im, i, k, t) = 0$  for all  $s, i, k, t$ , while  $MS(s, ma, i, k, t)$  could be different from 0 in some cases.

## 3.2 Growth

### 3.2.1 Mean growth in length and weight

Growth may be a function of food availability as well as of fish size, temperature and time. In a single-species model, *otherfood* can be used to make growth depend on food availability. In a model where growth is dependent on food availability, it would seem logical to calculate the growth in weight first, based on food consumption, and derive the growth in length from the growth in weight.

The consumption by an individual predator,  $PredCons(x, j, k, t)$ , is given by equation 17.

An example formula for calculating growth in weight from consumption (the 'Jones' growth function) is given in Stefánsson and Pálsson (1997), equation (7.2.2). In our notation that formula becomes

$$\Delta W(x, j, k, t) = \frac{PredCons(x, j, k, t)}{q_0 W(x, j, k, t)^{q_1}} - q_2 W(x, j, k, t)^{q_3} e^{q_4 T(k, t) + q_5 V_{swim}(x, l_x, j)} \quad (40)$$

where  $q_0, q_1, q_2, q_3, q_4, q_5$  are constants. These constants may be derived from analyses external to the model, or they could be estimated by the model. The values of  $q_0$  and  $q_2$  will depend on the length of the time step.  $V_{swim}(x, l_{x,j})$  is the swimming speed, which is dependent of the body length.

Equation 40 could be made more realistic by taking the energy content of the food into account and calculate the total amount of energy consumed by the predator. Such an approach was used for marine mammals in Bogstad et al. (1997).

If the length-weight relationship

$$W(x, j, k, t) = \beta_{1_{x,k,t}}(l_{x,j})^{\beta_{2_{x,k,t}}} \quad (41)$$

is constant over time, the mean length growth can be calculated by differentiating equation 41 with respect to length:

$$\delta W(x, j, k, t) = \beta_{1_{x,k}} \beta_{2_{x,k}} (l_{x,j})^{\beta_{1_{x,k}} - 1} \delta l(x, j, k, t) \quad (42)$$

which gives

$$\delta l(x, j, k, t) = \frac{\delta W(x, j, k, t)}{\beta_{1_{x,k}} \beta_{2_{x,k}} (l_{x,j})^{\beta_{1_{x,k}} - 1}} \quad (43)$$

Extensions to this formula are needed to make the model more realistic, and some extensions have already been implemented in Gadget. Reduction in weight (e.g. due to weight loss during spawning) is currently implemented in Gadget in such a way that it does not result in reduction in length (Stefánsson and Pálsson (1997), p. 40). Also, a fish in bad condition should increase its weight before its length starts to increase. A way of handling this is outlined in Stefánsson and Pálsson (1997). This implies that the weight also must be considered as a state variable which makes description of the model formulation much more complicated. We will thus not consider this issue further in the present paper.

Various functions describing mean growth in the single-species case are implemented. A common model for growth increments is based on the von Bertalanffy growth function

$$\delta l(s, i, k, t) = (L_\infty(s) - l_{s,i}) * (1 - \exp(-\mu(s, k, t)\Delta t)) \quad (44)$$

where  $L_\infty(s)$  and  $\mu(s, k, t)$  are parameters.

How to implement actual length growth around this mean, i.e. how to calculate the proportion of fish growing 0,1,2,... length groups will be dealt with in other papers. An introduction to this is given by Stefánsson (2001) and Bogstad et al. (2002). Björnsson and Sigurdsson (2003) used a beta-binomial distribution in their model.

The weight at length in a given time step can also be input as a number for each length group or as a formula for the weight-length relationship.

## 4 Comparing observations and model results

### 4.1 Background

In order to relate the model variables (number of fish in the stock, number eaten, number fished etc.) to the observations available, we need what here will be termed as an observation model. This is simply a description of how the available observations relate to model quantities. The intention of this section is to spell out in detail the comparisons made. We will present the various types of observations and describe which model variables they should be compared to. We will, not, however, discuss the choice of likelihood functions for such comparisons.

The highest detail level of observations available are length distributions of fish from a given trawl haul, acoustic abundance (back-scattering area) for each nautical mile, stomach content of individual fish etc. A model will generally use a coarser spatial and temporal scale than these individual observations, and thus the observations need to be aggregated in space and time. In this aggregation the statistical properties such as the sample size should be taken care of.

The total likelihood function is given by

$$L_{tot} = \sum_y w_y L_y \quad (45)$$

where  $L_y$  is the likelihood component for each set of observations  $y$  (e.g. length distribution of fish in the survey for given area and time) and  $w_y$  is the weighting factor. The weighting factors will be influenced by the sample size and other statistical properties of the observations.

Examples of models combining different sets of observations are given by Stefánsson (1998), Björnsson (1998), Frøysa et al. (2002) and Björnsson and Sigurdsson (2003).

The model parameters are generally assumed to be independent of time. For fisheries and survey-related parameters such as survey catchability and fleet effectivity one may want to allow for a time trend or to divide the observation data set into several periods and allow these parameters to vary between periods.

It is important to note that the model results are compared to the entire data set of observations simultaneously, and thus all model parameters will in principle be correlated.

## 4.2 Observation types

The following types of observations are available:

- Survey indices
- Commercial catch data
- Stomach content data
- Mark-recapture data

In addition we will consider how age distributions can be used in comparison of observations and model results for survey indices and commercial catch data.

In addition to the indices for species, length, area, fleet and survey used previously, indices for age ( $a$ ) and mature/immature ( $ma/im$ ) are included whenever appropriate.

## 4.3 Survey indices

For marine populations, the following survey indices are available:

- Trawl survey indices
- Acoustic indices
- Abundance estimates from sightings surveys

### 4.3.1 Trawl survey indices

These are usually given as abundance indices  $\hat{I}(d, s, i, k, t)$  representing the mean number of fish of each length group caught per trawling hour (or a swept area estimate) by survey  $d$ . The modeled equivalent of this,  $I(d, s, i, k, t)$ , is

$$I(d, s, i, k, t) = q_{d,s} \Xi_{d,s}(l_{s,i}) (N(s, i, k, t))^{\gamma_{d,s}} \quad (46)$$

if  $\gamma_{d,s} = 1$ ,  $q_{d,s}$  corresponds to the catchability of species  $s$  by survey  $d$ .  $\Xi_{d,s}(l_{s,i})$  describes the length selectivity of the survey.

For some stocks (e.g. herring, mackerel), trawl surveys of egg or larvae conducted shortly after spawning are used as measures of the spawning stock size. We then observe the number of egg or larvae  $\hat{N}^*(d, s, k, t)$ . The modeled equivalent is

$$N^*(d, s, k, t) = q_{d,s} \sum_{i=1}^{L_s} N(s, ma, i, k, t) fe(s, i, k, t) H(s, l_{s,i}, W(s, ma, i, k, t)) \quad (47)$$

where the additional index  $ma$  indicate mature individuals.

Here:

$fe(s, ma, i, k, t)$ : the proportion female in the mature stock of species  $s$ ,  $i$  in area  $k$  during time step  $t$

$H(s, l, W)$ : the fecundity (kg eggs/kg bodyweight) of fish of species  $s$  with length  $l$  and weight  $W$  (e.g.  $H(s, l, W) = \alpha l^\gamma W^\beta$ , ICES 2003).

The catchability  $q_{d,s}$  is in many cases set equal to 1, i.e. the estimate of egg or larvae abundance is considered to be an absolute one.

### 4.3.2 Acoustic abundance indices

The observations of acoustic abundance of fish from survey  $d$  are the total back-scattering area  $\hat{s}_A(d, s, k, t)$ , together with a length distribution from trawl samples  $\hat{D}(d, s, i, k, t)$ . The back-scattering area is converted to number of fish using a length-dependent formula for the acoustic target strength of an individual fish:

$$s_A(d, s, k, t) = q_{d,s} \sum_{i=1}^{L_s} \sigma_s(l_{s,i}) N(s, i, k, t) \quad (48)$$

where the target strength of an individual fish is given by

$$\sigma_s(l_{s,i}) = \alpha_s (l_{s,i})^{\beta_s} \quad (49)$$

where  $\beta_s$  usually is close to 2 (the echo-strength is close to proportional to the cross-section area of the fish). If the survey is considered an absolute estimate, the catchability  $q_{d,s}$  is set to 1.

The observed proportion of fish in a given length group is given by

$$\hat{\pi}(i|d, s, k, t) = \frac{\hat{D}(d, s, i, k, t)}{\sum_{i=1}^{L_s} \hat{D}(d, s, i, k, t)} \quad (50)$$

The modeled proportion of fish in a given length group is given by

$$\pi(i|d, s, k, t) = \frac{\Xi_{d,s}(l_{s,i}) N(s, i, k, t)}{\sum_{i=1}^{L_s} \Xi_{d,s}(l_{s,i}) N(s, i, k, t)} \quad (51)$$

$\Xi_{d,s}(l_{s,i})$  describes the length selectivity of the survey.

### 4.3.3 Sightings surveys

Such observations could be e.g. sightings surveys of whales with vessels as the observation platform, (Schweder et al., 1997), or estimates of pup production by seals using aerial surveys or visual counts at rookeries. The observation would then be the number of individuals observed in counting no.  $d$ ,  $\hat{I}(d, s, k, t)$  (the size distribution would generally not be available). The modeled equivalent would be assumed to be proportional to the abundance of the stock:

$$I(d, s, k, t) = q_{d,s} \sum_i N(s, i, k, t) \quad (52)$$

If the sightings survey is assumed to be an absolute estimate,  $q_{d,s}$  would be assumed to be equal to 1. Estimates of pup (age 0) abundance are usually used for estimating the total stock abundance in a similar way to egg surveys. The estimated abundance is  $\hat{I}(d, s, 0, k, t)$ , and the modeled equivalent is:

$$I(d, s, 0, k, t) = q_{d,s} \sum_{a=1}^{A_s} \sum_{i=1}^{L_s} N(s, a, i, k, t) fe(s, a, i, k, t) \gamma(s, a, i, k, t) \quad (53)$$

where  $fe(s, a, i, k, t)$  is the proportion of females and  $\gamma(s, a, i, k, t)$  is the number of pups born per female.

This is not implemented in Gadget.

## 4.4 Commercial catch data

At present, no adjustments are made for possible misreporting in the catch data.

### 4.4.1 Total catch in tonnes

The observation is the total commercial catch in tonnes  $\hat{C}(f, s, k, t)$ . The modeled equivalent is

$$C(f, s, k, t) = \sum_{i=1}^{L_s} BCatch(f, s, i, k, t) \quad (54)$$

where  $BCatch(f, s, i, k, t)$  is given by equations 28 or 31 for the BORMICON formulation and by equation 36 for the Fleksibest formulation.

### 4.4.2 Length distributions

For commercial catches we observe length distributions  $\hat{D}(i|f, s, k, t)$ . The proportion of fish in a given length group is then given by:

$$\hat{\pi}(i|f, s, k, t) = \frac{\hat{D}(f, s, i, k, t)}{\sum_{i=1}^{L_s} \hat{D}(f, s, i, k, t)} \quad (55)$$

The modeled proportion of fish in a given length group is given by

$$\pi(i|f, s, k, t) = \frac{Catch(f, s, i, k, t)}{\sum_{i=1}^{L_s} Catch(f, s, i, k, t)} \quad (56)$$

#### 4.4.3 Catch per unit effort

The observations here are the catch in biomass  $\hat{C}$  and the effort  $\hat{E}$  (e.g. trawling hours) by fleet, area and time. The catch per unit effort (CPUE) is then given by

$$CPUE(f, k, t) = \hat{C}(f, k, t) / \hat{E}(f, k, t) \quad (57)$$

In the model, this is assumed to be proportional to the biomass available to the fleet:

$$CPUE(f, k, t) = \nu_f \sum_{s=1}^{NS} \sum_{i=1}^{L_s} \Phi(f, s, i, k, t) \quad (58)$$

where  $\Phi(f, s, i, k, t)$  is given by equation 27.

This is not yet supported in Gadget.

## 4.5 Stomach content data

The model calculates *consumption*, while the observations reflect *stomach contents* at a particular point in time. The model has to convert between these two entities. Ideally one would convert the model consumption into stomach contents to compare with the data. This is not done in Gadget at present, but this approach is briefly discussed at the end of this section. Three ways of comparing stomach content observations and model results are currently implemented:

- Comparing absolute biomass consumed
- Comparing ratio of biomass consumed
- Comparing ratio of numbers consumed

The observations may either be the number of prey or the biomass of prey in each stomach, by prey species and size group. The model results are consumption (in biomass or number) per predator of each prey species and size group

per time step. In order to compare observations and model results, either the observations of stomach content or the model results (consumption rates) must be transformed in order to get comparable quantities.

It can thus be seen that there is a trade off between the utility of the comparison and the degree of manipulation required. This problem has been known for some time, and is mentioned in Stefánsson and Pálsson (1997).

Stomach evacuation rate and hence also consumption rate are in general non-linear functions of the observed stomach content. The evacuation rate model should thus be applied to each individual stomach, and the consumption calculated by Gadget can then be compared to the average consumption per predator calculated based on the evacuation rate model and the observations. The observations are  $\hat{SC}(x, j, r, s, i, k, t)$  which is the stomach content of prey group  $s, i$  in fish nr  $r$  sampled from predator group  $x, j$  in area  $k$  during time step  $t$ . The average consumption calculated from the observations and the evacuation rate model is given by

$$BC\hat{ons}(x, j, s, i, k, t) = \frac{\sum_{r=1}^{n(x, j, k, t)} Y(\hat{SC}(x, j, r, s, i, k, t), x, s, l_{x, s}, T(k, t))}{n(x, j, k, t)} \quad (59)$$

where  $n(x, j, k, t)$  is the number of stomachs sampled from group  $x, j$  in area  $k$  during time step  $t$  and  $Y(SC, x, s, l, T)$  is the consumption rate of prey  $s$  by predator  $x$  when the stomach content of prey  $s$  is  $SC$ ,  $l_x$  is the predator length and  $T$  is the temperature.

For the consumption of other food, we similarly get

$$B\hat{C}ons(x, j, other, k, t) = \frac{\sum_{r=1}^{n(x, j, k, t)} Y(\hat{SC}(x, j, r, other, k, t), x, other, l_x, T(k, t))}{n(x, j, k, t)} \quad (60)$$

An example of a functional form for  $Y(SC, x, s, l_x, T)$  given in Stefánsson and Pálsson (1997), which is derived from the work of Jones (1974), is

$$Y(SC, cod, s, l, T) = \alpha_{cod, s} 1.09^{T-6} l^{1.15} SC^{0.5} \quad (61)$$

In Jones (1974),  $\alpha_{cod, s}$  is not prey species dependent, but the evacuation rate and hence  $\alpha_{cod, s}$  will generally be dependent of prey species.

Björnsson (1998) gives an example of a multispecies model where this approach is used.

### 4.5.1 Comparing absolute biomass consumed

The modeled equivalent to  $B\hat{C}ons(x, j, s, i, k, t)$  in equation 59 is given by equation 20 for the BORMICON formulation, while the modelled equivalent to  $B\hat{C}ons(x, j, other, k, t)$  in equation 60 is given by equation 22.

### 4.5.2 Comparing ratio of biomass consumed

This component gives information on relative feeding levels between different prey. It does not give information on absolute levels. One calculates the proportion of each prey species and size group (including other food) in the diet from the consumption rate and the observed stomach content:

$$\hat{\pi}(x, j, s, i, k, t) = \frac{B\hat{C}ons(x, j, s, i, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} B\hat{C}ons(x, j, s, i, k, t) + B\hat{C}ons(x, j, other, k, t)} \quad (62)$$

and

$$\hat{\pi}(x, j, other, k, t) = \frac{B\hat{C}ons(x, j, other, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} B\hat{C}ons(x, j, s, i, k, t) + B\hat{C}ons(x, j, other, k, t)} \quad (63)$$

This is then compared to the proportion of each prey group in the model diet. For modelled food this is calculated from equation 20:

$$\pi(x, j, s, i, k, t) = \frac{BCons(x, j, s, i, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} BCons(x, j, s, i, k, t) + c_{other}(x, j, k, t)} \quad (64)$$

For other food, this is calculated from equation

$$\pi(x, j, other, k, t) = \frac{c_{other}(x, j, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} BCons(x, j, s, i, k, t) + c_{other}(x, j, k, t)} \quad (65)$$

### 4.5.3 Comparing ratio of numbers consumed

This is the only component to actually compare against unadjusted data. It does not give absolute levels or biomass of a specified prey as a fraction of

the diet. It can give information on the length distribution of prey eaten by a predator (i.e. the selection pattern of that predator). It can also be used to compare consumption of two or more similar modelled prey eaten by a predator (e.g. cod eating capelin and herring). Other food can not be taken into account in the comparisons.

The observed entities are the number of each prey in the stomachs,  $N\hat{P}rey(x, j, s, i, k, t)$ . The proportion in numbers is

$$\hat{\pi}(x, j, s, i, k, t) = \frac{N\hat{P}rey(x, j, s, i, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} N\hat{P}rey(x, j, s, i, k, t)} \quad (66)$$

This can then be compared to the proportion in number in the modeled diet, which can be calculated based on equation 21 for the BORMICON formulation.

$$\pi(x, j, s, i, k, t) = \frac{Cons(x, j, s, i, k, t)}{\sum_{s=1}^{NS} \sum_{i=1}^{L_s} Cons(x, j, s, i, k, t)} \quad (67)$$

#### 4.5.4 Comparing stomach content

Consumption rate can be transformed to a distribution of stomach content for individual fish by using a feeding model. This has been done for cod feeding on capelin by Magnússon and Aspelund (1997). In that work, only one prey group was considered. The extension to multiple prey groups may not be trivial.

## 4.6 Mark-recapture data

This is currently being re-implemented from scratch, and is thus not described in this document.

## 4.7 Age-based data

### 4.7.1 Age distributions

The observed entity is the number of fish in each age and length group in a survey,  $\hat{D}(d, s, a, i, k, t)$ , or in the commercial catch,  $\hat{C}atch(f, s, a, i, k, t)$ . From this the proportions of fish in each age group for a given length group can be derived:

$$\hat{\pi}(a|d, s, i, k, t) = \frac{\hat{D}(d, s, a, i, k, t)}{\sum_{a=1}^{A_s} \hat{D}(d, s, a, i, k, t)} \quad (68)$$

for survey  $d$  and

$$\hat{\pi}(a|f, s, i, k, t) = \frac{\hat{Catch}(f, s, a, i, k, t)}{\sum_{a=1}^{A_s} \hat{Catch}(f, s, a, i, k, t)} \quad (69)$$

for fleet  $f$ .

The modeled equivalent is

$$\pi(a|d, s, i, k, t) = \frac{N(s, a, i, k, t)}{\sum_{a=1}^{A_s} N(s, a, i, k, t)} \quad (70)$$

(same for all surveys  $d$ ) and

$$\pi(a|f, s, i, k, t) = \frac{Catch(f, s, a, i, k, t)}{\sum_{a=1}^{A_s} Catch(f, s, a, i, k, t)} \quad (71)$$

for fleet  $f$ .

#### 4.7.2 Mean length/weight at age in the catch

It is also possible to compare the mean length or weight at age in the observations and in the model. The observed mean length and weight at age in a fleet for a given time step are then given by  $LCatch(f, s, a, k, t)$  and  $WCatch(f, s, a, k, t)$ .

The corresponding model equivalents can be derived from the number caught and the weight by age and length group in the model:

$$LCatch(f, s, a, k, t) = \frac{\sum_{i=1}^{L_s} Catch(f, s, a, i, k, t) l_{s,i}}{\sum_{i=1}^{L_s} Catch(f, s, a, i, k, t)} \quad (72)$$

and

$$WCatch(f, s, a, k, t) = \frac{\sum_{i=1}^{L_s} Catch(f, s, a, i, k, t) W(s, a, i, k, t)}{\sum_{i=1}^{L_s} Catch(f, s, a, i, k, t)} \quad (73)$$

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