

dst²

Development of structurally detailed statistically testable models of marine populations

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Part III

Case Studies

Chapter 8

Introduction

An important part of the dst² project was the inclusion of several case studies. These case studies were intended to reflect important differences between the ecosystems involved. Waters around Iceland were chosen to reflect a case study with fairly comprehensive data sets, the Celtic Sea for its complex food web and North Sea herring for its migration patterns. The Barents Sea had initially been included as a case study, later dropped but is included here for completeness since a considerable portion of project funding effectively became a part of this case study.

As the project developed, it became clear that some of the initial model proposals were infeasible, mainly due to severe data problems. This illustrates two aspects of Gadget. Firstly, it is a general framework and the implemented models have developed as the data availability and quality have become clear. Secondly, it is very important for any user of these marine data sets to be on top of not only what data exist, but also how they have been collected, potential errors in the data and so forth.

The papers in this final part of the report describe these various case studies. These reflect various levels of complexity, i.e. varying spatial scales, variable numbers of species etc. The case studies should demonstrate beyond any doubt that these interactions can be modelled and they can be modelled using appropriate statistical methods.

Chapter 9

Iceland

9.1 Definition of areas in Icelandic waters

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Introduction

A hierarchical spatial structure is required which represents spatial areas suitable for use in Gadget and for storage of the data in the datawarehouse. These areas should reflect hydrography, bathymetry, species distributions and to a lesser extent fishing controls. The data should be aggregated at a level where use of the original data is seldom required.

For modelling, the spatial structure needs to allow for adequate definitions of spatial stock structure, migration patterns and predator-prey overlap. Each area should also be considered relatively homogeneous in terms of bathymetry and hydrography.

The areas originally defined for Bormicon are described in Stefansson et al (1997). For the datawarehouse it was decided that the smallest unit, the gridcell, should be a statistical subrectangle (1/2 degree longitude and 1/4 degree latitude). Subdivisions and divisions are composed of these gridcells.

For Gadget, the Bormicon areas, mapped onto gridcells, become the divisions and the boundaries between the subdivisions correspond to the 200m, 1000m and 1500m depth contours. Some modifications to this scheme were made to take into account fishing regulations, hydrography and the size of the resulting areas.

The appropriateness of this spatial structure, with respect to species composition, was tested using cluster analysis of species assemblage data.

Bormicon Areas

The original Bormicon areas, as described in Stefansson et al (1997), are shown in fig. 9.1. Considering bathymetry (fig 9.2), with Iceland situated on two ridges (the south-east to north-west Faroes-Greenland ridge, to the south-west the Reykjanes ridge and to the north-east the Jan Mayen ridge) results in a split into four areas. The Icelandic shelf (at ~ 500m) is a further natural split into on-shelf and off-shelf with area 7 (see fig 9.1) separate. Hydrography, to a large extent reflects the bathymetry (fig 9.3) but sea temperature indicates a further split of the northern area. The remaining spatial structure was defined according the spatial distribution of cod, shrimp, Greenland halibut, capelin and nephrops.

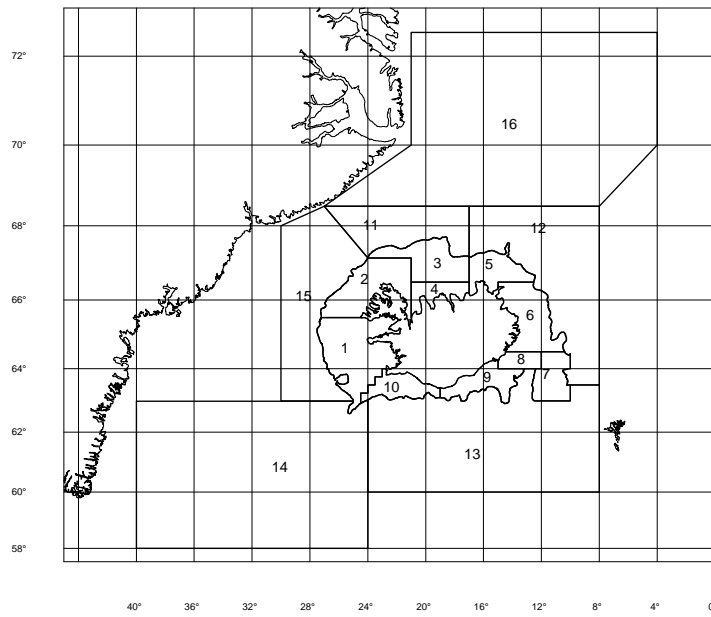


Figure 9.1: The original Bormicon areas

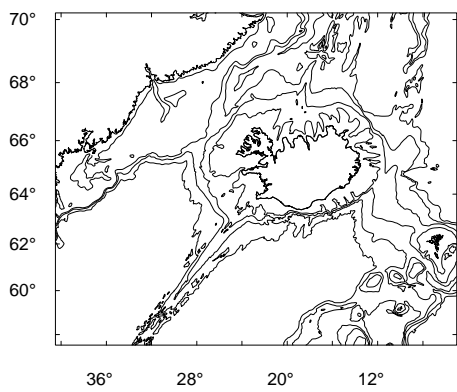


Figure 9.2: Bottom topography

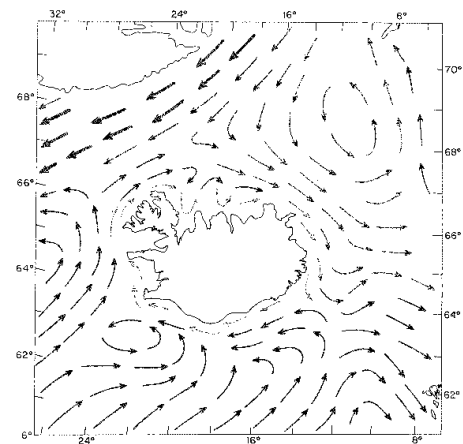


Figure 9.3: Ocean currents

The Gadget Spatial Hierarchy

The numbering system for Gadget is slightly different to that for Bormicon. In the datawarehouse, divisions in Icelandic waters start at 100. So division 1 becomes 101 and the subdivisions of division 101 are 1011, 1012 etc.

The range of the current spatial hierarchy has been partly determined by the data which have been included in the datawarehouse. As more species are input, the area may be extended.

Divisions

The divisions within the 500m depth contour are derived from the Bormicon areas (fig. 9.4, with grid-cells being the smallest spatial unit considered. Some changes result from using a slightly different 500m depth contour. Other deviations from the original scheme are:

- the northern boundary between areas 2 and 3 is further south to follow the 200m depth contour.
- the southernmost section of the boundary between areas 2 and 4 is slightly further east to avoid splitting a shrimp fishery.
- areas 3 and 4 have been combined into a single division which is divided into subdivisions.
- area 8 has been incorporated into divisions 5 and 7. The reassignment of area 8 was based on the observed length distributions of cod and haddock.

Off the Icelandic coastal shelf, there are more differences between the Bormicon and Gadget spatial divisions. The Gadget divisions are predominantly derived from the bathymetry:

- the Reykjanes ridge separates divisions 109 and 114, which represent the Irminger Basin and Iceland Basin respectively.
- the Iceland-Faeroe Rise separates divisions 113 and 114.
- division 110 represents the Greenland coastal shelf to 500m depth.

Subdivisions

The coastal shelf subdivisions are based on the 200m depth contour (fig. 9.6). Exceptions to this are subdivisions 1011 and 1012 which represent regions with gear restrictions and 1054 (formerly area 8) which covers a frontal region. As some scientists prefer to analyse data from this region (1054) separately (or to exclude it from analyses) it has been included as a subdivision.

Subdivisions off the coastal shelf, are mainly in the vicinity of the Reykjanes ridge (south west) and the Iceland-Faeroe Rise (south east).

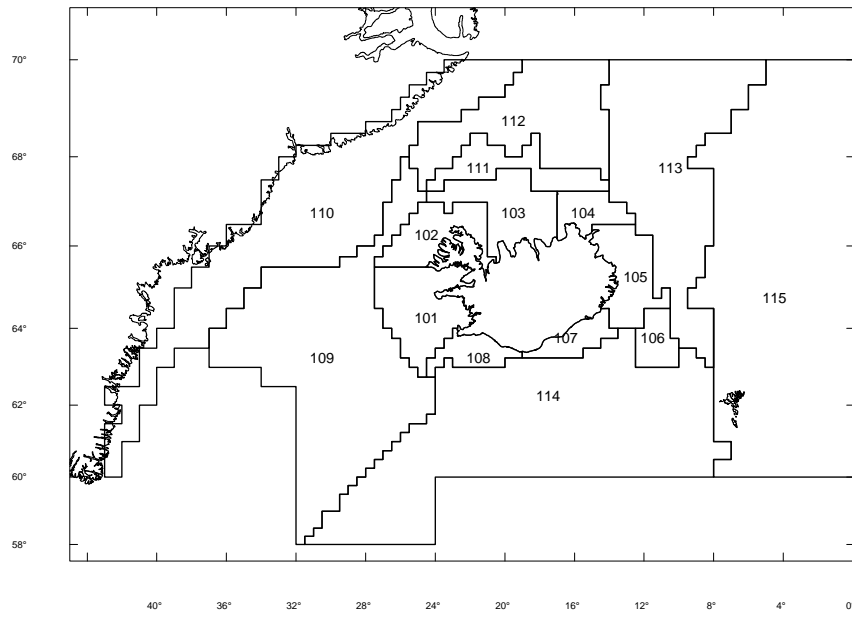


Figure 9.4: Gadget divisions

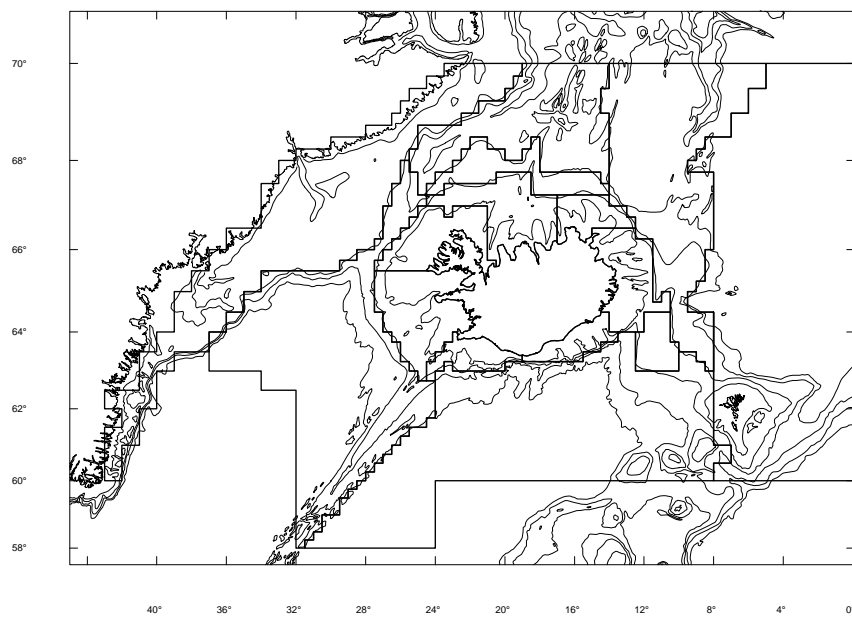


Figure 9.5: Gadget divisions with the 500m, 1000m and 1500m depth contours.

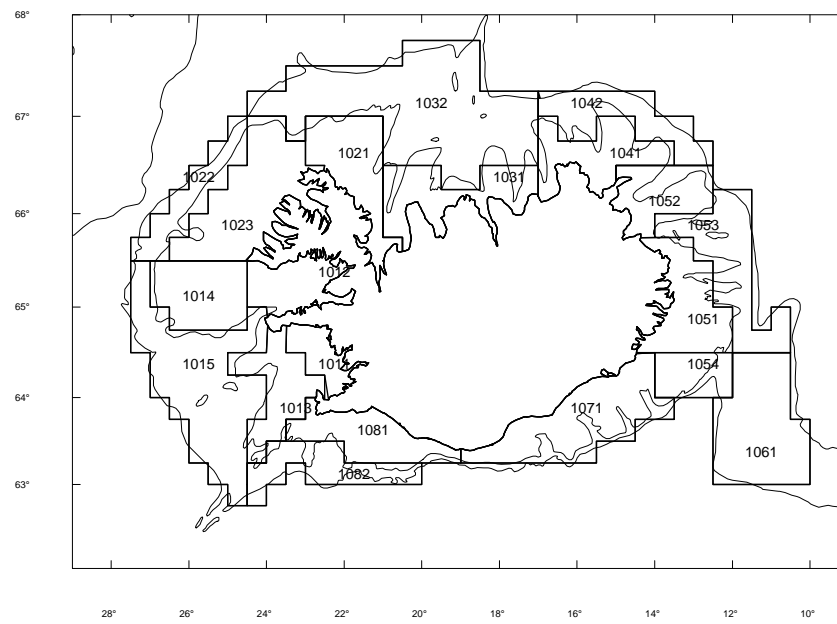


Figure 9.6: Gadget subdivisions within the 500m depth contour, with the 200m and 500m depth contours.

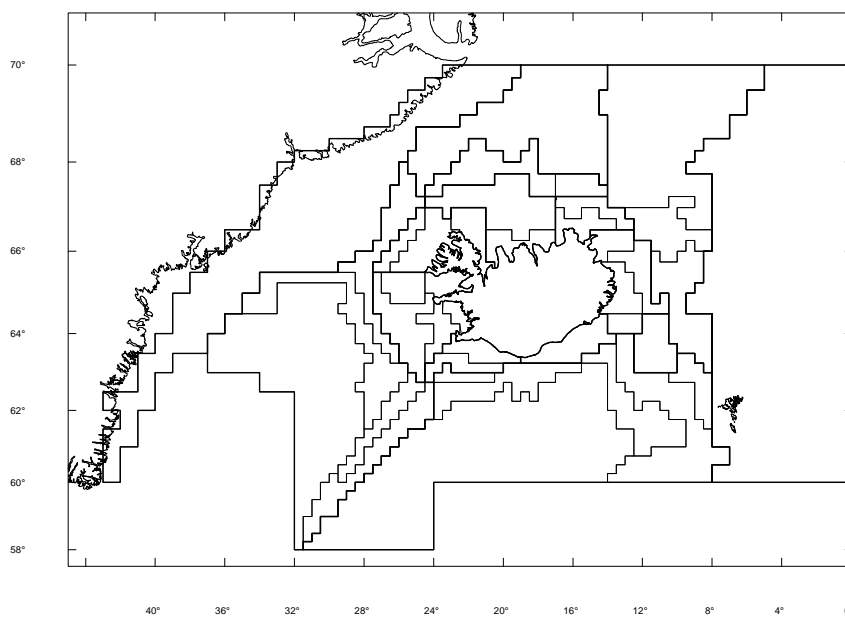


Figure 9.7: Gadget subdivisions

Data

Data from two surveys are used in the analyses: the Icelandic (Spring) Groundfish Survey from 1989 to 2002 and the Autumn Survey for the years 1996 to 2001. As the Groundfish Survey was designed for cod it is mostly on the Icelandic shelf covering depths to 500m. This area is represented by divisions 101-108. There are few data off the shelf and these were excluded from the analyses. The survey takes place in March each year and years prior to 1989 were excluded as species identification was inconsistent. The Autumn Survey includes some areas off the coastal shelf but 2002 was excluded as the number of species identified was considerably lower than previous years.

The species considered from both surveys are: cod, haddock, saithe, whiting, redfish (*Sebastes marinus*), Atlantic wolffish, starry ray, Greenland halibut, dab, long rough dab, moustache sculpin and *Sebastes viviparus*. Additional species in the analyses of the Autumn Survey data are roundnose grenadier, greater Argentine and deep water redfish (*Sebastes mentella*). Pelagic species such as capelin and herring were not included.

The abundance data were aggregated over all available years and within subrectangles, generating the total for each species and subrectangle. The fourth root of the total was then scaled to a mean of zero and variance equal to one. The surveys were analysed separately.

Cluster Analysis

Cluster analysis was used to define similar subrectangles. The partitioning around medoids method “pam” in Splus 6.0 was applied to the scaled abundance data. No spatial restrictions were placed on clustering of the subrectangles and the spatial proximity of was not taken into account in the analyses.

Partitioning around medoids operates on the dissimilarity matrix, minimizing the sum of dissimilarities. The required number of clusters is predefined, and an equivalent number of medoids are computed. Each observation is then assigned to the nearest medoid minimizing the sum of dissimilarities of each observation to the associated medoid.

A silhouette score is calculated for each observation which represents the difference between its average dissimilarity to other observations in the cluster it is assigned to and its average dissimilarity to observations in the second best cluster. The silhouette score is therefore an indication of the appropriateness of the classification. Average silhouette scores can be calculated for all observations providing an indication of the most appropriate number of clusters and by cluster to indicate which clusters are poorly or well defined.

Clustering was carried out on all the data together and then for the northern and southern regions separately.

Results

March groundfish survey

Cluster analysis of the entire region into 3 clusters indicates differences between the north (102, 103, 104, 105), south (101, 107, 108) and division 106 (table 9.1, fig. 9.8). Cluster 1 predominantly represents 106, cluster 2 the southern area and cluster 3 the north.

The main effect of further splitting the area into 5 clusters is a separation in the north, with divisions 102 consisting predominantly of cluster 5 and 103 and 104 consisting predominantly of cluster 4 (table 9.2, fig. 9.9).

	101	102	103	104	105	106	107	108	North	South	106
1	11	5	12	3	6	16	6	0	26	17	16
2	47	9	1	0	4	0	20	24	10	91	0
3	0	34	41	23	40	1	0	0	138	0	1

Table 9.1: March groundfish survey data in 3 clusters by division and by north and south

	101	102	103	104	105	106	107	108
1	11	5	9	3	6	16	5	0
2	37	1	1	0	1	0	14	17
3	4	1	2	0	0	0	6	7
4	0	6	30	15	20	1	0	0
5	6	35	12	8	23	0	1	0

Table 9.2: March groundfish survey data in 5 clusters by division

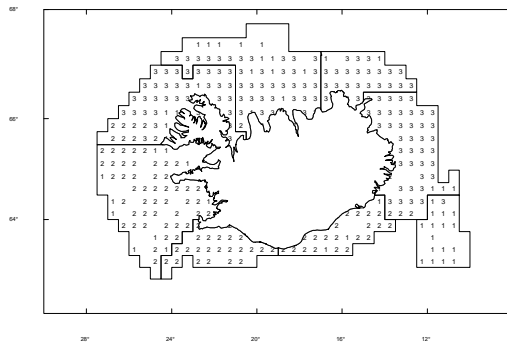


Figure 9.8: March groundfish survey data in 3 clusters

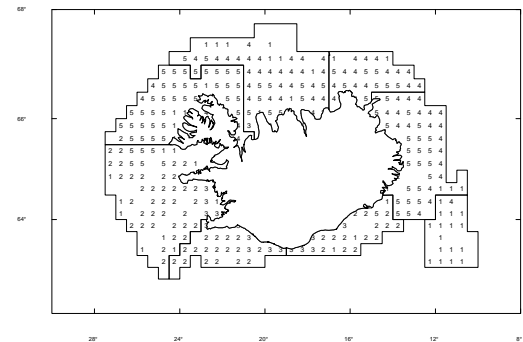


Figure 9.9: March groundfish survey data in 5 clusters

Clustering the northern divisions (102, 103, 104, 105) into 4 clusters reveals some inshore-offshore differences (fig. 9.10). Cluster 4 is coastal (subdivisions 1021, 1022, 1031) and cluster 1 is predominantly the offshore parts of division 102 and subdivision 1054 (previously area 8) (table 9.10).

	1021	1022	1023	1031	1032	1041	1042	1051	1052	1053	1054
1	4	12	9	1	7	2	0	3	1	2	6
2	1	2	0	1	12	1	2	2	1	5	1
3	6	6	1	7	18	10	10	6	10	10	0
4	2	5	0	8	0	1	0	2	0	1	0

Table 9.3: March groundfish survey data: northern divisions in 4 clusters by subdivision

Clustering the southern divisions (101, 107, 108) into 3 clusters also indicates an inshore-offshore pattern of species composition (fig. 9.11) with cluster 3 only being found along the coast (subdivisions 1011 and inshore parts of 107 and 1081) and cluster 2 mainly found in subdivision 1015 the most offshore cluster (table 9.4).

	1011	1012	1013	1014	1015	1071	1081	1082
1	1	8	3	10	13	16	8	10
2	2	2	1	2	11	4	0	0
3	3	1	1	0	0	6	6	0

Table 9.4: March groundfish survey data: southern divisions in 3 clusters by subdivision

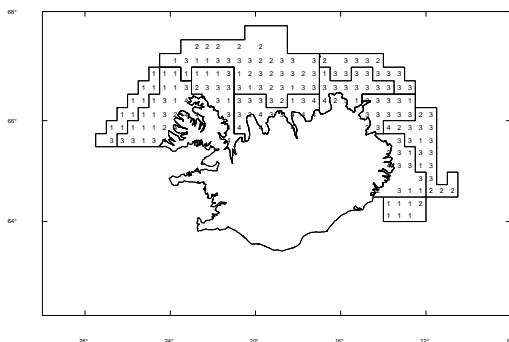


Figure 9.10: March groundfish survey data from the northern divisions in 4 clusters

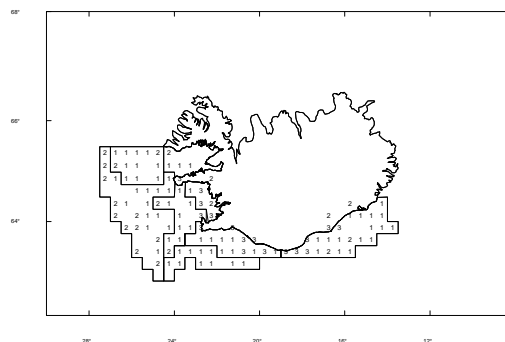


Figure 9.11: March groundfish survey data from the southern divisions in 3 clusters

Autumn survey

Cluster analysis of the entire region into 2 clusters, separates the area into on-shelf and off-shelf (fig. 9.12). With 5 clusters (table 9.5, fig. 9.13) the off-shelf area is split into 2 areas. There is a southwest off-shelf cluster (cluster 1 in table 9.5) incorporating divisions 109 and 114 (along with some of 101 and 108) and in the north cluster 2, which mainly included 111 and 113 with the outer area of 103. The deeper part of division 101 is represented by cluster 3, with the shallow part of 101 along with 108 and 107 in cluster 4. Cluster 5 represents most of divisions 102, 103, 104 and 105.

	101	102	103	104	105	106	107	108	109	110	111	112	113	114
1	4	1	0	0	0	2	3	6	31	0	0	0	0	10
2	0	1	17	6	5	4	0	0	9	3	22	3	16	3
3	27	6	0	0	2	2	2	4	1	0	0	0	0	2
4	8	1	1	0	0	0	5	8	0	0	0	0	0	0
5	3	21	26	13	19	0	3	0	0	1	0	0	0	0

Table 9.5: Autumn survey data in 5 clusters by division

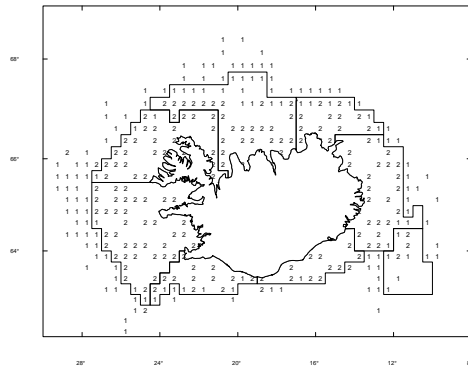


Figure 9.12: Autumn survey data in 2 clusters

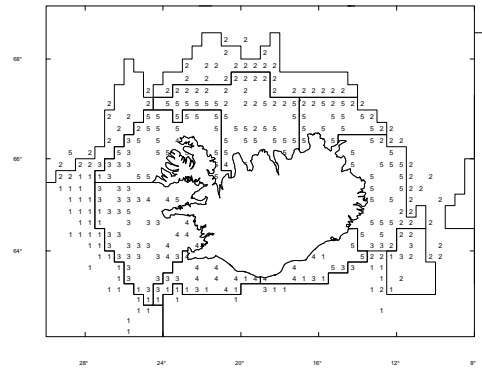


Figure 9.13: Autumn survey data in 5 clusters

Cluster analysis of the northern area into 5 clusters mainly indicates differences related to distance from shore/depth (tables 9.6 & 9.7 and figure 9.14). Cluster 5 is closest to shore, with clusters 2, 4, 3 and 1 tending to move progressively further offshore.

	102	103	104	105	110	111	112	113
1	1	2	0	0	2	13	3	9
2	23	5	4	10	0	0	0	0
3	1	15	6	4	1	9	0	7
4	1	14	7	10	1	0	0	0
5	4	8	2	2	0	0	0	0

Table 9.6: Autumn survey data: north divisions in 5 clusters

	1021	1022	1023	1031	1032	1041	1042	1051	1052	1053	1054
1	0	1	0	1	1	0	0	0	0	0	0
2	6	8	9	2	3	4	0	5	1	0	4
3	0	0	1	0	15	0	6	0	1	2	1
4	0	0	1	1	13	3	4	0	2	8	0
5	1	3	0	8	0	2	0	2	0	0	0

Table 9.7: Autumn survey data: northern on-shelf subdivision in 5 clusters (off-shelf divisions as in table 9.6)

Clustering the southern region into 6 clusters also produces clusters indicating differences in species composition relating to distance from shore/depth (fig. 9.15).

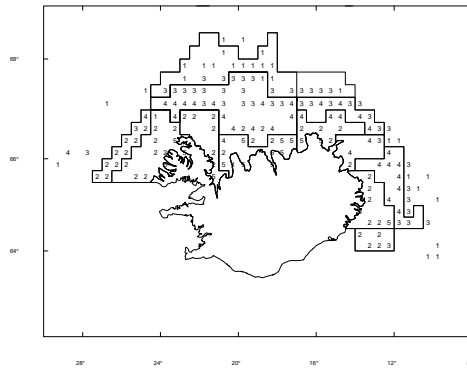


Figure 9.14: Autumn survey data from northern divisions in 5 clusters

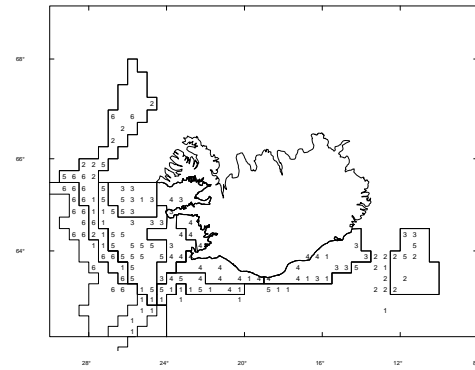


Figure 9.15: Autumn survey data from the southern divisions in 6 clusters

Discussion

Distinct differences in species composition are indicated between the northern divisions (divisions 102, 103, 104, 105), the southern divisions (101, 107, 108), division 106 and those off the Icelandic shelf (deeper than 500m). Within the northern and southern regions, differences in species composition are related to distance from shore or depth. The clusters obtained from the survey data are in sufficient agreement with the divisions and subdivisions for these to be considered appropriate for data storage and area disaggregated modelling.

References

Stefansson, G. and O. K. Palsson (1997). Bormicon a boreal migration and consumption model. Technical Report 58, Marine Research Institute.

9.2 Standardised fisheries database for Icelandic waters

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Introduction

The standardised fisheries database (SFD) for Icelandic waters has been established primarily to aid the development of Gadget models. The position of the SFD in the dst² project is illustrated in fig. 9.16.

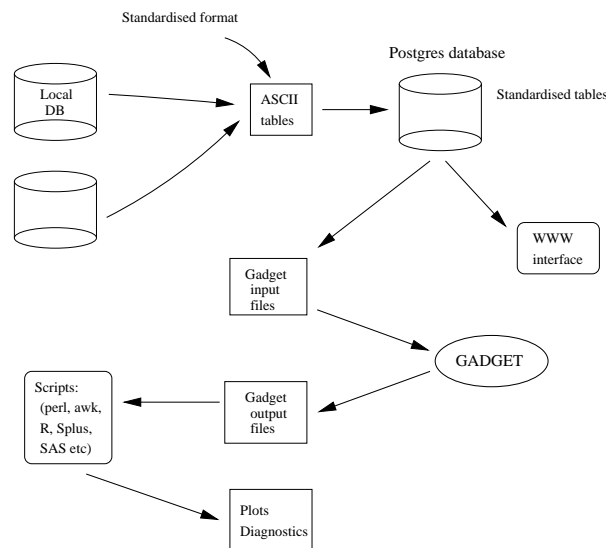


Figure 9.16: Structure of data processing for the standardised fisheries database and Gadget

Data are extracted from the institute database, aggregated, error checked and output as ASCII tables (full definition in Section 2.3). These tables are uploaded into the hierarchical SFD (the tabular structure is defined in Section 2.2). Data can be extracted from the SFD using PostgreSQL (from the command line or using a browser interface) or using routines which can extract data either into the format required for Gadget or for stock assessment. Use of the SFD to create input files for Gadget models simplifies the process of creating new Gadget models.

Database structure

The parts of the SFD covered here are: biological sampling (Station → Species → Sample → Length → Age), stomach tables (Station → Species → Predator → Prey → Prey length/Prey maturity) and log book data (Station → Species → Catch) each of which comprises part of the hierarchical structure, along with mark-recapture (Tagging), landings (Landings) and acoustic (Acoustic) data which are separate tables. The structure of the part of the SFD currently containing data is illustrated in fig. 9.17. The hierarchical structure means that for data to be uploaded a corresponding record (ie identical unique key) must be available at the level above.

The landings table was not in the original SFD definition but it was decided to include it, at least for Icelandic waters, as the existing record of landings is disaggregated by subdivision using log book data which involves manipulating the data. It contains the official landings data by month, species and stock along with vessel and gear class information.

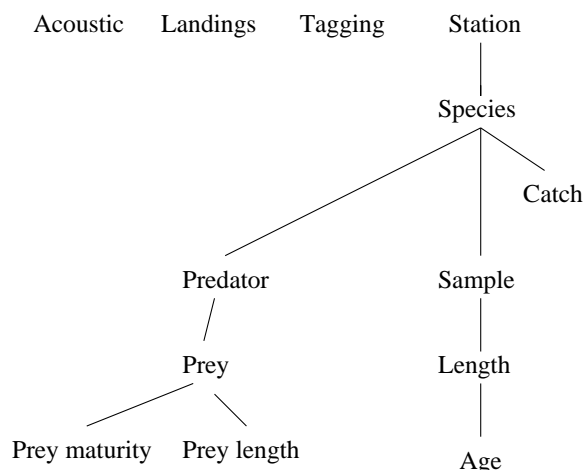


Figure 9.17: Standardised fisheries database structure

Data sources

The areas of the database considered so far are: sampling data, log book data, official catch statistics, stomach data, tagging data and acoustic data.

Landings statistics

All data apart from the landings statistics are collected by the Marine Research Institute. Since September 1992, landings statistics have been collected by the Directorate of Fisheries, prior to that data were collected by Fiskifélag Íslands and those from 1982 to 1992 are available as ASCII files. The data collected by the Directorate of Fisheries are stored in an Oracle database.

Marine Research Institute data

Data at the Marine Research Institute are stored in an Oracle database. This database system has been operating since 1985, with data prior to 1985 being input by year moving back in time. Data are currently being entered for 1972. These data are input into different tabular structures than the post 1985 data and are more thoroughly checked for errors. Simultaneously checks are being made to data forward in time in the main database and these data loaded into the format of the older data but the existing tables are not corrected subsequently. The differences in the structure of the 2 groups of tables and changes to years available in each group (and data quality) needs to be monitored carefully.

The data storage format is similar for most species with capelin and herring the most important exceptions. In the tables recording biological samples (commercial and research) whenever SeaScale (an automatic system used to record and upload data into the institute database) is used, capelin and herring are input in the standard format. Care needs to be taken that this is taken into account when extracting data.

Position is often known, both at the start and end points of each tow, but for older data sometimes only the statistical rectangle (1 degree longitude, 1/2 degree latitude) and subrectangle (1/2 degree longitude, 1/4 degree latitude), or the rectangle alone, are known. The position of shrimp data is identified by an additional system of area definitions.

Stomach data are stored in two formats: pooled data where the stomachs of fish within a length class were pooled and individual sampling when the length of each fish, often along with age, sex and maturity, are available as well as the stomach contents. Individual sampling became the standard method in 1993.

In 1991 log books were made mandatory for vessels larger than 10 tonnes and in September 1999 for all vessels. Limited log book data also exist for some trawlers back to the 1970's.

Acoustic data are not currently stored in the Oracle database but files of interpreted data are available for the capelin survey.

Extraction of the data into the ASCII file format

Data are extracted from the MRI Oracle database into the ASCII standard format using sequences of views and mapping tables.

Tables have been created in SQL which map the codes used in the institute database with those used in the SFD. The conversion of codes is then done by joining the appropriate tables. This makes it easy to see and alter the mappings. For the biological sampling, mark-recapture and stomach data all processing of the data is done using a sequence of SQL tables and views.

The codes used in the SFD are defined in the Look up tables (<http://www.hafro.is/~vojtech/dw>).

In the case of acoustic data the available data files are transformed into the appropriate format within the PostgreSQL database and exported in the AFEF.

Standardised fisheries database definitions

Spatial scale

The finest spatial resolution at which the Icelandic waters SFD stores data is subdivision. Gridcell is defined as a statistical sub-rectangle but no data are currently being stored at this level. The hierarchical spatial structure is described in Section 9.1.

Station positions in the institute database are assigned to a gridcell and mapped from the gridcell to subdivision. Where gridcell is not available, the statistical rectangle is known and an alternative mapping is available for rectangle to subdivision.

In the case of shrimp data, there is an additional set of mappings which can be used to identify subdivision from additional spatial units used in the recording of these data.

Temporal scale

Data are stored by year, quarter and month.

Vessel class and subclass

Vessel class is defined by length < 12m, 12 – 24m and > 24m as for the Celtic Sea and North Sea.

At present, vessel subclasses are research, commercial and foreign. It would be useful to be able to identify some particular types of vessel, such as freezer trawlers and distinguish between boats which are controlled by number of days fishing and quotas, but this cannot be done directly from the database.

Gear class and subclass

Gear class refers to the type of fishing gear, with the range of gear types defined in the institute database considerably reduced. Table 9.8 contains the SFD gear class definitions.

SFD code	Gear type
101	long line
102	gillnets
103	hand line
105	Danish seine
106	bottom trawl
107	pelagic trawl
109	nephrops trawl
110	purse seine
114	shrimp trawl
115	dredge
117	trap
120	various gears

Table 9.8: SFD gear class definitions for Icelandic waters

Gear subclass is only used for cod where it is mesh size (inches) for gillnets. For other gear types the mesh size is referred to (at least approximately) by the combination of gear type, year and sampling type.

Sampling type

Sampling type distinguishes between sampling of commercial catches, various surveys and research sampling not associated with a survey. Table 9.9 contains the SFD sampling type definitions.

SFD code	Sampling type
101	sea sampling
102	harbour sampling
103	sampling by fishermen
110	research, not survey
130	Icelandic ground fish survey
131	offshore shrimp survey
133	0-group survey
134	gillnet survey
135	autumn survey
137	inshore shrimp survey

Table 9.9: SFD sampling type definitions for Icelandic waters

Species information*Length divisions*

The accuracy at which fish lengths are stored is species dependent (Table 9.10).

Maturity stages

Four maturity stages are normally used but shrimp have separate codes and are included as being immature or mature (Table 9.11):

Stocks

Herring is recorded as either being Icelandic summer spawning or Norwegian spring spawning.

Species	length interval
cod	10mm
haddock	10mm
herring	5mm
capelin	5mm
shrimp	0.5mm
redfish	10mm

Table 9.10: Length intervals

Code	description
1	immature
2	prespawning
3	spawning
4	resting
6	mature
10	immature shrimp
11	mature shrimp

Table 9.11: Maturity stages

Shrimp are identified as either being inshore or offshore. As the inshore stocks are limited to small areas, subdivision is sufficient for further definition of inshore stocks in Gadget.

Aggregation of data

The aim of the aggregation is to store data on a scale where the necessity of returning to individual records is minimal but to reduce the size of the database.

Biological sampling

Data are aggregated either by summing or taking the mean. For each record at year, month, subdivision, gear type, species etc the total number of stations, along with the total number of fish sampled, aged, weighed is recorded. In each lengthcell, sex and maturity stage the number of fish is recorded, along with the mean weight and standard deviation of weight. Similarly, mean weight is recorded for age, length, sex and maturity.

The survey index is calculated to be a scaling factor, taking into account the number of fish counted but not measured and the length of the tow. This is done for the Icelandic groundfish survey and the autumn survey.

When ungutted weight is not available but gutted weight is, then gutted weight is used multiplied by a scaling factor.

For capelin and herring data, information on the ship, survey and year is used to identify the data storage method used in the database, to ensure the data are extracted in the correct form for the SFD.

Despite maturity stage and sex being available with the length data in the institute database, they were not used, as the hierarchical structure of the SFD rejected many of these data as they do not agree with the data on maturity and sex in the age table. This is probably due to the data being entered inconsistently. For this reason all data pertaining to maturity stage and sex are taken from the age table in the institute database.

Stomach data

The pooled and individual samples are extracted separately but the aggregation methods are similar and the data are output in the same form. The samplingstrategy column is used to indicate the type of data with 105 and 106 indicating individual and pooled stomachs respectively.

The most common prey are identified to species level (Table 9.12), others are included in as a prey group eg fish, benthos. The grouping system is that used in the institute database.

Latin name	English common name
<i>Gadus morhua</i>	cod
<i>Melanogrammus aeglefinus</i>	haddock
<i>Sebastes marinus</i>	golden redfish
<i>Anarhichas lupus</i>	Atlantic wolffish
<i>Hippoglossus hippoglossus</i>	Atlantic halibut
<i>Hippoglossoides platessoides</i>	long rough dab
-	flatfish
<i>Clupea harengus</i>	herring
<i>Mallotus villosus</i>	capelin
<i>Micromesistius poutassou</i>	blue whiting
<i>Nephrops norvegicus</i>	Norway lobster
<i>Pandalus borealis</i>	deep water prawn
<i>Sebastes viviparus</i>	Norway haddock
Myctophyidae	lanternfish
Lumpenidae	blennies
<i>Lycodes</i> sp.	eelpout
<i>Sebastes</i> sp.	redfish
Gadidae sp.	gadoids
Ammodytidae sp.	sand eels

Table 9.12: Prey included to species or family level in the SFD.

For each predator cell (ie by subdivision, month, species, age, length etc) the total number and weight of each prey group/species is calculated and the corresponding proportion by weight and number.

When prey lengths are stored the total length distribution of each prey species (in numbers and as a proportion) for each predator cell is calculated. Prey sex is also included in this table but is seldom recorded except for capelin in cod stomachs. The final table on prey maturity and weight only includes data on capelin from cod stomachs. The format of the Oracle tables, means that it is not possible to include the maturity and weight data below the length data in the table hierarchy despite the sampling scheme allowing for this.

Digestion stage cannot be included in the SFD, despite being available in the database. The hierarchy of the SFD requires it to be available at all levels and its availability is limited in the database.

Mark-recapture data

Unlike the other tables, mark-recapture data are stored as individuals and the spatial resolution is finer. The gridcell of release and recapture (when appropriate) of individual fish is recorded whenever available.

When fish are double tagged, only one tag is recorded in the SFD. Only data where the release position is known and stations from which records on uncaptured fish are available are included in the SFD.

Log book data

Log book records of catches are used to estimate the catches by subdivision. These are recorded in the table catch both as the values calculated directly from the log books and also scaled to the total landings (by gear type) for the year. When log books are not available, landing harbour indicates the subdivision small boats fished in. This cannot be assumed for larger vessels but a longer time series of log books is available for them.

Landings

The landings data are aggregated by month, vesselclass, vesselsubclass, gearclass, gearsubclass, species and stock.

Data validation

An integral part of the data extraction procedure is to check the source data for potential errors. Additional checks are also done outwith the extraction routines. The aim is to notify the database administrator of errors in the institute database and have them changed at source rather than exclude them from the SFD. This allows for data to be checked, improves the institute database and prevents the exclusion of fish which are merely unusual. When potential errors are found, the original paper records are checked and if necessary otoliths reread.

Most of the error checks within the extraction routines are done using predefined database tables which contain the bounds for each species and data type.

Tests outside the extraction routines

The coordinates (start and end position) are compared with each other and with the statistical rectangle and subrectangle defined in the database whenever data fall outside the existing area definitions,

The timing and gear type of surveys are checked. This has indicated a problem with the current structure of the database and led to a modification of the institute database which enables more accurate identification of surveys.

Maturity and sex codes are checked to ensure they only include defined values.

Any problems with the hierarchy are identified when the data are uploaded into the SFD.

Generic error checks

Database tables of expected bounds for several data types for all species have been created. These are used for more than one data type.

- Minimum and maximum length (range dependent on sampling type.)
- Minimum and maximum age.
- Minimum and maximum length at age.
- Minimum and maximum weight at age.

Biological sampling tables

As the institute database is not strictly hierarchical, it is possible for a length to be recorded at a station in the age file, but not be recorded in the length file. Such errors (which in the past were a side effect of the sampling procedure) are identified. The stations for which more fish have been entered into the age than the length table are also identified.

The problem with the hierarchy also affects the extraction of data relating to maturity and sex.

Stomach data tables

There are some instances where the biological data about predators does not agree with the corresponding data in the age table. It was found that this is a problem with the script to load the stomach data and these fish are not included in the SFD.

The lengths of prey are checked and those outwith a set of bounds are excluded from the SFD. More than one unit of measurement appears to have been used within a prey species causing a wide range of values to be entered into the database. This is the only exception to the policy of including potential errors due to the large number of errors being returned by the scripts.

Mark-recapture data

There are instances where the length of recaptured fish is less than the release length. Although these can be identified, in most cases the discrepancy cannot be resolved. The date of recapture is also checked against the date of release. Fish tagged at age 1 (except when juveniles were being tagged) or less according to their age at recapture are also identified. With the herring data there are some problems: in most cases, only returned fish have been entered in the MRI database as most tagging was done by Norwegian scientists off the Norwegian coast and this has limited the number of data which have been included in the SFD.

Uploading data

Upload of the ASCII file exchange format (AFEF) data into the SFD is possible using the PHP program `dst2up.php`. This program recognises the AFEF format and SFD structure and consistently uploads data into particular SFD tables. Problematic lines that could not be uploaded for some reason are reported in an error file for later scrutiny. For further detail on data import see Section 2.4.

Status of data in the standardised fisheries database

The current status of data in the SFD is summarised in tables 9.13 & 9.14. The tables are described in Section 2.3. Some minor alterations will be made to these data and they will be reuploaded as corrections are made to the MRI database. Data input to the MRI database should be uploaded regularly to the SFD.

Data type	Tables	Species	Years
Biological sampling	1, 12, 5, 6, 7	cod, haddock, capelin, herring	1976 - 2004
Biological sampling	1, 12, 5, 6	shrimp, redfish	1976 - 2004
Stomachs	1, 12, 13, 14, 15, 16	cod, haddock, herring	1979 - 2004
Mark-recapture	10	cod, herring	1991 - 2004
Log book	1, 12, 4	cod, haddock, capelin, herring, shrimp	1982 - 2002
Landings	17	cod, haddock, capelin, herring, shrimp	1992 - 2004

Table 9.13: Status of data loaded in the SFD for Icelandic waters

species	Table 6 LEC	Table 7 AGE	Table 10 TAG	Table 13 PRD
cod	650000	320000	145000	60000
haddock	280000	145000		2043
redfish	130000	20000		
shrimp	115000			
capelin	65000	65000		
herring	45000	45000	59	73
total	1285000	595000	145000	60000

Table 9.14: Number of rows in the Icelandic waters SFD (to the nearest 5000) by table and species.

Extracting data

Data can be extracted from the SFD from the command line using PostgreSQL, using php data extraction routines and with a web browser. The extraction routines which are described more fully in Section 2.5 output data either in a format suitable for Gadget or for stock assessment methods such as VPA.

Gadget

The extraction procedure for Gadget is described fully in Section 2.5.

Creating a Gadget model data set using the extraction package requires a set of scripts. Table 9.15 describes seven sets of commands (each with a filename as indicated) which can be used to output a single species cod model. Likelihood data are from one commercial fleet and two surveys. The likelihood data output from this example are more extensive than would be used in an actual model in order to illustrate the keywords required for the different data types.

The most important demarcation in the extraction of data is between input data and the likelihood data. In some cases all the input files, excepting the fleet data, can be output from a single script. For the likelihood data, however, a new file is required for each fleet or survey. The prefix is required in all scripts to name the output files.

The data groups used in tables 9.15 and 9.16 are described in table 9.17 and in the examples would be contained in a separate file `cod.grp`.

To extract data a typical command would be:

```
dst2input.sh single/Control/fltctl single/Data GFLT
```

Input files

GSPE is a template for the stockfile and requires editing by the user, it assumes that there is renewal (ie recruitment) and standard names are used for the initial value file, renewal file and aggregation files. Some default data types are used: for the initial value file GINI and recruitment file GREC `samplingtype` 130 is the default, although another survey can be selected; for the reference weight file GAVG data from `samplingtypes` 130 and 135 are used and in GREC the weight-length relationship coefficients are taken from a look up table. In GREC `agemin` is assumed to be the age of renewal, if a different age is required then another script would be created with the required `agemin`. For the predicted years, renewal is assumed to equal that of the final year of data selected. It is possible to estimate recruitment data for each year separately (ie different mean and standard deviation of length at age for each year) or to aggregate over the entire time period (same mean and standard deviation of length at age for all years).

When the fleet data are output, the prediction file is created automatically, as is the fleet file which requires editing. The option `fleetscale` scales the catch of the selected commercial fleets to the total catch by year. The catch in kilogrammes for the surveys is input by the user in `survey` and is a dummy value which is essential as it allows the modelled data to be compared with the survey likelihood data.

As temperature data has not been entered into the SFD, temperature for the area file is selected by the user and a single temperature is output for all areas and timesteps.

Likelihood files

Catch and survey likelihood files have different filetypes, the `s` suffix indicates a survey file and `c` a catch file. When a survey filetype is selected, the `gearclass`, `gears subclass`, `vesselclass`, `vessels subclass` keywords are not used and the extraction is based solely on the selected `samplingtype`. For catch filetypes, `samplingtype` is assumed to be from 101, 102 and 103.

The `zerotimestep` keyword is only used for likelihood data and removes all rows when no data are available for a year, area, timestep combination. The `althreshold` keyword is used to remove timesteps with fewer age samples, with `althreshold` set as the minimum number allowed.

The likelihood file is automatically output along with the likelihood data with each subsequent request for likelihood data appended to the existing likelihood file. The appropriate aggregation files are also output with the likelihood data. As these can be overwritten by subsequent requests, files may need to be renamed during the data extraction procedure.

	Input data			Likelihood data			
fi lename	init.ext	ft.ext	rec.ext	catch1.ext	catch4.ext	igfs.ext	aut.ext
keyword	initial values	fbets	renewal	catch		survey	
hostname	haffugl	haffugl	haffugl	haffugl	haffugl	haffugl	haffugl
database	oko3	oko3	oko3	oko3	oko3	oko3	oko3
user	vojtech	vojtech	vojtech	vojtech	vojtech	vojtech	vojtech
groupfile	cod.grp	cod.grp	cod.grp	cod.grp	cod.grp	cod.grp	cod.grp
filetype	GSPE, GARE, GTIM, GAVG, GINI	GFLT	GREC	GLDc, GALDc, GAVWc	GALKc, GAVLc	GLDs, GALDs, GAVLs, GAVWs GALKs	GLDs, GALDs, GAVLs, GAVWs GALKs
years	82-02	82-02	82-02	82-02	82-02	85-02	85-02
areas	IN	IN	IN	IN	IN	IN	IN
timestep	QTR	QTR	3	QTR	QTR	3	10
timesteplabel			1			1	4
gearclass		COD-ALL		COD-ALL	COD-ALL		
vesselsubclass		102		102	102		
fbetscale		1					
samplingtype		130 135	130			130	135
species	COD	COD	COD	COD	COD	COD	COD
lengthcell	10		10	20	40	20	20
lengthcellmin	100		100	100	100	100	100
lengthcellmax	1400		1400	1400	1400	1400	1400
agemin	1		1	1	1	1	1
agemax	12+		5	12+	12+	12+	12+
lmax	1400		1400	1400	1400	1400	1400
amax	14			14	14	14	14
stockname	cod	cod	cod	cod	cod	cod	cod
fbetnames		comm		comm	comm		
surveynames		igfs aut				igfs	aut
prediction	2006	2006	2006				
switch		1					
survey		30000 20000					
zerotimestep				0	0	0	0
alkeyscount	1		1	1	1	1	1
althreshold	1	1	1	100	100	100	100
temperature	5						
outputdir	Input	Input	Input	Input	Input	Input	Input
prefix	cod	cod	cod	cod	cod	cod	cod

Table 9.15: An example of the extraction routines for a simple single species Gadget model

Multistock likelihood data

There are two other types of likelihood data which can be used in multistock and multispecies models: stock distribution and stomach content. Examples of keywords to extract these data types are given in table 9.16.

keyword	Stock distribution				Stomach contents
	Catch		Survey		
	by age	by length	by age	by length	biomass ratio
hostname	haffugl	haffugl	haffugl	haffugl	haffugl
database	oko3	oko3	oko3	oko3	oko3
user	vojtech	vojtech	vojtech	vojtech	vojtech
groupfile	cod.grp	cod.grp	cod.grp	cod.grp	cod.grp
filetype	GSTOc	GSTOc	GSTOs	GSTOs	GPRB
years	82-02	82-02	85-02	85-02	82-02
areas	IN	IN	IN	IN	IN
timestep	QTR	QTR	IGFS	IGFS	HALF
gearclass	COD-ALL	COD-ALL			
vesselsubclass	102	102			
samplingtype			130	130	
species	COD	COD	COD	COD	COD
lengthcell	1400	40	1400	40	100
lengthcellmin	100	100	100	100	100
lengthcellmax	1400	1400	1400	1400	1400
agemin	1	1	1	1	1
agemax	12+	12+	12+	12+	12+
lmax	1400	1400	1400	1400	1400
amax	14	14	14	14	14
maturitystage	1 2,3,4	1 2,3,4	1 2,3,4	1 2,3,4	
sex	F	F	F	F	
preys					CAP COD *
stockname	codi codm	codi codm	codi codm	codi codm	codm
fleetnames	comm	comm			
surveynames			igfs	igfs	
zerotimestep	0	0	0	0	0
outputdir	Input	Input	Input	Input	Input
prefix	cod	cod	cod	cod	cod

Table 9.16: Extraction routines for stock distribution and stomach content likelihood data

definition type	identifier	group(s)
years	82-02	1982 1983 1984 1985 1986 1987 1988 1989 1990 1991 1992 1993 1994 1995 1996 1997 1998 1999 2000 2001 2002
division	IN	101,102,103,104,105,106,107,108
timestep	QTR	1,2,3 4,5,6 7,8,9 10,11,12
timestep	IGFS	3
timestep	HALF	1,2,3,4,5,6 7,8,9,10,11,12
gearclass	COD-ALL	101,102,103,105,106

Table 9.17: Group file commands

Stock assessment

Data in formats appropriate for stock assessment, such as length distributions, age length distributions and catch in numbers at age can be extracted from the SFD using the same keywords as the Gadget data but with different filetypes ie ALK, LD etc.

9.3 A simple implementation of Gadget for cod in Icelandic waters

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Abstract: Gadget is a statistical modelling framework which can be used to create multi-species, multifleet, multiarea models. The development of a complex multispecies model requires understanding of the modelled single species population. Simple single species models also are essential in evaluating whether more complex models increase understanding of the population dynamics. In this paper, Gadget is illustrated using a single species case study with two stock components on one area. Features of the implementation include immature and mature stock components, maturation, predation of the immature stock component and two fleets. Parameter estimation is done using maximum likelihood based on a variety of datasets. The estimated parameters relate to growth, maturation, fleet selection, recruitment, the initial population and consumption. Likelihood data include survey indices, biological samples from the catch and survey and stomach data. Optimisation of the model, along with a protocol to estimate appropriate weighting of the likelihood components are described. The effect of reduced data availability on parameter estimation is also considered, both by aggregating the likelihood component data (eg using coarser length categories) and by excluding age data from the likelihood components.

Keywords: Gadget, statistical model, maximum likelihood, predation, cod.

Introduction

Fishery science deals with the analysis of the interactions between fisheries and the ecosystem, possibly taking into account economic and social aspects. A computer program, Gadget, has been developed to undertake such analysis in as objective a manner as possible, using formal statistical modelling approaches. This paper gives a simple example of the use of Gadget to describe a species consisting of two stock components, immature and mature fish, in a single area. Extensions to more species and areas are described.

Data are routinely collected from the ecosystem, mainly by sampling and measuring fish in various types of surveys and from the fishery in the form of recording the catches, effort and biological sampling of the catches. These two types of biological samples routinely include measurements of the total amount caught, length measurements of individual fish, expensive age measurements from a subset of these and stomach content analysis from an even smaller subset.

Different models of the population dynamics of fish stocks have been able to utilise varying amounts of these data. In recent decades models have been developed to use all of the data through likelihood components when describing species and fleet interactions in spatially disaggregated models.

The Gadget environment has been developed to utilise as many of these data as possible, using appropriate assumptions on each data set.

Basic model setup

Models described in this paper are implemented using the computer program Gadget (Begley 2004), which is a derivative of Bormicon (Stefansson and Palsson 1997; Stefansson and Palsson 1998), which

uses concepts developed in earlier work such as MULTSPEC (Tjelmeland and Bogstad 1989) and MSVPA (Helgason and Gislason 1979). Gadget can be used to implement a wide variety of ecosystem models with only a few possibilities occurring in the present case study.

The model is a parametric statistical model with parameters which can be fitted using maximum likelihood. Internally, the model tracks the number of fish by age and length within each area, time step and stock unit. The development of the ecosystem of all such units is deterministically projected or simulated forward in time resulting in a single realisation of the development of the ecosystem. A single such simulation results in a variety of information including stock trends, mean length and so on, for each stock unit. These simulation results can be compared to data through (negative logs of) likelihood functions. A search algorithm can subsequently be used to estimate values of the unknown parameters.

Denote by N_{almsrt} the number (N) of fish of species s , age a , length l and maturity stage m , alive in region r and timestep t . This group of fish is a subset of the entire collection of fish of a given species. Such a collection will be referred to as a subpopulation (or substock). Mathematically, this is just a collection of numbers, but they are usually unknown and will need to be estimated using statistical techniques.

Normally there are only two maturity stages within the model, immature and mature fish ($m = 0, 1$). In many cases only a fixed species, area, time step and maturity stage are considered and in this case such indices are omitted and the notation is simplified to e.g. N_{al} .

In order to distinguish between predator and prey species in an interaction, the following notation is used:

- s a general species.
- p a prey species.
- P a predator species.
- l a prey length group.
- L a predator length group.

Accordingly, N_{lp} denotes the number of individuals of a prey species p of length l and N_{LP} the numbers in length group L of a predator P . The notation is solely for convenience as there is no reason mathematically to exclude one predator's prey from being another species' predator.

Several processes can affect such a group of fish and cause a change in numbers in the group. The change in numbers can be either due to a transfer of fish between groups or mortality. The various processes available as model components in Gadget are listed here, but a detailed description of components used in the present case study is given in the following section.

- Migration:

Migration is not used in the present case study. The migration a subpopulation undertakes on a given time step can be described by matrices, $A_{almst} = (a_{almsr_1r_2t})_{r_1=1, \dots, R}^{r_2=1, \dots, R}$, containing the proportion $a_{almsr_1r_2t}$ of the population of the subpopulation that moves from area r_2 to area r_1 and R is the number of areas. Hence, if $u = (u_1, \dots, u_R)$ are abundance numbers by area for an age-length-maturity-species group in a subpopulation, the area distribution after the migration has taken place, is $A_{almst}u$.

- Maturation:

Maturation involves shifting fish from a subpopulation of immature fish to a subpopulation of mature fish. This is done using proportions (as in the migration process), which are designed to mimic the resulting proportion of mature fish in each age-length cell.

- Consumption:

Predation causes mortality in the prey stock and can be used to determine the growth of the predator.

- Individual growth:

Within population dynamics models growth in length may be implemented through growth in weight since the weight increase is more naturally linked to consumption. In this case, the target weight increase, ΔW is a function of consumption and fixing a length-weight relationship of the form $W = aL^b$ can give an approximate average length increase through e.g. a Taylor approximation. Alternatively, as used in the present case study, the length growth is according to a specified functional form and a length-weight relationship is used to implement growth in weight.

Regardless of which method is used to compute ΔW , the length increase ΔL needs to be implemented through an update mechanism which moves fish between length groups in such a fashion that the average movement corresponds to a length growth of ΔL . Growth in length is therefore modelled through the use of growth update matrices. The matrices are described in a parametric manner but the resulting growth needs to match the average growth of ΔL .

- Natural mortality:

In addition to predation/fishing, “other” natural mortality is implemented in the usual fashion, viz

$$N_{a,t+1} = e^{-M_a \Delta t} N_{a,t}.$$

- Ageing:

The last time step of a year involves increasing the age by one year, except for the oldest age group which is a plus group.

- Spawning:

A (mature) subpopulation may generate offspring and lose biomass. This possibly results in spawning mortality.

A case study

The primary case study considered in the present paper considers two stock components of cod, i.e. mature and immature cod in Icelandic waters which are considered a single area. This will illustrate biological assumptions which need to be made and several statistical estimation issues.

Since mature cod consume immature cod, the present setup will illustrate statistical incorporation of stomach content data into the estimation procedure, as well as a variety of other data sources.

The emphasis of the case study is the illustration of complex estimation issues and how these can be solved. It is important to note that using simpler models tends to ignore these issues rather than solve them. This becomes particularly obvious when Gadget is used for estimation, since the approach permits the user to either estimate or fix values of parameters and as it turns out, values for, or relationships between parameters do need to be assumed since they are in some cases very poorly determined.

Several important multispecies interactions are known to be of importance in the marine ecosystem off Iceland (Stefansson et al. 1998b).

This particular case study does not take into account capelin, the major food source of cod. Hence the effect of consumption on the growth of the predator will not be included as a part of the model, though this is known to be an important factor (Magnusson and Palsson 1991; Steinarsson and Stefansson 1991). For the same reason, temperature or other environmental factors are not included (though they certainly could be). The environmental effects are known to exist and be considerable (Stefansson et al. 1998b) and should be included, at least as a factor affecting metabolism if capelin is included, though these effects may also be taken into account to describe catchability changes (Stefansson and Eiriksson 1998).

On the other hand, predation as a source of mortality can be important (Bogstad et al. 1994) and this is taken into account in the present model, but only with regard to the predation of mature cod on immature cod. Other factors, such as marine mammals may potentially be important (Stefansson et al. 1998a).

The biological model: Component processes

Growth

For immature cod, growth is assumed to be according to a von Bertalanffy equation (9.1).

$$L_t = L_\infty (1 - e^{-Kt}), \quad t \in \mathbf{R}_+, \quad (9.1)$$

Suppose fish of a given age, a , happen to be of length l . The growth is given by

$$\Delta L = L_\infty \left(1 - \frac{L}{L_\infty}\right) (1 - e^{-K\Delta t}) \quad (9.2)$$

$$\simeq K(L_\infty - L)\Delta t, \quad (9.3)$$

where the approximation is either based on the Taylor approximation (9.3) to the exponential function or, alternatively, the approximation is simply based on discretising an appropriate differential equation. Although the approximation is commonly used, it is not quite adequate for general use in Gadget since it is virtually impossible to simulate exact processes using the approximation and hence the exact formula (9.2) will be preferred to (9.3) in this case study.

In the present paper the growth in weight and growth in length will be assumed to be linked and a length-weight relationship of the form

$$W = cL^b \quad (9.4)$$

is used as a basis. In this relationship, c becomes the condition factor, $c = W/L^3$ when $b = 3$ but c has little direct meaning otherwise.

It should be noted that when l is greater than L_∞ , growth should become negative according to the growth equation. The implementation of the equation in Gadget does not allow for l to be greater than L_∞ which should exceed the maximum length defined in the model.

Also, the average growth of a group of fish next needs to be translated into a new distribution of these fish in a subsequent time step. This will be handled in subsequent sections.

Updating length distributions

Fish population dynamics are modelled in MULTSPEC and Gadget through forward simulations of fish populations, allowing fish to migrate between areas, die, grow, mature and spawn. The basic unit in these models is the number of fish in a certain model unit or “cell”. The fish in a “cell” are in the same age and size group, in the same region and time step. When this basic model formulation is used, the numbers in a “cell” need to be updated during a given time step, so as to reflect all processes being modelled. In addition to growth, these processes include migration, spawning, natural and fishing mortality.

Starting with a specified average length increment (ΔL) fish need to be distributed from their initial length class into upper length classes in a reasonable manner. Simple techniques may use only few upper length intervals and use a simple ad-hoc update scheme. The update scheme should eventually be evaluated in terms of its ability to provide adequate eventual length distributions. This sets some immediate bounds on the dispersion at each time step, since an overly high or low variance in the length update will quickly result in inadequate final length distributions at age for the oldest ages.

The length update scheme can most easily be implemented through a look-up table, where a discrete set of ΔL -values is provided along with the distribution to be used for reallocating the length group when the chosen growth is ΔL . This approach, used in earlier Bormicon, MULTSPEC and Fleksibest implementations (e.g. Stefansson and Palsson (1997)), is undesirable for many reasons. Firstly, the setup is completely rigid as there is no built-in parameter to describe possible deviations of growth from

the specified distribution and hence data on growth may adversely affect parameters in other parts of a complex model only because of incorrect specification of the rigid relationship. Secondly, a simple discrete (rounded) lookup provides a nondifferentiable likelihood function which will result in estimation problems later on.

What is needed is a way to specify a flexible parametric distribution with enough parameters to allow minimal flexibility to track length distributions of an age group, yet with enough parsimony in parameters to allow for the estimability of the parameters involved.

Consider fish of a specified length, L , which are destined to grow on average ΔL , according to the growth model. A model for the update will assign probabilities, p_j of a fish in the original cell growing by j length groups. Denote the absolute length increment corresponding to j length groups by δl_j . These probabilities must then satisfy the obvious restrictions

$$\begin{aligned}\sum_j p_j &= 1 \\ \sum_j p_j \delta l_j &= \Delta L.\end{aligned}$$

Since the present approach is length-based, the weight needs to be updated in synchrony with the length increase. Consider therefore fish of length L with an average weight of W , which are due to increase in length by δl_j from length L . Although it is possible to use Taylor approximations to the length-weight relationship, as implemented in Bormicon, a more internally and mathematically consistent approach is to maintain length-weight relationships exactly. This can be done by defining the upcoming weight increment of this group of fish as

$$\delta w_j = c(L + \delta l_j)^b - cL^b.$$

The mean weight in the receiving group is subsequently updated using prior and incoming numbers and mean weight in the group.

The result of this approach is that if fish start out so that the length-weight relationship holds exactly for all length cells, then this relationship is maintained throughout the simulation. In the present case study, however, the initial weight at length is determined from smoothed data and hence the length-weight relationship is not precisely maintained.

A formal model for the growth update is defined in Section 4.2.

Alternative growth formulations

An alternative set of growth functions is obtained by basing length growth on weight growth and computing weight growth from consumption. In order to verify different methods of implementing growth, it is useful to be able to link these approaches together and this can be done in Gadget (Begley 2004).

The general case will involve consumption and therefore growth in length and growth in weight will not always conform strictly to a length-weight relationship. Notably, if fish do not get enough food, they will typically lose weight but not get shorter. This effect can be accounted for within Gadget but is not implemented in the present case study.

Predation, including fishing and consumption

The consumption of a prey by a predator is defined through the following set of equations. Consider a fixed area and time step so the notation can be simplified to indicate only the length of predator and prey.

The suitability function, $S_{P,p}$ is viewed as a function of two variables, the length of the predator and prey.

$S_{P,p}(l, L)$ the suitability of length group l of prey p as food for length group L of predator P .

As a function of l , over the domain of prey length groups, the form of this function can be for example, strictly increasing or dome shaped. The function needs to reflect the relative desirability of one prey size group to another for a given predator size group.

In this case study the suitability function is given by

$$S_{P,p}(l, L) = \begin{cases} p_0 + p_2 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_4}} & \text{if } \ln \frac{L}{l} \leq p_1 \\ p_0 + p_2 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_3}} & \text{if } \ln \frac{L}{l} > p_1, \end{cases} \quad (9.5)$$

with five parameters allowing an asymmetric relationship about the optimal predator prey size ratio.

Define the auxiliary function ϕ_P by

$$\phi_P(l, L, p) := S_{P,p}(l, L) N_p(l) W_p(l), \quad (9.6)$$

which simply weights the prey biomass according to its suitability. This is used to define the *feeding level*

$$\psi_P(L) := \frac{\sum_{l,p} \phi_P(l, L, p)}{\sum_{l,p} \phi_P(l, L, p) + A}, \quad (9.7)$$

where $A = A_1 A_2$ is a constant, commonly separated into the size of the area, A_1 and a constant A_2 representing the prey density at which consumption is half the maximum consumption.

The *target consumption*, i.e. the amount which length group L of P will consume of length group l of p , assuming that enough food is available, is then given by the equation

$$\tau_{P,p,L,l} = N_P(L) H_P(L, T) \psi_P(L) \frac{\phi_P(l, L, p)}{\sum_{l,p} \phi_P(l, L, p)}, \quad (9.8)$$

where T denotes area-specific temperature and the function H is termed the *maximum consumption* which is given by

$$H_P(L, T) = m_0 e^{(m_1 T - m_2 T^3)} L^{m_3}. \quad (9.9)$$

For each prey an upper limit needs to be set on the total amount consumed by all predators so as not to obtain more consumption than available biomass. Consumption is limited to 95% of the available biomass. This is implemented by scaling target consumption by all predators through the understocking likelihood component, given by the equation

$$\ell = \sum_{\text{time areas}} \sum_{\text{predators}} \left(\sum U \right)^g,$$

where U is the understocking that has occurred in the model and g is a constant.

Commercial catches can be implemented using the predation procedure, by setting the *target catch* directly equal to the observed catch and using the same scaling mechanism as for (other) predators when prey biomass is too low to sustain total predation (including catches).

Alternatively, commercial or survey catches can be set to be linearly related to the abundance numbers of the preys. In this case, the amount caught of length group l of the prey p on the area a and time step t by fleet P is

$$\tau_{P,p,L,l} = cE_{t,a}\phi_P(l, L, p) \quad (9.10)$$

$$= cE_{t,a}S_{p,P}(l, L)N_p(l)W_p(l) \quad (9.11)$$

where the effort measure $E_{t,a}$ is a parameter, c is a constant and L is a number appropriate for scaling the suitability function into a selection pattern for the fleet.

Available raw and basic data summaries

Data collection

Biological data are collected by the Marine Research Institute as a part of a standard monitoring programme and data on landings are collected by the Directorate of Fisheries. In both cases all data are stored in Oracle data bases. The data of interest to the current case study are:

- Landings data by species, fleet and month.
- Age, length and maturity measurements from surveys and biological sampling of the catch.
- Stomach data
- Survey indices

Data Warehouse

Data input to Gadget is normally through a data warehouse, which is used to store data at a minimally aggregated level (i.e. highly disaggregated) and described in Chapter 2. In this case study data from the MRI data base are aggregated onto the subdivisions set out in Section 9.1. Aggregations are through simple arithmetic summaries (averages or sums, as appropriate). Input data files and likelihood data files can be extracted from the data warehouse with the user defining the level of aggregation to be output.

Data and likelihood functions

As indicated in Stefansson (1998), a statistical multispecies model can be based on a variety of different data summaries, but care must be taken not to use the same information twice, e.g. both through mean length at age and as length distributions with age-length keys.

It is important to aggregate the data to a level at which coverage of the selected length/age interval is adequate as zeros are taken to mean zero. Timesteps with low sampling or sampling restricted to a limited range of length/age groups may result in zeros which are an artifact of sampling and unrepresentative of the population. This is true for all likelihood components.

The data used in the current analysis consist of measurements from commercial catches and the two main groundfish surveys. Not all months have measurements for all fleets and in particular the groundfish surveys each occur only in a single month. Each of these data sets is linked to the model through a likelihood component. Given the problems inherent in mixing likelihood components corresponding to different probability distributions and in particular the known problems with a multinomial distribution being inadequate for length distributions, only normal distributions are used and each negative log likelihood component is simply a (weighted) sum of squares.

Data used in the case study are:

Input data:

- Landings data are obtained from the Directorate of Fisheries data base.

Biological sampling likelihood data:

- Length distribution, aggregated on 2 cm intervals, from sea and harbour sampling of commercial catches by month from 1984 to 2002.
- Length distribution, aggregated on 2 cm intervals, from the March groundfish survey (Palsson et al. 1989) from 1985 to 2002.
- Age length composition, aggregated on 4cm intervals, from commercial catches by month from 1984 to 2002.
- Age length composition, aggregated on 4 cm intervals, from the March groundfish survey (Palsson et al. 1989) from 1985 to 2002.
- Age composition from the March groundfish survey (Palsson et al. 1989).
- Age composition of the commercial catches by month from 1984 to 2002.

These likelihood data are of the same class – biological sampling – with all ages aggregated for the length distributions and all lengths aggregated for the age distributions. The sum of squares likelihood function is

$$\sum_{time} \sum_{areas} \sum_{ages} \sum_{lengths} (p_{tral} - \pi_{tral})^2$$

where

p is the proportion of the data sample for that time/area/age/length combination

π is the proportion of the model sample for that time/area/age/length combination.

Stock composition likelihood data:

- Number immature and number mature at length in 2cm length classes from the March groundfish survey (Palsson et al. 1989).

This groundfish survey is undertaken at a time when the maturity stage is easily determined and is unaffected by the potential biases due to targeting of the mature stock component by the commercial fleet. Although the maturation process in Gadget can be age and length dependent, in this case study only length is taken into account and ages are aggregated.

The sum of squares likelihood function for this component is

$$\sum_{time} \sum_{areas} \sum_{ages} \sum_{lengths} \sum_{stocks} (p_{tral} - \pi_{tral})^2$$

where

p is the proportion of the data sample for that time/area/age/length/stock combination

π is the proportion of the model sample for that time/area/age/length/stock combination.

Survey index likelihood data:

- Three survey indices from the March survey (Palsson et al. 1989) (figure 9.18) with one datum for each group for the years 1985–2002.

- Three survey indices from the autumn survey (Sigurdsson et al. 1997) (figure 9.18) with one datum for each group for the years 1995–2002.

Three indices are calculated for each survey by splitting the length distribution into three groups with the division based on the 'typical' structure of the length distribution for the survey over all years. These groups represent age 1, age 2 and age 3 and older.

The likelihood component for these data is the sum of squares of a log linear regression with the slope and intercept estimated or with the slope fixed and only the intercept estimated.

$$\ell = \sum_{time} \left(\ln(I_t) - (\alpha + \beta \ln(N_t)) \right)^2$$

where I is the observed survey index and N is the corresponding index calculated in the model.

In this case study, the slope and intercept are estimated for length groups 1 and 2 with the slope fixed to 1 for the third length group.

In figures 9.18 & 9.19 it can be seen that for length groups 1 and 2, the surveys provide similar information for the overlapping years (correlations of 0.59 and 0.92 for length groups 1 and 2 respectively) but there is conflicting information from the third length group (correlation of -0.15), which could be due to differences in the spatial distribution or depth in the water column of the mature stock component at the time of the surveys.

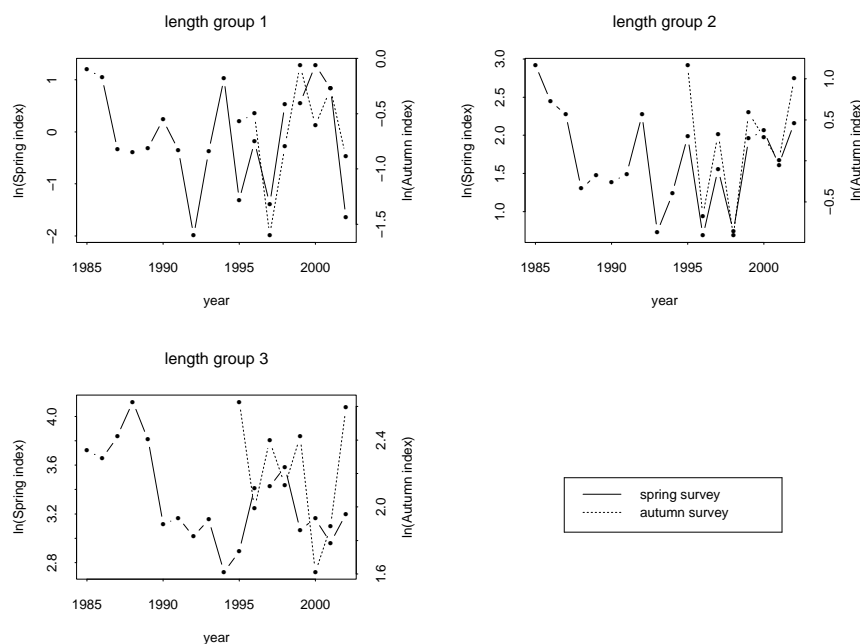


Figure 9.18: Survey indices for the spring and autumn surveys for each length group, with the y axis for the spring survey on the left and for the autumn survey on the right.

For both the spring and autumn surveys there is a positive relationship between length group 1 and 2 indices, as indicated in figure 9.3) with correlations of 0.84 and 0.66 for the spring and autumn surveys respectively.

Stomach content likelihood data:

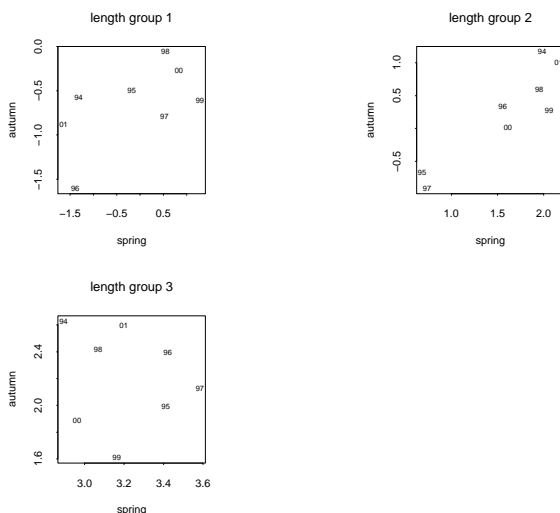


Figure 9.19: Scatter plots of the autumn survey vs the spring survey for each length group on a log scale.

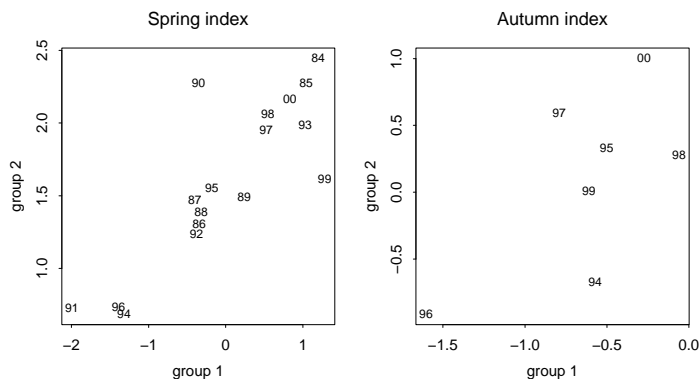


Figure 9.20: Scatter plots of the length group 2 index against the length group 1 index for each survey on a log scale with each point labelled with the cohort year.

- Composition of stomach contents as ratios of prey biomass by species (i.e. cod or other) aggregated over all predator lengths from the March groundfish survey for 1985–2002.
- Composition of stomach contents ratios of prey biomass by species (i.e. cod or other) aggregated over all predator lengths from other stomach sampling projects.
- Length distribution of prey by predator length groups as biomass ratios from the March groundfish survey for 1985–2002. Predators are aggregated into 10cm length groups and prey into 4cm length groups.
- Length distribution of prey by predator length groups as biomass ratios from other stomach sam-

pling projects. Predators are aggregated into 10cm length groups and prey into 4cm length groups.

The likelihood component for the stomach data biomass ratios is given by

$$\sum_{time} \sum_{areas} \sum_{prey} \sum_L \sum_l (p_{prey,L,l} - \pi_{prey,L,l})^2$$

where

p is the proportion of the data sample for that time/area/prey/predator size group/prey size group combination

π is the proportion of the model sample for that time/area/prey/predator size group/prey size group combination

Species biomass ratios and prey length distributions are available for all years of the spring groundfish survey. Data other than those from the spring survey are available for 39 timesteps from 1994 onwards with prey length distributions for all but 2 of the steps with cod prey recorded.

It should be noted that a particularly simple sum of squares is used as the log likelihood in all cases. There are several reasons for this, all somewhat technical (e.g. Section 5.5).

Model Implementation

The model runs from 1984 to 2002 on one area with two cod components – immature and mature. The immature are aged 1 to 10 and the mature ages 3 to 12, with the final age a plus group. Immature fish mature according to the maturation function and any not mature by the end of their tenth year move into the mature component. A single commercial fleet operates.

- Length growth is defined by equation 9.2 with k estimated within Gadget and L_∞ fixed to a value estimated directly from sampled catch and survey data. The betabinomial parameter β is fixed to 1000 with maximum length group growth $n = 10$.

Weight growth is according to equation 9.4 with different weight length relationships for the immature and mature components. The values of c and b were calculated from survey data and subsequently fixed.

- The function for maturation is:

$$M(l_t, a_t) = \frac{1}{1 + e^{-\alpha - \beta l_t - \gamma a_t}} \quad (9.12)$$

As maturation in this case study is only a function of length, the age parameter γ is set to zero. β the length of 50% mature and the rate α are estimated within the model.

- Mortality at age is fixed.
- The mean and standard deviation of length of the initial populations were calculated from survey data and output from the datawarehouse. The weight-length relationships used for weight growth were also used for the initial population.
- The number at age of the initial population (ages 2 to 12) is estimated within the model, with the age distribution estimated and then a multiplier used to scale the population abundance.
- Mean and standard deviation of length of the age 1 recruits estimated from the March survey for each year.
- The number of age 1 recruits for each year (1984–2002) is estimated within the model.

- To enable the age structure of the initial population to be estimated independently of the survey indices there is an additional parameter (*mult*) which can be used to scale the abundance of the initial population with the age structure fixed.
- Selection of the spring survey and commercial catch are described by:

$$S(l, L) = \frac{\delta}{1 + e^{-\alpha - \beta l - \gamma L}} \quad (9.13)$$

with $\gamma = 0$, $\delta = 1$ and α and β estimated for each fleet separately.

- Selection of immature cod by mature cod is defined by equation 9.5 with $p_0 = 0$, $p_2 = 1$ and the other parameters estimated within the model.
- As cod growth is not linked to consumption, there is no constraint from growth on the total consumed. If consumption in the wild is taken to be half that of maximum consumption estimated from feeding experiments, then parameter estimates are available. Maximum consumption is defined in equation 9.9 and can be parameterised from the daily food intake equation from Jobling (1988) to

$$H_P(L, T) = m_0 e^{(0.104T - 0.000112T^3)} L^{2.406}$$

assuming that $W = 0.01L^3$ with W in grammes and L in cm.

If the prey is cod, with an energy content of 4.2kJ/g then $m_0 = 1.98 \times 10^{-5}$ results in consumption of half the monthly maximum in kilograms. For the *target consumption* $\tau_{P,p,L,l}$ to then be half the maximum possible consumption, the *feeding level* is then required to be $\psi_P(L) = 1$ which is achieved by setting the constant $A_2 = 0$.

Technical details

As noted by several authors (e.g. Methot (1989)), considerable attention needs to be given to the weights attributed to each negative likelihood component. Weights here are obtained based on the method proposed by Stefansson (1998) & Stefansson (2004). The initial weights are set to the inverse of the negative likelihood function at the initial parameter values, which are arbitrarily chosen. At this stage the total negative likelihood score at the starting point is equal to the total number of components. The specially developed iterative reweighting scheme of Stefansson (2004) is subsequently used for estimation.

Each component is taken in sequence, first the weight of that component is multiplied by 1000, the likelihood function is then minimized and the result for this particular likelihood component is taken as a measure of how well the model can best fit to this data set. That best (minimum) value, scaled to the number of data points (degrees of freedom), is used as a variance estimate, to become an inverse final weight for this component. While the number of terms is easily determinable for some likelihood components, such as survey indices, it is less clear how many should be assigned to data types such as age-length keys for which many values are expected to be zero. In this example, the degrees of freedom for age-length keys were estimated by deciding upon a number of potentially informative length cells for each year/step/age cell. As there is only one datum for each survey index in each year, the equivalent indices for the spring and autumn surveys are weighted simultaneously.

Ideally the subsequent point estimate would be based on these iteratively chosen weights. Unfortunately, the different likelihood data sources, even with similar objective functions, are not equivalent. In particular, the survey indices are considerably more constrained than the biological sampling data (i.e. length distribution, age length keys and age distributions). For this reason the final parameter estimation is done sequentially with the order of parameter estimation, to a certain extent, model dependent. There is, however a general procedure. Parameters associated with the biological sampling likelihood components are estimated first with the weights on all likelihood components as estimated from the iterative

procedure. These parameters (e.g those for growth and the age structure of the initial population) are then fixed and the weights on the likelihood components set to zero. Parameters associated with the survey indices (including the initial population multiplier) are then estimated.

Results

Parameter estimation and model evaluation are described for a variety of models: a basic cod model with two stocks (immature and mature) and no predation, the same model with predation by mature cod, the basic model with no age disaggregated likelihood data and the basic model with the likelihood data aggregated in 10cm length groups. In each model there are a variety of data components and the emphasis of different datasets can be seen to push the solution in different directions.

Model with no predation: model 1

The minimum sum of squares from the iterative weighting procedure described on page 363 are given in table 9.18 for the biological sampling and maturity ratio likelihood components and table 9.19 for the survey index components. Bounds and understocking are zero for all optimised runs and ignored here.

Tables 9.18 & 9.19 illustrate the conflicting information from the different data sources. For example, in table 9.18 the minimum sse from weighting the survey age distribution (ADs) is 0.094 whereas the same component has a score of 0.534 (a value 5.7 times greater) when the catch age distribution is heavily weighted. The information from these data sources is clearly contradictory within the structure of this implementation of Gadget.

	mat	LDs	LDc	ALKs	ALKc	ADs	ADc	base	final
mat	0.131	0.36	0.403	0.274	0.336	0.229	0.325	0.307	0.294
LDs	0.612	0.046	0.126	0.18	0.142	0.164	0.122	0.17	0.07
LDc	3.745	2.744	1.184	4.2	2.629	19.13	1.895	3.372	1.646
ALKs	0.534	0.273	0.84	0.088	0.152	0.11	0.169	0.155	0.213
ALKc	7.931	5.838	15.02	3.804	2.983	13.9	3.278	4.312	5.13
ADs	2.3	0.768	1.679	0.279	0.501	0.094	0.534	0.604	0.716
ADc	29.02	13.19	49.65	14.13	8.726	55.43	7.422	15.4	13.09

Table 9.18: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation. The baseline values are given in the column 'base' and those of the final run in column 'final'. These components are from the biological sampling likelihood components (LD – length distribution, ALK – age length key, AD – age distribution, with s and c indicating whether survey or catch data) and the ratio of immature to mature fish (mat).

The difference in information deriving from the different components is particularly large for the survey indices (table 9.19). For example the likelihood scores for length group 1 are seven to eleven times greater when length groups 2 or 3 are heavily weighted.

	I_1	I_2	I_3	base	final
I_{1S}	1.119	12.46	11.2	3.837	3.699
I_{2S}	3.527	0.512	6.189	0.634	0.825
I_{3S}	1.578	1.199	0.56	1.243	0.649
I_{1A}	0.156	1.148	1.203	0.75	0.769
I_{2A}	2.207	0.005	3.793	0.01	0.001
I_{3A}	1.525	1.005	0.424	0.995	1.194

Table 9.19: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation – with two indices heavily weighted in each optimisation. The base run values are given in the column ‘base’ and those of the final run in the last column. These components are survey indices where I_i , $i = 1, 2, 3$ are the length groups and the S, A subscripts indicate the spring and autumn surveys.

The weights determined from the iterative procedure are shown in table 9.20 along with the ratio of the sum of squares from the final model to the minimum for each component (tables 9.18 & 9.19). As a result of incorporating information from the different data sources, the final sse for each component is greater than the minimum from the iterative weighting. For length group 2 of the survey indices, the total score is greater although the score for the autumn index alone is lower in the final model. The ratio of final see to minimum sse suggests that relatively more information is retained from the catch than the survey data (table 9.20).

Component	Weight	sse_f/sse_m
mat	6032	2.24
LDs	26333	1.52
LDc	10358	1.39
ALKs	34200	2.42
ALKc	8335	1.72
ADs	2307	7.62
ADc	236	1.76
I_{1S}	16.09	3.31
I_{2S}	35.18	1.61
I_{3S}	32.13	1.16
I_{1A}	51.35	4.93
I_{2A}	1514	0.20
I_{3A}	18.87	2.82

Table 9.20: Component weights calculated from the minimum sums of squares and sse_f/sse_m , the ratio of the sums of squares from the final model (sse_f) with the minimum sse (sse_m) from the iterative weighting.

Parameter estimation using the weights in table 9.20 was done in three stages. 1) all likelihood data were used, 2) growth, selection (catch and survey) and initial population parameters were fixed, the LD, ALK and AD weights were set to zero and the initial population multiplier was used 3) maturity parameters fixed and the maturity likelihood data to zero. The parameters estimated from the procedure are shown figure 9.21.

Plots of the fitted log-linear regression are shown in figure 9.22. The slopes for length group 1 are 1.64 and 0.54 for the spring and autumn surveys respectively and for length groups 2 the slopes are 1.62 and 1.83. The highest weight of the survey indices is for length group 2 of the autumn survey (table 9.19) and consequently the modelled population fits this component particularly well. For the survey indices, the largest decreases between the likelihood score from the weighted run and the final run are for length groups 1 and 3 of the autumn survey which can be seen to have the worst fit to the modelled population (figure 9.22).

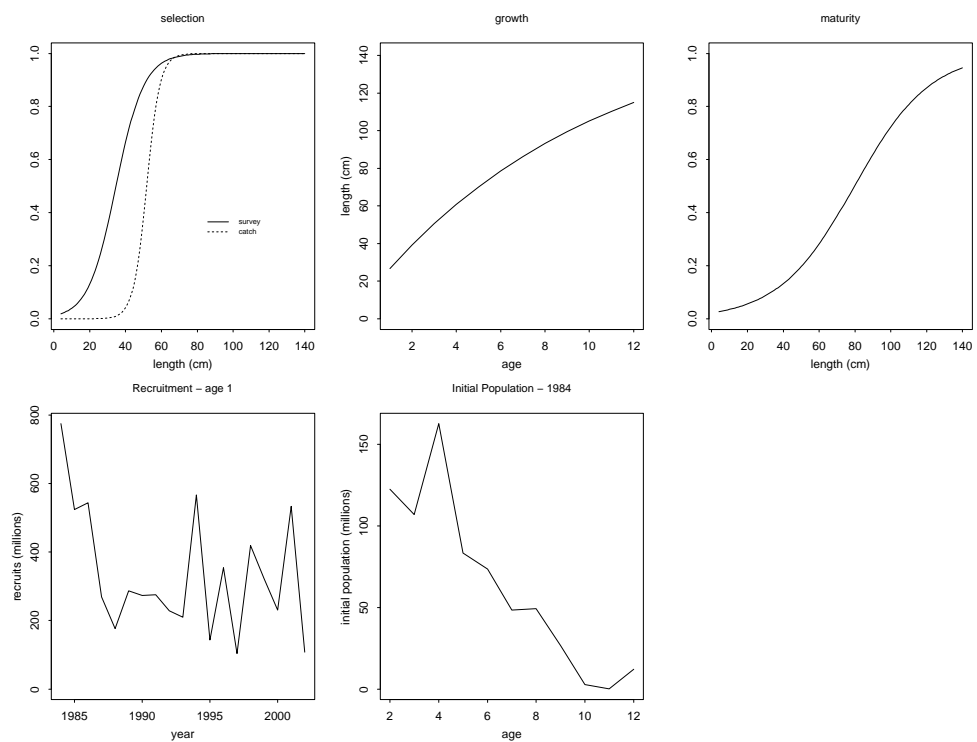


Figure 9.21: Parameter estimates from the final optimisation: selection patterns of the spring survey and catch, growth, maturation, number of age 1 recruiting into the model and the initial population age 2–12

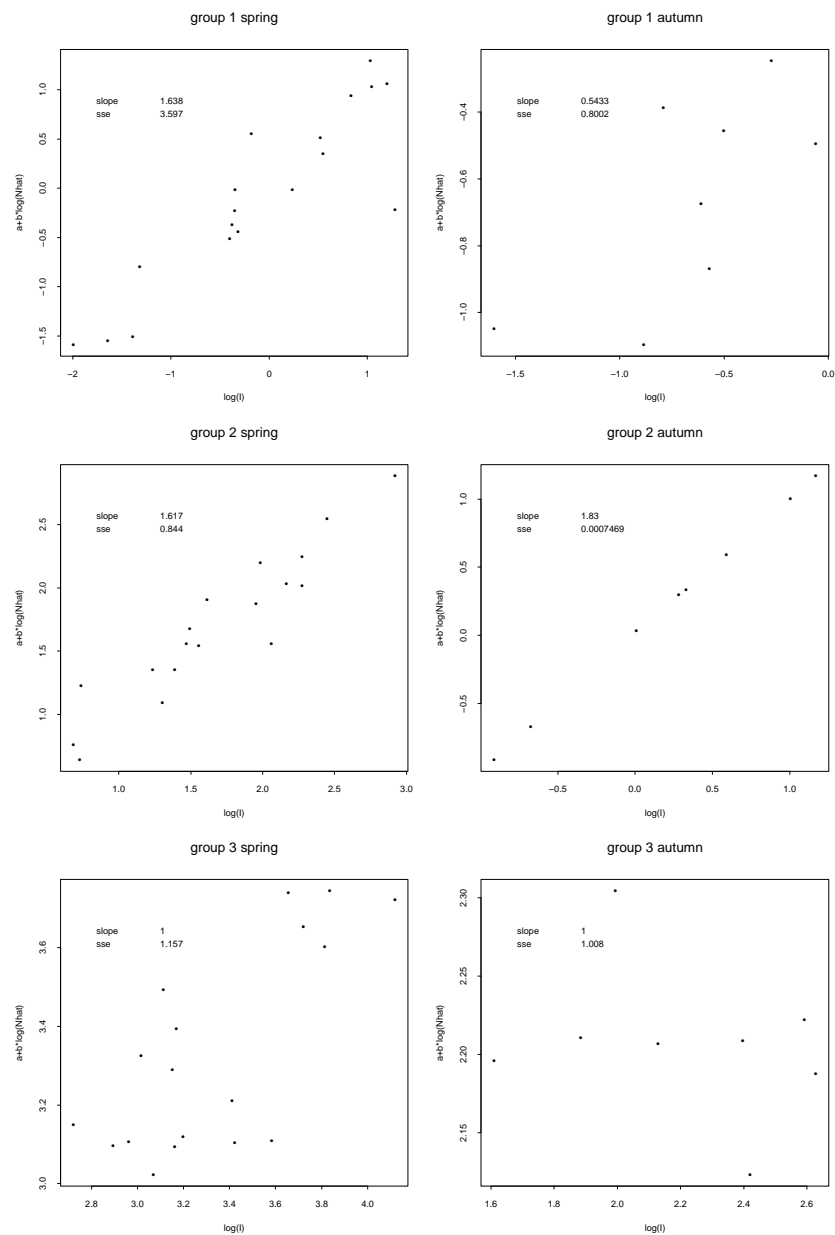


Figure 9.22: Plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b \cdot \log(N)$ the regression fitted to the modelled population.

Model with predation: model 2

The minimum sums of squares from the iterative weighting procedure are given in table 9.21 for the biological sampling and maturity ratio components and table 9.22 for the survey indices. In addition, table 9.23 contains the minimum sums of squares for the stomach data likelihood components. Bounds and understocking are zero for all optimised runs. The similarities in the values from model 1 and model 2 (comparing tables 9.18 & 9.21 and tables 9.19 and 9.22) indicates that the parameter settings for the optimisation routines and the results of the optimisations are adequate.

	mat	LDs	LDc	ALKs	ALKc	ADs	ADc	base	final
mat	0.085	0.472	0.462	0.209	0.328	0.963	0.358	0.222	0.235
LDs	0.3729	0.037	0.139	0.168	0.126	0.148	0.124	0.083	0.07
LDc	10.3	6.315	1.087	6.502	2.742	16.99	2.516	1.514	1.523
ALKs	0.2219	0.246	0.611	0.081	0.162	0.191	0.2	0.141	0.211
ALKc	8.733	7.001	12.06	5.033	2.98	10.32	3.123	3.762	5.121
ADs	1.113	0.687	1.25	0.226	0.546	0.107	0.615	0.397	0.717
ADc	40.44	21.76	28.19	17.35	8.718	19.97	7.339	8.508	12.7

Table 9.21: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation. The base run values are given in the column 'base' and those of the final run in the last column. These components are from the biological sampling likelihood components and the ratio of immature to mature fish. Row and column labels are identical to those in table 9.18.

	I_1	I_2	I_3	base	final
I_{1S}	1.262	13.85	15.97	2.541	3.756
I_{2S}	4.726	0.529	4.51	1.409	0.797
I_{3S}	1.935	2.046	0.564	1.27	0.636
I_{1A}	0.102	1.316	1.501	0.557	0.757
I_{2A}	2.768	0.008	3.793	0.233	0.002
I_{3A}	1.3	1.249	0.2	1.023	1.183

Table 9.22: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation. The base run values are given in the column 'base' and those of the final run in the last column. These components are survey indices. Row and column labels are identical to those in table 9.19.

The addition of predation into the model involves the inclusion of relatively sparse data. While data are available on the proportion of cod in the diet of cod, the low proportion means that length sampling of cod prey is limited and the data sparse. Further aggregation of the data either by predator length group or prey length group could lead to little information on the optimal predator length:prey length relationship or the shape of the selection curve. The sparseness of the likelihood data means that the difference between the likelihood score when heavily weighting the prey length distributions, PLs and PLo, compared to weighting the other components is much less than for other data types (table 9.23).

	PBs	PLs	PBo	PLo	base	final
PBs	0.003	0.025	0.016	0.023	0.017	0.014
PLs	87.28	65.46	95.59	67.8	70.89	82.55
PBo	0.181	0.193	0.154	0.192	0.175	0.171
PLo	79.58	68.23	88.29	65.81	71.07	76.85

Table 9.23: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation. The base run values are given in the column ‘base’ and those of the final run in the last column. These components are stomach content data.

Figure 9.23 illustrates the difference in predicted recruitment when emphasis is put on the different survey length groups. While there are similarities e.g. all plots have a peak in 1994 followed by a low value in 1995, there are many differences between the estimated values. The correlations between the recruit series are:

Indices	cor
I_1 and I_2	0.28
I_1 and I_3	0.60
I_2 and I_3	0.52

It should be noted that length group 1 provides no information for 1984 as the first survey index is for 1985.

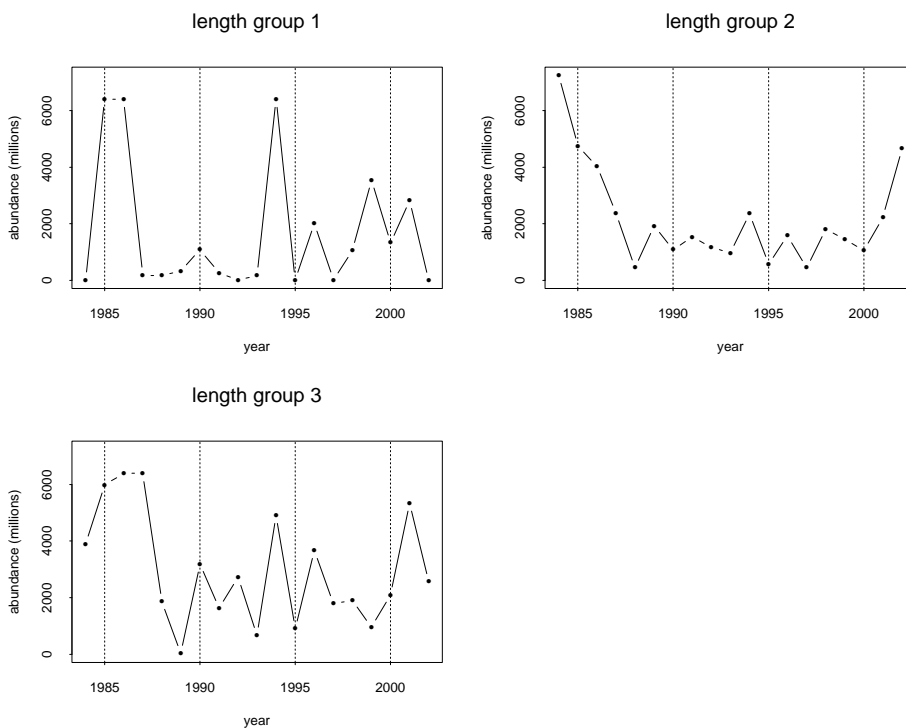


Figure 9.23: Recruitment estimated from the iterative weighting procedure. The plots show recruitment estimated with the survey data for length group 1, length group 2 and length group 3 heavily weighted respectively.

As parameter estimation using the prey biomass components (to estimation consumption of other food) needs to be done at the same time as estimation using the survey indices, which estimate the total abundance, the prey biomass data from the survey (PBs) were not included in the later stages of the estimation procedure as the weight was so large (table 9.24). The spring survey stomach content biomass

ratios are almost the same in every year resulting in a low minimum sse. The sparse data for the prey length distributions, however, result in low weights for these components.

The survey indices with the least difference between the minimum sse and the sse with the final parameters are length groups 2 for both surveys and length group 3 for the spring survey (table 9.24). This is reflected in the fit of the indices to the modelled abundance (figure 9.25).

Component	weight	sse_f/sse_m
mat	9364	2.76
LDs	32992	1.89
LDc	11283	1.40
ALKs	37200	2.60
ALKc	8344	1.72
ADs	2019	6.70
ADc	239	1.73
I_{1S}	14.26	2.98
I_{2S}	34.03	1.51
I_{3S}	31.90	1.13
I_{1A}	78.74	7.42
I_{2A}	1062	0.25
I_{3A}	39.98	5.92
PBs	10529	4.67
PLDs	3.71	1.26
PBo	507.81	1.11
PLo	3.42	1.17

Table 9.24: Component weights calculated from the minimum sums of squares and sse_f/sse_m , the ratio of the sums of squares from the final model (sse_f) with the minimum sse (sse_m) from the iterative weighting.

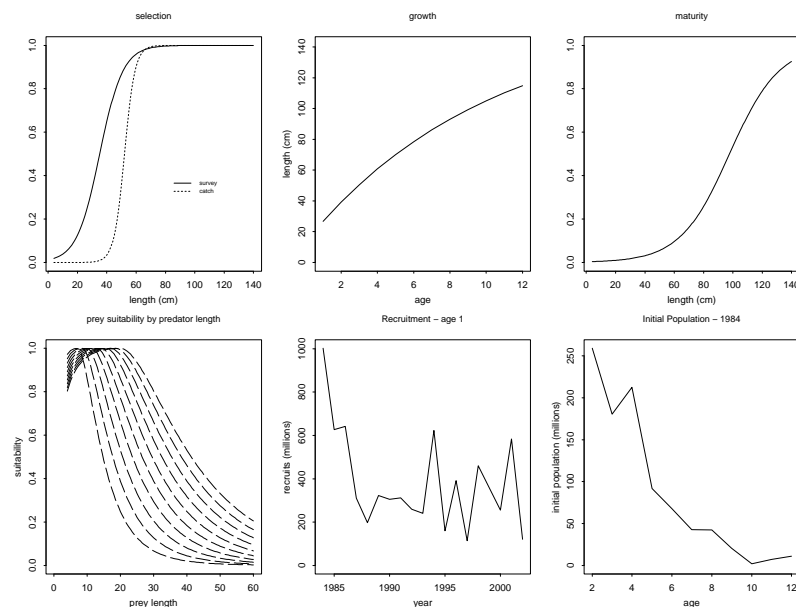


Figure 9.24: Parameter estimates from the final optimisation: selection patterns of the spring survey and catch, growth, maturation, selection curve of cod prey by cod predators for a selection of predator lengths, the number of age 1 recruiting into the model and the initial population age 2–12

Plots of the fitted log-linear regression are shown in figure 9.25. The slopes for length group 1 are 1.66 and 0.59 for the spring and autumn surveys respectively and for length groups 2 the slopes are 1.62 and 1.86. These estimated slopes are similar to those for model 1. The low consumption of cod by cod in Icelandic waters is not expected to have much impact on the population dynamics and there is no evidence here that it does.

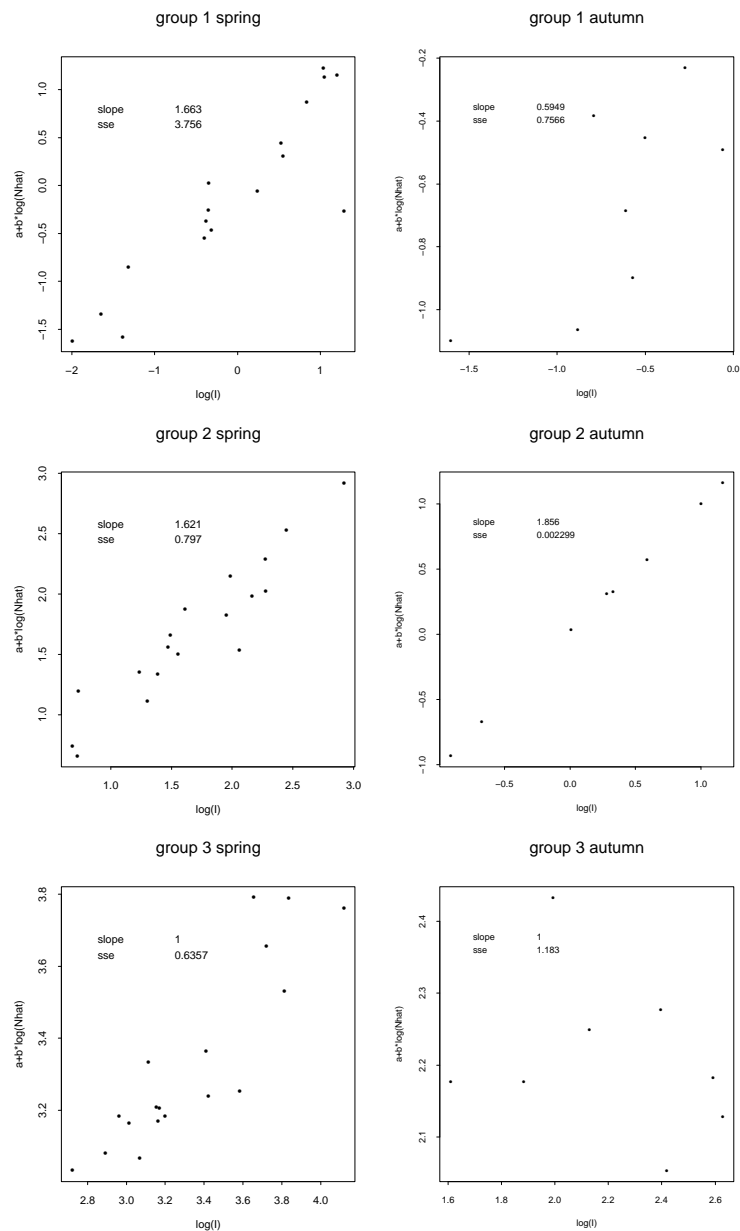


Figure 9.25: Plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b \cdot \log(N)$ the fitted regression to the modelled population.

Residuals

The fit of the model to the likelihood data can be considered in more detail by considering residuals from the fit of length distribution components and modelled catch length distributions calculated as $p_{y,s,l} - \pi_{y,s,l}$ where $p_{y,s,l}$ is the observed length distribution as proportions by year and step and $\pi_{y,s,l}$ is the modelled catch length distribution as proportions by year and step.

The patterns in the residuals from the survey length distribution likelihood component and the modelled survey catch (figures 9.26 & 9.27) and equivalent residuals for the catch length distribution component and modelled commercial catch (figure 9.28) indicate that growth in this implementation of Gadget may be insufficiently flexible. It is, however, to be expected that the length distributions from the modelled population will be smoother than those observed as samples are affected by intra-haul correlation (Pennington and Volstad 1994) with fish of a similar length being caught together (Hrafinkelsson and Stefansson 2002).

A model with growth affected by consumption might increase the flexibility of growth, as might variable growth rates for different years or time periods. For the catch data, disaggregating the commercial fleet into different gear types, which apart from having different selection patterns also operate during different seasons, might also improve the model.

Commercial catch residuals from January 1985 are considerably greater than those from other timesteps (figure 9.28) and possibly should be removed from the model.

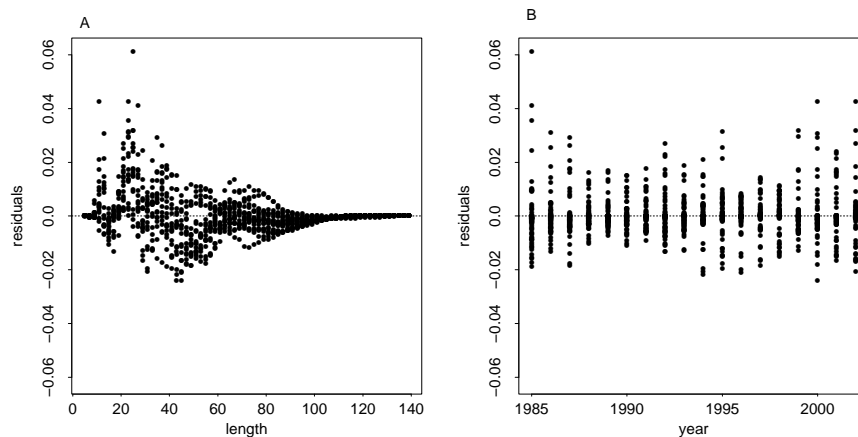


Figure 9.26: Length distribution residuals from the spring survey. A) by 2cm length group and B) by year.

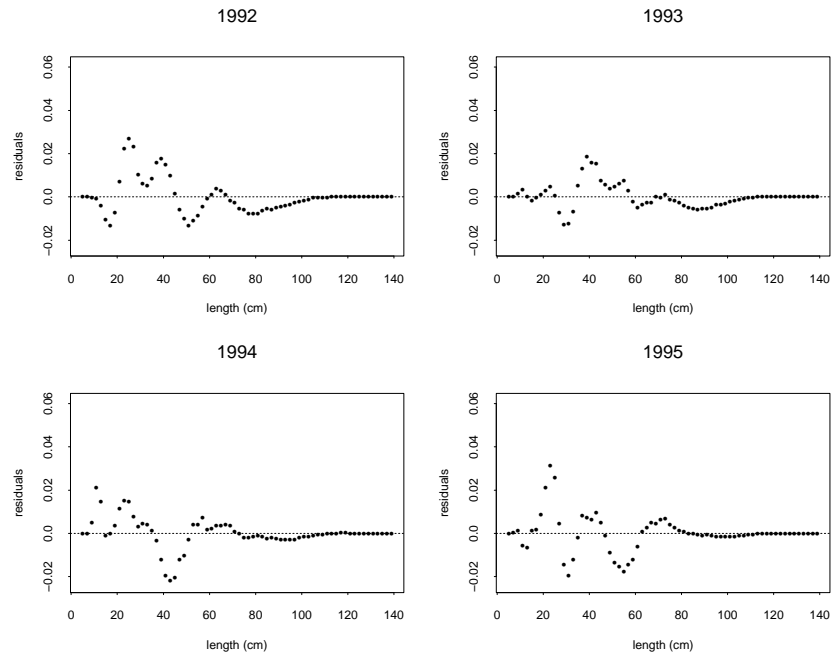


Figure 9.27: Length distribution residuals from the spring survey for an arbitrary selection of years 1992–1995

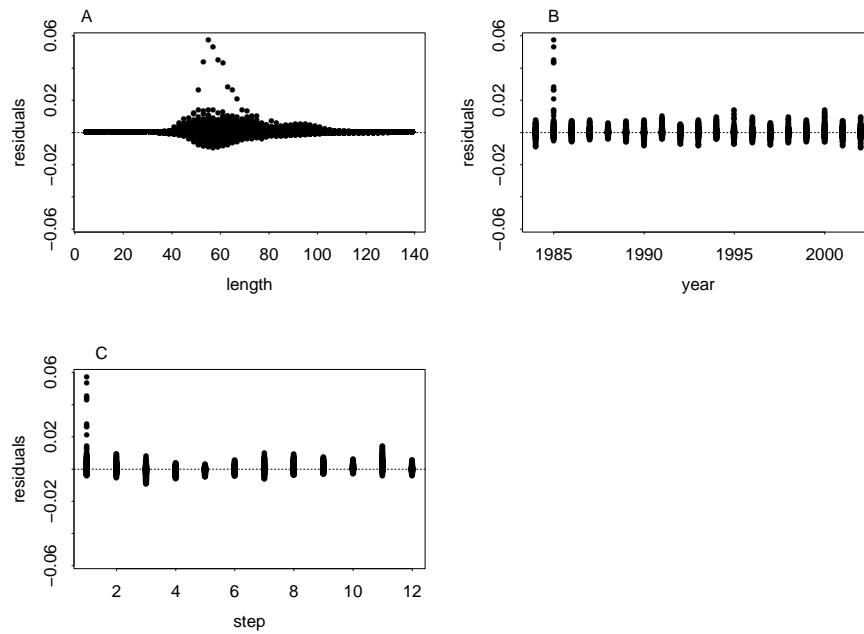


Figure 9.28: Length distribution residuals from the catch data. A) by 2cm length group, B) by year and C) by month.

The total likelihood score by year, step and component can also be plotted as in figures 9.29 for the survey data and figures 9.30 & 9.31 for the catch data. The poorer fit for the maturity data for the initial years may be affected by the initial distribution of fish between the immature and mature stock components. As both the maturity and age-length keys components (and to a lesser extent the age distribution data) have relatively high scores for 1985–1989 it is more likely that the cause is the otolith sampling protocol for the survey which was subsequently changed.

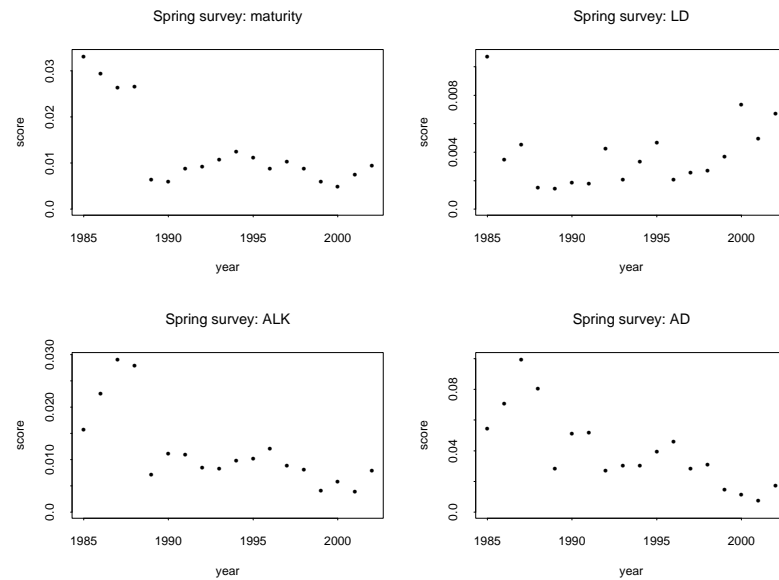


Figure 9.29: Likelihood scores by year for the spring survey components: maturity, length distribution, age length keys and age distribution.

It can be seen in figure 9.30 that the likelihood data do not fit all years equally, with higher likelihood scores for the years 1995–1999 for all biological sampling datasets. There is also a seasonal pattern (figure 9.31) with higher and more variable scores in the spring. Disaggregating the commercial fleet by gear type might reduce some of the seasonality in the likelihood scores. Including a separate gill net fleet is of particular interest as gill net use is seasonal and used to target larger spawning fish. The sampling of the gill net fishery during the spawning season is also disproportionately large in relation to landings.

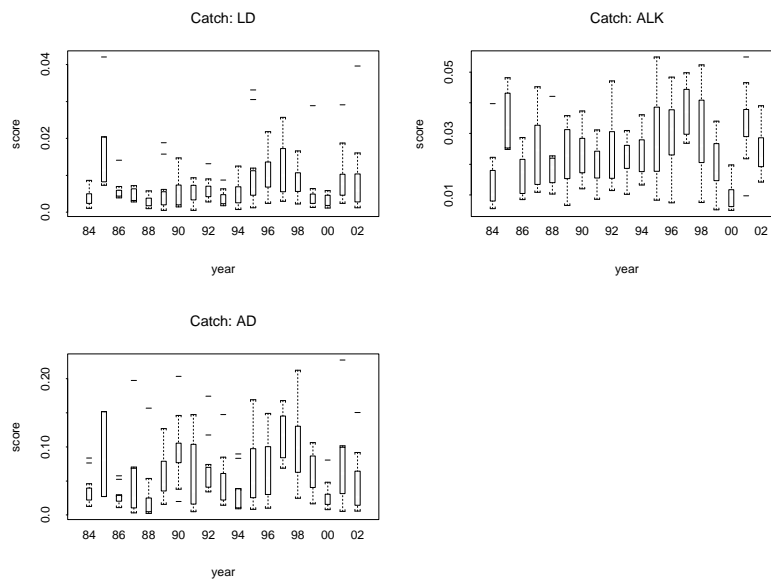


Figure 9.30: Boxplots of the likelihood scores by year for the commercial catch components: length distribution, age length keys and age distribution.

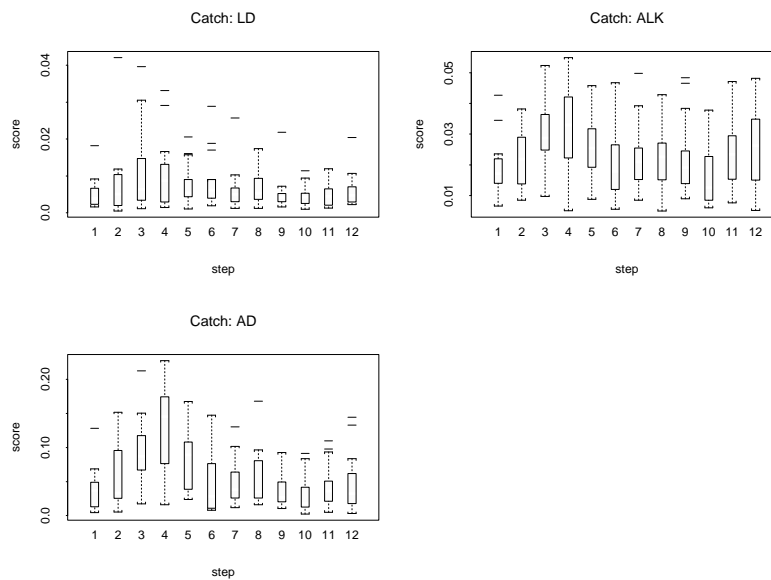


Figure 9.31: Boxplot of the likelihood scores by month for the commercial catch components: length distribution, age length keys and age distribution.

Model with no age data: model 3

For model 3, model 1 is repeated with no age data likelihood components. The remaining likelihood components are: length distributions for the spring survey and catch, the ratio of immature to mature by length group and the survey indices by length groups. Apart from the growth function being fixed and different initial parameters the procedure is the same as with age data.

The minimum sums of squares from the iterative weighting procedure are in table 9.25 for all components.

	mat	LDs	LDc	I_1	I_2	I_3	base	final
mat	0.136	0.363	0.39	1.086	0.565	1.2	0.348	0.283
LDs	0.532	0.037	0.082	0.484	0.268	0.503	0.155	0.064
LDc	11.11	3.008	1.625	12.77	7.216	8.815	3.752	1.409
I_{1S}	10.63	3.268	14.9	1.438	12.73	11.94	5.271	3.694
I_{2S}	6.685	1.402	6.685	2.863	0.331	6.204	0.34	0.523
I_{3S}	5.345	0.98	14.23	1.791	1.929	0.56	1.148	0.651
I_{1A}	0.918	0.642	0.806	0.162	1.028	1.202	0.592	0.646
I_{2A}	1.874	0.344	0.45	1.588	0.058	3.793	0.075	0.071
I_{3A}	1.722	0.964	1.441	1.333	0.967	0.418	0.998	1.165

Table 9.25: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation. The base run values are given in the column 'base' and those of the final run in the last column. These components are from the biological sampling likelihood components and the ratio of immature to mature fish. Row and column labels are identical to those in table 9.18.

Table 9.26 contains the weights calculated from the iterative procedure and the ratio of the sum of squares from the final model to the minimum for each component. In most cases, the difference between the minimum and final sse is less than for models 1 and 2 as there are fewer data sets providing conflicting information. The final parameter estimates are shown in figure 9.32.

Component	weight	sse_f/sse_m
mat	5836	2.08
LDs	32701	1.73
LDc	7548	0.87
I_{1S}	12.52	2.57
I_{2S}	54.41	1.58
I_{3S}	32.15	1.16
I_{1A}	49.44	3.99
I_{2A}	137.55	1.22
I_{3A}	19.12	2.79

Table 9.26: Component weights calculated from the minimum sums of squares and sse_f/sse_m , the ratio of the sums of squares from the final model (sse_f) with the minimum sse (sse_m) from the iterative weighting.

Plots of the fitted log-linear regression are shown in figure 9.33. The slopes for length group 1 are 1.61 and 0.58 for the spring and autumn surveys respectively and for length groups 2 the slopes are 1.64 and 1.70. As before the highest weight of the survey indices is for length group 2 of the autumn survey (table 9.25) but the weight is considerably lower than for models 1 and 2. The sse from the log-linear regression is correspondingly higher at 0.07 for model 3 compared to 0.0007 and 0.002 for models 2 and 3 respectively.

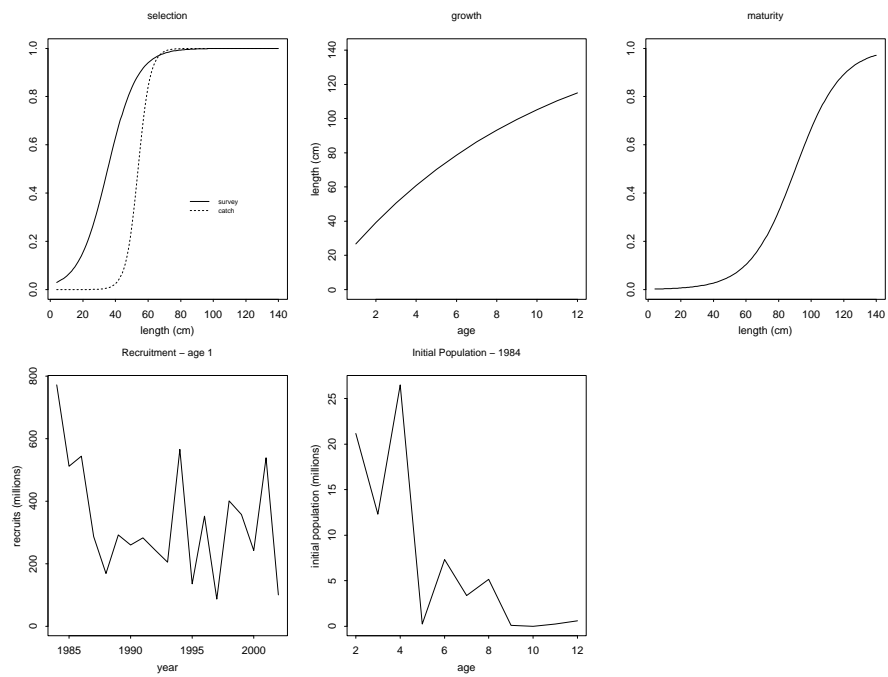


Figure 9.32: Parameter estimates from the final optimisation: selection patterns of the spring survey and catch, growth (fixed), maturation, number of age 1 recruiting into the model and the initial population age 2–12

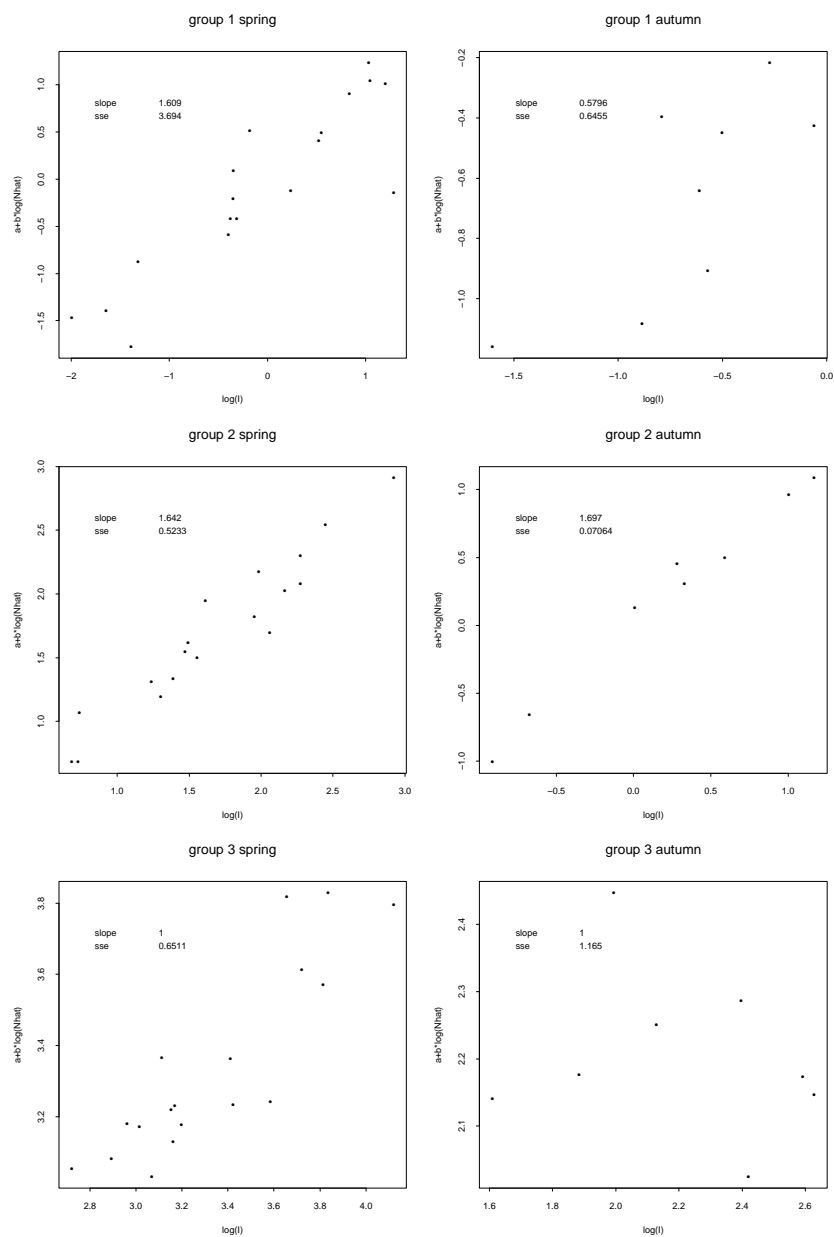


Figure 9.33: Plots of the log linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b \cdot \log(N)$ the fitted regression to the modelled population.

Model with aggregated likelihood components: model 4

Model 4 is equivalent to model 1 with the length distribution, age-length key and maturity ratio likelihood components aggregated in 10cm length groups. Survey indices are identical to those used for the other models. All parameters are estimated as for model 1.

Tables 9.27 & 9.28 contain the minimum sum of squares from the iterative weighting procedure. The minima for the length data in table 9.27 are greater (by as much as a factor of 4) than those for model 1.

	mat	LDs	LDc	ALKs	ALKc	ADs	ADc	base	final
mat	0.371	1.803	1.485	0.811	1.358	2.081	1.154	1.246	1.407
LDs	2.442	0.203	0.370	0.739	0.496	0.557	0.359	0.697	0.331
LDc	17.240	8.465	4.621	48.920	11.440	40.010	5.807	14.760	6.059
ALKs	1.292	1.796	1.721	0.136	0.309	1.119	0.377	0.334	0.397
ALKc	21.720	34.390	34.210	17.180	6.258	33.350	8.418	9.747	11.200
ADs	2.609	1.609	1.485	0.149	0.506	0.103	0.489	0.614	0.625
ADc	30.540	43.240	50.810	31.310	8.927	51.350	7.375	16.850	14.660

Table 9.27: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation. The base run values are given in the column 'base' and those of the final run in the last column. These components are from the biological sampling likelihood components and the ratio of immature to mature fish. Row and column labels are identical to those in table 9.18.

The minimum sums of squares for the indices are similar to those for model 3 which was started with similar initial parameter values. Initial parameter values can affect the weighting of the survey indices as they influence the weight of the baseline run.

	I_1	I_2	I_3	base	final
I_{1S}	1.463	12.520	11.95	4.726	3.835
I_{2S}	3.519	0.334	6.187	0.355	0.525
I_{3S}	2.155	1.167	0.516	1.230	0.638
I_{1A}	0.136	1.061	1.238	0.624	0.628
I_{2A}	3.640	0.055	3.793	0.078	0.070
I_{3A}	1.677	1.005	0.449	0.994	1.183

Table 9.28: Minimum sums of squares from iterative optimisations with each column representing a run with that component heavily weighted. The values in bold are the sums of squares of the heavily weighted component in each optimisation – with two indices heavily weighted in each optimisation. The base run values are given in the column 'base' and those of the final run in the last column. These components are survey indices where I_i , $i = 1, 2, 3$ are the length groups and the S, A subscripts indicate the spring and autumn surveys.

Table 9.29 contains the weights calculated from the iterative procedure and the ratio of the sum of squares from the final model to the minimum for each component. As indicated by the minimum sums of squares the weighting of the survey indices is similar to that for model 3. In most cases, the ratio is greater for model 4 than for the other models, indicating that the final model fit is poorer to these aggregated likelihood datasets.

The final parameter estimates are shown in figure 9.34 where it can be seen that the parameter estimates are, in most cases similar to those from the earlier models.

Plots of the fitted log-linear regression are shown in figure 9.35. The slopes for length group 1 are 1.59 and 0.58 for the spring and autumn surveys respectively and for length groups 2 the slopes are 1.63 and 1.67. Despite being considerably lower than for models 1 and 2, the highest weight of the survey indices is still for length group 2 of the autumn survey (table 9.29). The sse from the log-linear regression is correspondingly higher at 0.07 for model 4 compared to 0.0007 and 0.002 for models 1

Component	Weight	sse_f/sse_m
mat	436.187	3.79
LDs	1238.938	1.63
LDc	690.760	1.31
ALKs	11134.020	2.92
ALKc	2040.213	1.79
ADs	2103.213	6.09
ADc	247.322	1.99
I_{1S}	12.303	2.62
I_{2S}	53.957	1.24
I_{3S}	34.863	1.28
I_{1A}	58.737	1.57
I_{2A}	146.065	4.61
I_{3A}	17.833	2.64

Table 9.29: Component weights calculated from the minimum sums of squares and sse_f/sse_m , the ratio of the sums of squares from the final model (sse_f) with the minimum sse (sse_m) from the iterative weighting.

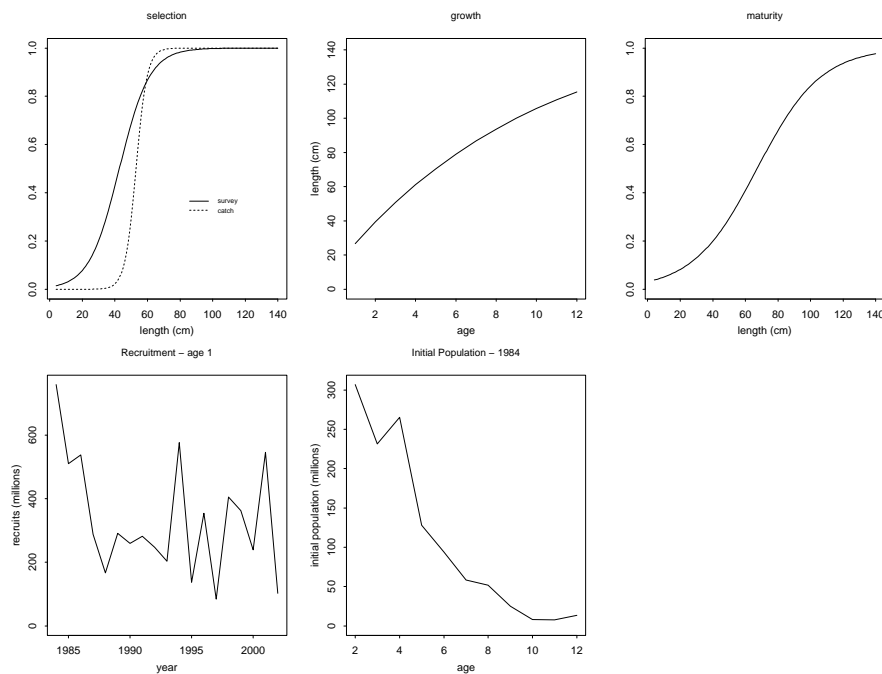


Figure 9.34: Parameter estimates from the final optimisation: selection patterns of the spring survey and catch, growth (fixed), maturation, number of age 1 recruiting into the model and the initial population age 2–12

and 2 respectively. In general, the sse for the indices are closer to those for model 3 than models 1 and 2, indicating the effect of the initial parameters on the resulting weights and fit. The slopes and intercepts are, however, similar for all models.

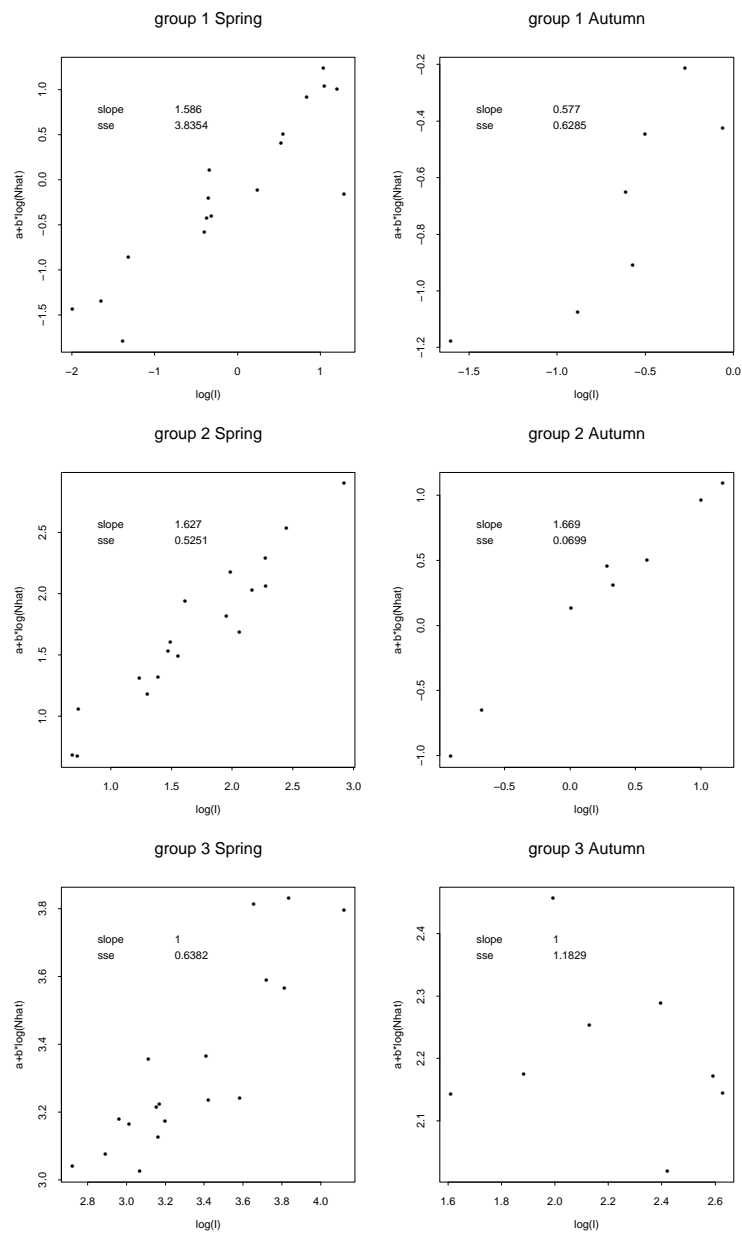


Figure 9.35: Plots of the log-linear regression as estimated in Gadget for model 4, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b*\log(N)$ the fitted regression to the modelled population.

Model comparison

The tables summarising the iterative weighting procedures for the four models (tables 9.18, 9.19, 9.20, 9.21, 9.22, 9.23, 9.25, 9.26, 9.27, 9.28 & 9.29) along with the plots of the estimated parameter values (figures 9.21, 9.24, 9.32 & 9.34) indicate consistency in both optimisation and parameter estimation for the first three models despite the differences between the models and initial parameter values.

A comparison of the estimation of the selection pattern and growth (for the models with age data) is shown in figure 9.36. Estimation of both growth and the selection pattern of the commercial fleet are similar but the survey selection differs when estimated from the aggregated data in model 4. From the length distributions in figure 9.37 it can be seen that aggregating the survey index loses more information than aggregating the catch data due to the range of lengths in the datasets.

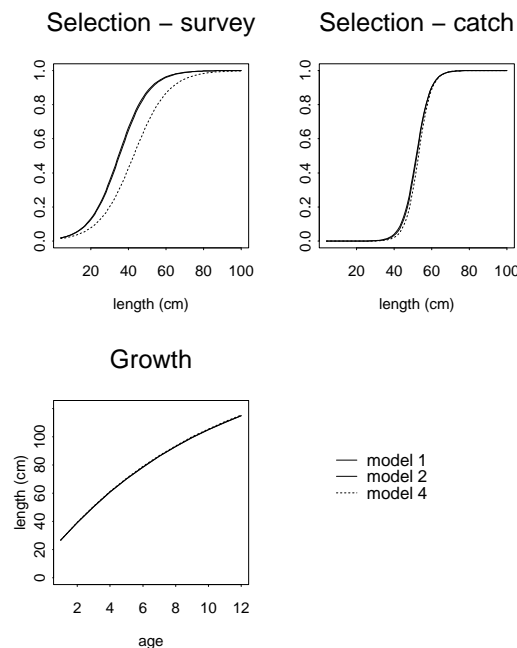


Figure 9.36: Comparison of selection and growth estimated by the models with age data.

The consistency of the estimated parameters is illustrated further in figure 9.38 where the estimated recruitment and initial population are compared directly for all the models. There is slightly more recruitment estimated from model 2, which is to be expected with predation, but otherwise recruitment parameters are similar. There is greater variability in the estimates of the initial population, particularly for model 3 with no age data. Most importantly, the stock biomass predicted by each of the models is similar, as shown in figure 9.39. Differences in the initial population result in different levels of biomass for the first few years, with the trajectory similar for models 1 & 2 and models 3 & 4. This is likely to be a result of the different weights assigned to the survey indices in these models. Differences in spawning stock biomass result from slightly different maturation ogives being estimated.

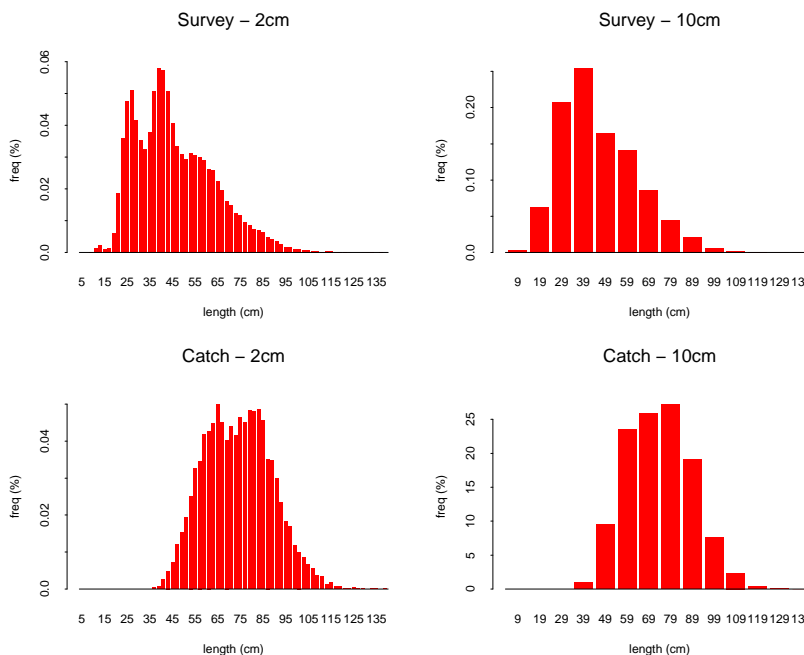


Figure 9.37: Length distribution from March 1990 for the survey and commercial catch aggregated on 2cm and 10cm.

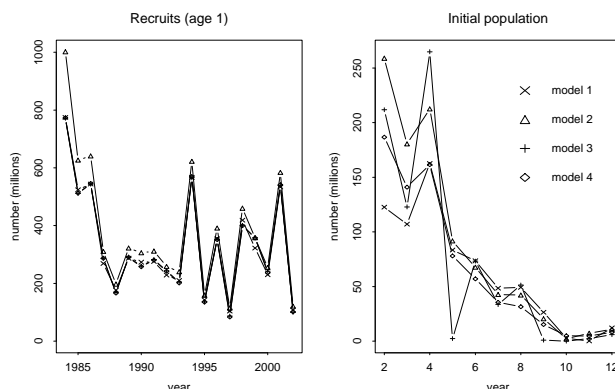


Figure 9.38: Comparison of the number of recruits (age 1) and the initial population (age 2–12) estimated by the four models.

Discussion

In this paper it has been demonstrated that it is possible to parameterise a statistical fisheries model using a formal statistical methodology. In these examples more data sources (seventeen likelihood datasets in model 2) and biological processes have been combined in such a model than before. Although these are single species models, it should be noted that there are two stock components which, in the case of model 2, interact. It was found that while it is possible to estimate a considerable number of parameters, it is necessary to fix some.

These examples are data-rich but with judicious use of available data the methodology also seems promising for less data-rich environments. As demonstrated in model 3, with fixed growth the lack of age data does not adversely affect estimates of recruitment or stock biomass. In the case of more

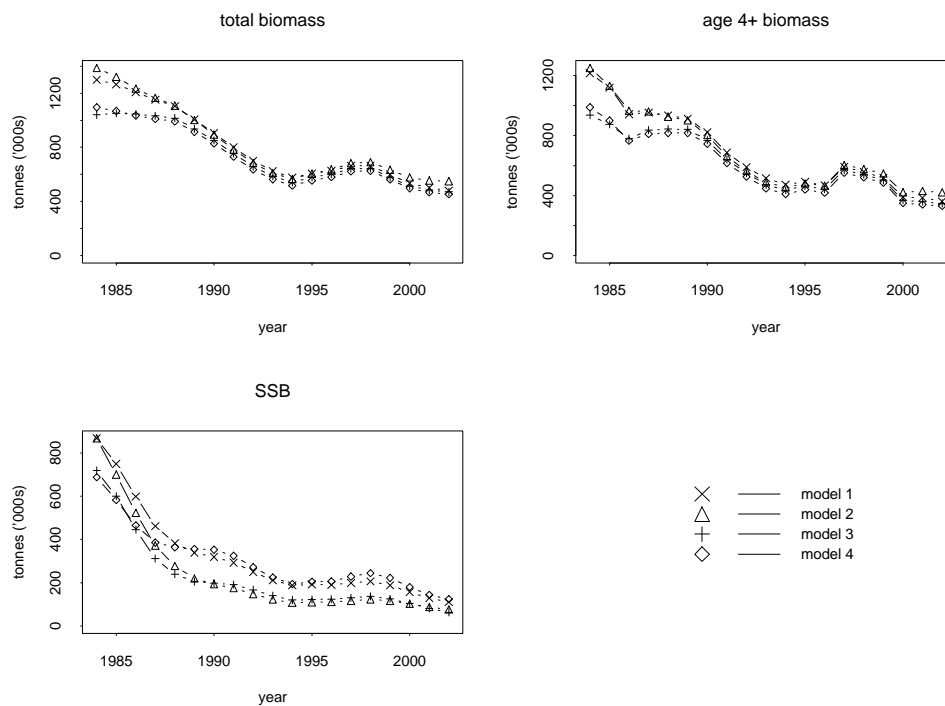


Figure 9.39: Comparison of the biomass estimated by the four models, for: total (age 1+) biomass, age 4+ biomass and spawning stock biomass.

aggregated likelihood components, parameter estimation in most cases was similar to that with more detailed likelihood data and the estimation of recruitment and stock biomass was also similar.

While there are indications that these implementations are too stiff with respect to growth, disaggregating the commercial fleet and/or allowing for variations in growth rate (both of which are currently possible within the Gadget framework) may help resolve some of these issues.

The potential for the initial parameter values to affect the weighting of survey likelihood components (in the model formulation used here) and in turn the final parameter estimates needs to be considered further. In this case, both the pattern and level of recruitment was the same but given very conflicting information from different surveys this might not be the case.

As an extension to this work, there is a need to demonstrate the methodology for the more complex multi-area case.

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9.4 Gadget models of cod-capelin-shrimp interactions in Icelandic waters

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Abstract: In Icelandic waters there are known to be strong links between cod and capelin and between cod and shrimp, with the condition of cod related to capelin abundance and shrimp abundance affected by predation by cod. The development of a model to assess the importance of capelin abundance to cod, and the corresponding impact of the capelin fishery on cod is therefore of some importance. Similarly, in assessing the abundance of shrimp, understanding the impact of cod predation might be expected to improve both the understanding of population dynamics and abundance estimates. Modelling these scenarios requires multispecies, multiarea, multifleet models. In both cases the spatial overlap of the predator and prey needs to be taken into account. There are also large temporal changes in the availability of capelin as prey as they are only present on the Icelandic shelf for part of the year. Each of these species has different modelling requirements and differing levels of data availability. The development of models to address these issues is described, with levels of model complexity compared and evaluated.

Keywords: Gadget, multispecies, statistical model, cod, capelin, shrimp, migration

Introduction

The marine ecosystem off Iceland contains several important players. Considered in isolation, the cod (*Gadus morhua*) stock is an important demersal species whose population dynamics have been studied extensively (e.g. Stefansson (1992) and Schopka (1994)). An interesting twist on the population dynamics is cannibalism, which appears to exist, though not of a dominating importance (Bogstad et al. 1994). The cannibalism has been taken into account when evaluating utilisation strategies for the cod stock (Baldursson et al. 1996).

The capelin (*Mallotus villosus*) is a very abundant (though also highly variable) prey species and has also been studied extensively (Vilhjalmsson 1994). When considering the part of the ecosystem related to commercial species, the most studied link is between cod and capelin, where capelin is an important food for cod (Magnusson and Palsson 1989; Magnusson and Palsson 1991a). Both of these finfish species sustain fisheries of considerable commercial importance (MRI 2004).

Shrimp (*Pandalus borealis*) is also a commercially important species, and another important link is between cod and shrimp, where predation by cod forms a considerable part of the mortality on the shrimp (Magnusson and Palsson 1991b). This effect has been captured using models of interactions as a part of routine assessments of shrimp (Stefansson et al. 1994; MRI 2004).

The various links between these three species have been studied using simple regression analyses (Stefansson et al. 1998b). The analyses support these conclusions but are difficult to convert into absolute numbers, though not impossible (Steinarsson and Stefansson 1996). These links have been used to develop harvest control rules for cod (Danielsson et al. 1997), as have sequences of more complex links (Stefansson et al. 1998a).

Models of marine ecosystems tend to be simplified in different ways depending on the purpose of the analysis conducted. As noted above, a very simple model can be in the form of a simple linear regression, possibly taking into account the statistical properties of the data. A very detailed model of the predation process could be a strictly mathematical model with no recourse to data fitting. Many

model types fall somewhere in between these extremes, taking into account a varying level of detail in the mathematical model of the biological process and the statistical description of the data to which the model is fitted.

Although the simple models should be expected to illustrate the most important relationships, several problem issues arise. These include variable species overlap, seasonal and stage-dependent migratory behaviour as well as competing mortality factors which can only be sensibly considered in joint analyses.

The models to be developed in this paper are therefore implemented using the scheme set out in Stefansson and Palsson (1998) and implemented using a computer program, Gadget, described in detail in Section 4.1 and Begley (2004). These models are statistical in nature, i.e. they are based on fitting to data using likelihood functions. They are also parametric in that a prediction is based on a parameter value alone, ideally using data only through the formal data fitting procedure. Finally, these models can take into account spatial and temporal variation in the species under consideration.

When developing these models it has proved important to first develop single-species models of fairly high quality for each species in question. Given the different data availability for e.g. cod and shrimp, these models become very different in nature. Thus, although the models may be internally age-disaggregated, there are no true age data for shrimp. Similarly, although most traditional assessments of cod in the North Atlantic use catches in numbers, disaggregated by age, such data are highly processed and the present paper uses data closer to the original samples, in accordance with common statistical procedure.

Earlier versions of such models have been used to analyse the cod-capelin interactions (Bjornsson 1998), based on Bormicon (Stefansson and Palsson 1997). Most of the earlier work has relied heavily on unproven and hardwired assumptions and weights given to different data sources. Given the problems in such approaches (Stefansson 1998), the emphasis in the present paper is on the cod-shrimp interaction, using appropriate statistical estimation methods at each stage of model development.

Model definition

The fishery for the offshore shrimp stock takes place mainly in the Gadget divisions 103, 104, 105 and 111 (figure 9.40). The definition of these divisions is described in Section 9.1. The cod stock, however, is predominantly found on the Icelandic shelf (< 500m). The simplest spatial resolution for a cod-shrimp stock model is to develop a two area model with a northern area incorporating divisions 103, 104 and 105 and a southern area of 101, 102, 107 and 108. Within the model, shrimp only exist on the northern area, whereas cod are on both and migrate between the two areas.

Given the spatial structure of the final cod-shrimp model, two preliminary single species models can be developed independently. This enables the impact of cod predation on shrimp to be assessed, and given the difficulties of estimating migration, it is more efficient to work with a simpler model in the first instance.

One of the aims of the cod model is to estimate migration of cod between the areas using the methodology described in Section 4.4. A simpler alternative would be to fix the migration rates to values estimated externally to Gadget, e.g. using the method described for capelin by Dereksdottir et al. (2003).

The interest in linking cod and shrimp is in the impact of predation on shrimp rather than the effect of consumption on cod. As shrimp is not a major part of the diet of cod (Magnusson and Palsson 1991b), consumption of shrimp is not considered to have a significant impact on cod growth (Bjornsson 1998) and in this implementation cod growth is independent of consumption.

The approach to parameter estimation, through iterative weighting of each likelihood component is similar to that described in Section 9.3 and will not be discussed here.

Input data and likelihood component data were extracted from the datawarehouse described in Chapter 2 with the original data sources and aggregation methods described in Section 9.2. In all cases, except

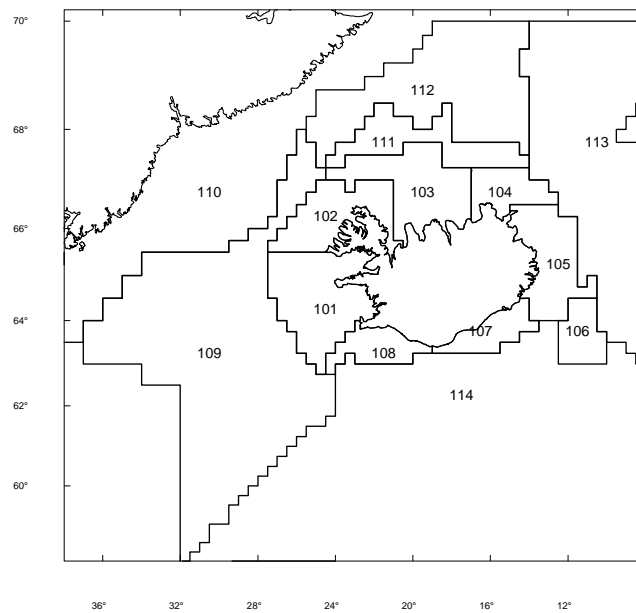


Figure 9.40: Map showing some of the datawarehouse divisions for the area around Iceland.

tagging data, the likelihood functions are those used for the cod models in Section 9.3.

Shrimp model

Data and likelihood functions

Age data are only available for shrimp by using methods to disaggregate length frequency data (e.g MacDonal and Pitcher (1979)). Age disaggregation is problematic, especially for the older ages as the modes in the length distribution are difficult to identify. As can be seen in figure 9.41, only the modes of the first three cohorts are easily distinguished. For this reason, age data are only used in this model to initialise the population and to determine the growth parameters which are then fixed.

Data used in the shrimp model are:

Input data:

- Landings data obtained from the Directorate of Fisheries data base.

Biological sampling likelihood data:

- Length distribution, aggregated on 1mm intervals, from sampling of commercial catches by month from 1988 to 2002.
- Length distribution, aggregated on 1mm intervals, from the main net of the offshore shrimp survey from 1988 to 2002 (Skuladottir et al. 2000).

Survey index likelihood data:

- Four survey indices from the main net of the offshore shrimp survey (figures 9.41 & 9.42) with one datum for each group for the years 1988–2002.
- Two survey indices from the juvenile bag of the offshore shrimp survey (figures 9.41 & 9.42) with one datum for each group for the years 1988–2002.

Four indices are calculated for the main net (and two for the juvenile bag) by splitting the length distribution into groups, with the division based on the ‘typical’ structure of the length distribution for the survey over all years. The first three length groups are considered to be cohorts. The division of the length distributions into groups is illustrated for two years in figure 9.41. The length group divisions are identical for the two data sources and are derived from length distributions on 0.5mm intervals. The intervals in cm are: (0.60,1.10), [1.10,1.65), [1.65,2.15) and [2.15,3.20) for groups 1–4. This provides two survey indices for the younger shrimp, with likelihood components that can be weighted simultaneously in the iterative weighting scheme. The appropriateness of these divisions as indicators of cohorts varies between years but as the indices are identified as length groups rather than age groups and the two sources of survey indices are collected simultaneously this is not a problem.

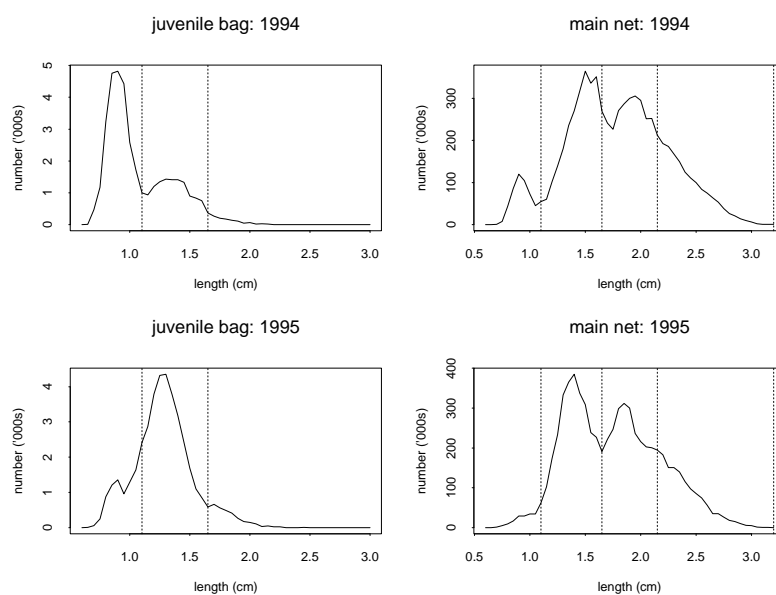


Figure 9.41: Length distributions from 1994 and 1995 for the juvenile bag and main net of the offshore shrimp survey. The vertical lines indicate the division into length groups for the survey index likelihood components.

For the shrimp surveys, the slope and intercept of the log-linear regression between the survey and modelled data are estimated for length groups 1 and 2 with the slope fixed to 1 for the third and fourth length groups.

In figures 9.42 & 9.43 it can be seen that for length groups 1 and 2, the trends from the juvenile bag and main trawl net are similar for length group 1 (correlations between nets of 0.687 and 0.540 for length groups 1 and 2 respectively) although the time series do not entirely agree. The selection of shrimp in the two nets is different, with the smaller meshed juvenile bag expected to be a more reliable indicator of length group 1 and the main net for length group 2.

Comparing length groups within nets by cohort (figure 9.44), the relationship between length groups 1 and 2 is considerably stronger in the main net than the juvenile bag (correlations of 0.645 and 0.140 respectively). There is also a strong correlation (0.667) between length groups 2 and 3 of the main net and between length group 1 of the juvenile bag and length group 2 of the main net (correlation of 0.732).

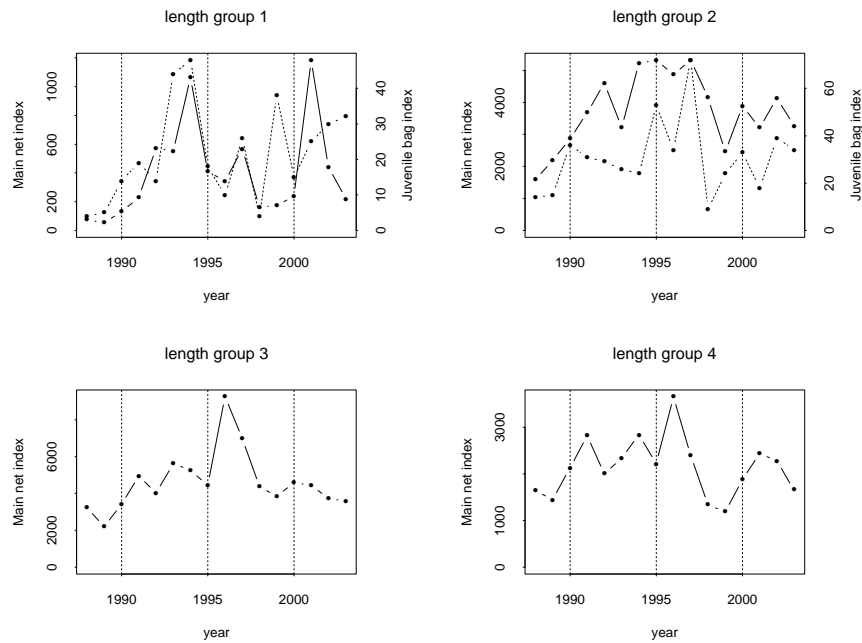


Figure 9.42: Survey indices for the offshore shrimp survey for both nets by length group. For length groups 1 and 2, the y axis for the main net is on the left and for the juvenile bag on the right with the index for the main net represented by the solid line and the juvenile bag by the dashed line.

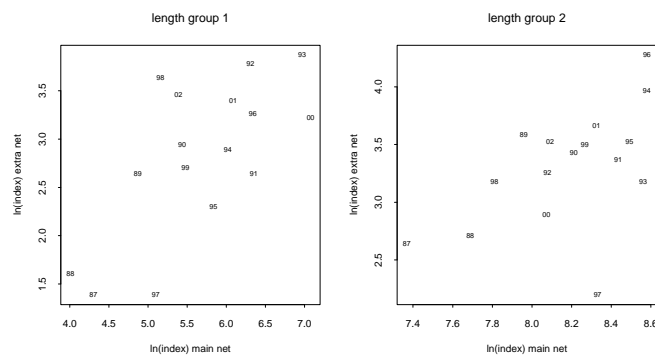


Figure 9.43: Scatter plots of the (ln transformed) offshore shrimp survey abundance indices. On the left, length group 1 from the main net is plotted with length group 1 from the juvenile bag and on the right, the equivalent plot for length group 2. Each point is labelled with the cohort, assuming group 1 is age 1.

Model Implementation

The model runs from 1988 to 2002, with monthly timesteps, on one area with two shrimp components – male and female. The males are aged 1 to 6 and the females 3 to 8, with the final age a plus group.

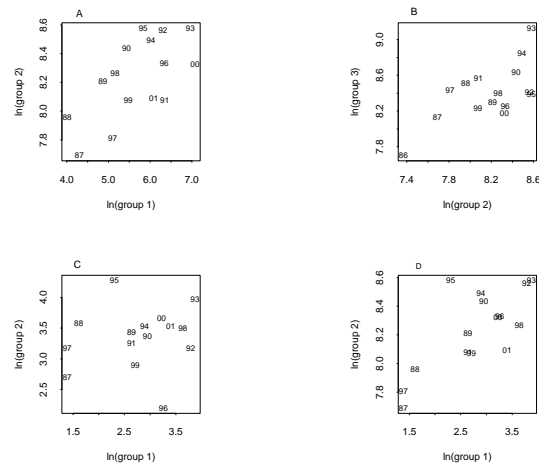


Figure 9.44: Scatter plots by cohort of the (ln transformed) offshore shrimp survey abundance indices. A) length group 1 vs length group 2 from the main net, B) length group 2 vs length group 3 from the main net C) length group 1 vs length group 2 from the juvenile bag and D) length group 1 from the juvenile bag vs length group 2 from the main net. Each point is labelled with the cohort, assuming group 1 is age 1.

Males become female through a maturation function and any not female by the end of their sixth year automatically move into the female stock component. The female component is not split further into immature and mature. A single commercial shrimp fleet operates along with a shrimp survey.

Variable natural mortality has been identified as an important control on the population dynamics of shrimp (Fu and Quinn 2000) and in Icelandic waters predation by cod has been estimated to be high in relation to the catch of the shrimp fishery (Magnusson and Pálsson 1991b). As the aim of developing the shrimp model is however to link it with a cod model to investigate the importance of cod predation on shrimp population dynamics, in this implementation natural mortality is constant for all years.

- Length growth is according to the von Bertalanffy function as described in Section 9.3 with k and L_{∞} fixed to 0.17 and 3.501 for both the male and female stock components. The von Bertalanffy parameters were calculated from data (Skuladottir pers. com.). The betabinomial parameter β is fixed at 20, with maximum length group growth $n = 10$ and length intervals of 0.025cm.
- The weight-length relationship is fixed, $W = aL^b$, with different values for the male and female components (Skuladottir pers. com.).
- The transition from male to female is implemented using the maturation function described in Section 9.3 as a function of length. The parameters defining sex change are estimated from shrimp survey data and fixed.
- Natural mortality at age is fixed to 0.4 for all males, 0.5 for females aged 3 to 6 and 0.6 for age 7 and 8 females. Natural mortality has been set to be higher for females than males as Clark et al. (2000) report that mortality increases sharply after first hatching for mature females for Gulf of Maine shrimp. In some other areas however, natural mortality of males is believed to exceed that of females due to greater predation on smaller shrimp (Fu et al. 2001).
- The mean and standard deviation of length of the initial populations were fixed, and based on a von Bertalanffy curve fitted to data (Skuladottir pers. com.). The weight-length relationships used for weight growth were also used for the initial population.

- The number at age of the initial population (ages 2 to 7) is estimated within the model, with the age distribution estimated and then a multiplier used to scale the population abundance.
- Mean and standard deviation of length of the age 1 recruits are fixed according to the data used to initialise the population.
- The number of age 1 recruits for each year (1988–2002) is estimated within the model.
- To enable the age structure of the initial population to be estimated independently of the survey indices, there is an additional parameter (*mult*) which can be used to scale the abundance of the initial population with the age structure fixed.
- The fleet selection pattern is the same as that used in Section 9.3 with the length at 50% selected ($L_{50\%}$) and the slope estimated for each fleet.

Results

Parameter estimation was done in two stages using the weights from table 9.30:

1. all likelihood data were used,
2. growth, selection (catch and survey) and initial population parameters were fixed, the weights on the length distribution were set to zero and the remaining components were to estimate recruitment and the population abundance.

The higher weight for length groups 1 and 2 is on the juvenile bag and main net respectively (table 9.30) which is the expected relationship given the survey design. The weights on length groups 3 and 4 of the main net are arbitrary as there are no equivalent data with which to iteratively weight these length groups. A heavy weight on a component containing one datum per year will result in that component fitting perfectly (if optimised for long enough) which means that more than one source of survey index is required for at least some years.

Component	Weight	sse_f/sse_m
LDs	5479.45	1.209
LDc	1795.12	1.067
I_{1J}	24.74	1.463
I_{2J}	19.18	3.976
I_{1M}	6.04	0.852
I_{2M}	38.05	0.939
I_{3M}	<i>20.00</i>	
I_{4M}	<i>5.00</i>	

Table 9.30: Likelihood component weights and sse_f/sse_m , the ratio of the sums of squares from the final model (sse_f) with the minimum sse (sse_m) when that component is heavily weighted. The components are the LD – length distribution, with s and c indicating whether survey or catch data and the survey indices with I_i , $i = 1, 2, 3, 4$ indicating the length group and the J, M subscripts indicate the juvenile bag and main net of the offshore shrimp survey. The weights in italics were not estimated from the iterative procedure.

Parameters, fixed and estimated, along with the predicted stock biomass, for a single timestep, and observed catch are shown in figure 9.45.

Plots of the fitted log-linear regression are shown in figure 9.46 with the residuals in figure 9.47. The slopes for length groups 1 and 2 are similar for both data sources, with greater values for the larger meshed main net. As expected the fit of the model to the juvenile bag index is better for length group 1 and to the main net index for length groups 2.

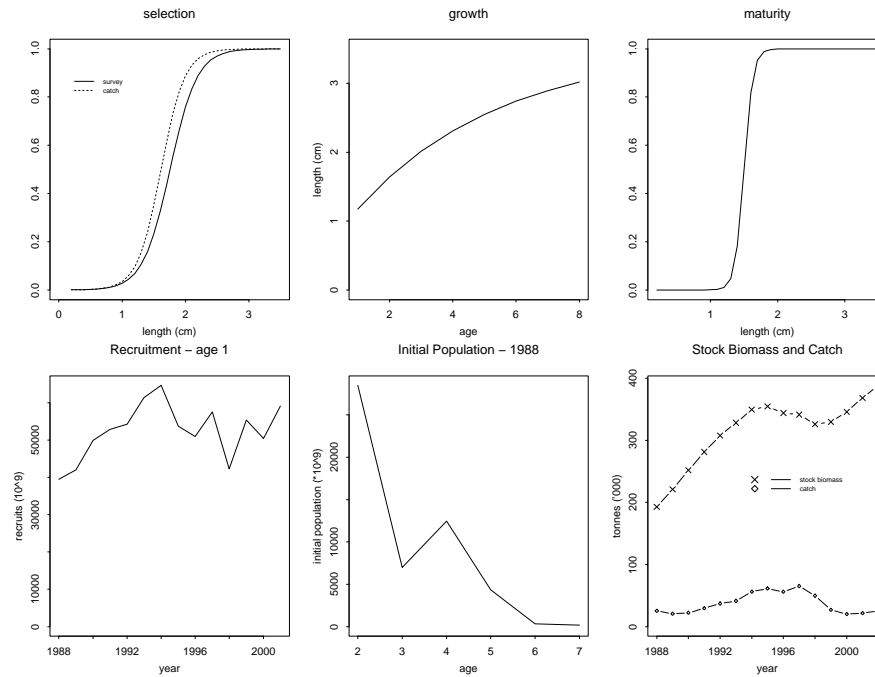


Figure 9.45: Parameter estimates from the final optimisation: selection patterns of the offshore survey and catch, growth (fixed), sex change (male to female – fixed), number of age 1 recruiting into the model and the initial population ages 2–7. The estimated stock biomass and the observed catch are also shown.

The residual plots for length groups 3 and 4 (figure 9.47) show that the model overpredicts the group 3 and 4 indices for the final years, while underestimating those for the middle years. This is reflected in the biomass plot in figure 9.45 where the total stock biomass can be seen to increase from 1998 onwards, whereas the catch decreased in these years. As the first two length groups fit the index data for this time, the problem is entirely due to an over prediction of the abundance of older shrimp. It is possible that this is a result of not taking into account annually varying mortality. With mortality constant for all years and fixed growth and fleet selectivity, recruitment and catch determine the modelled stock structure and abundance. For a stock, such as shrimp, with high predation mortality, natural mortality can be a more important determinant of stock dynamics than recruitment (Fu and Quinn 2000). Another possible cause for the over prediction of older shrimp could be the increased mortality of females after hatching which has been observed for Gulf of Maine shrimp (Clark et al. 2000).

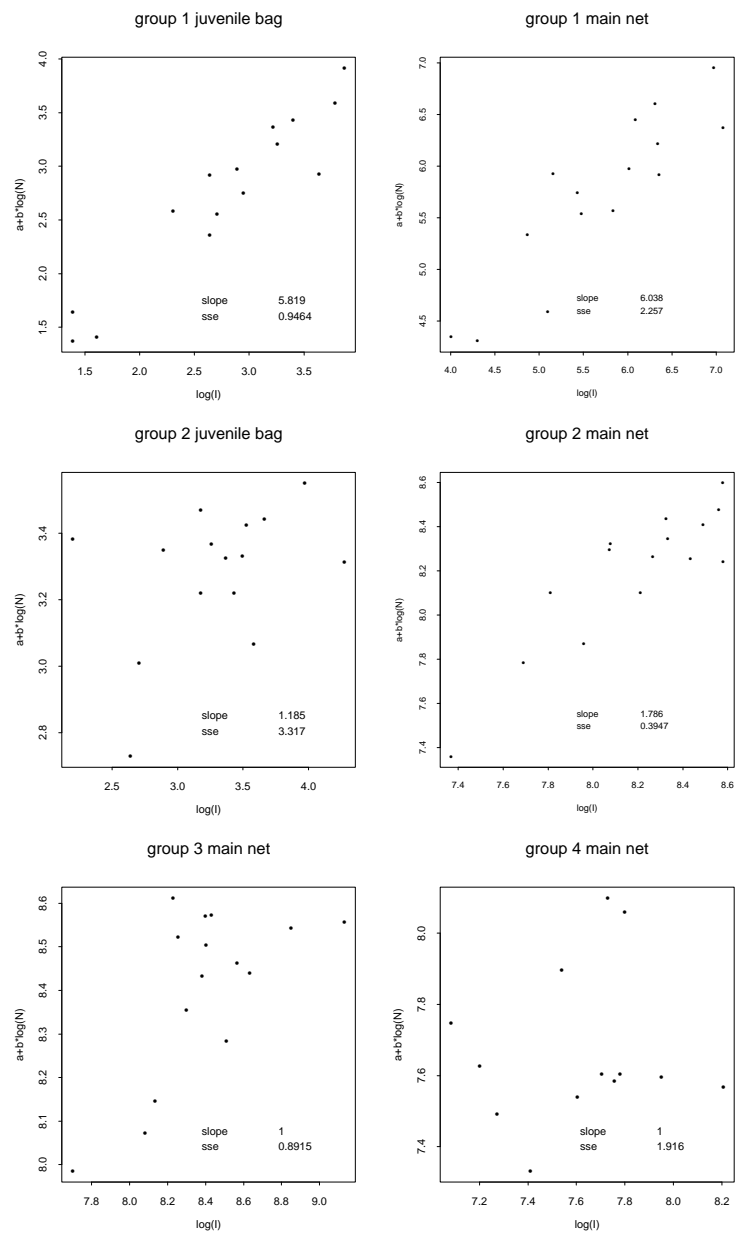


Figure 9.46: Plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b \cdot \log(N)$ the model estimate of the survey index.

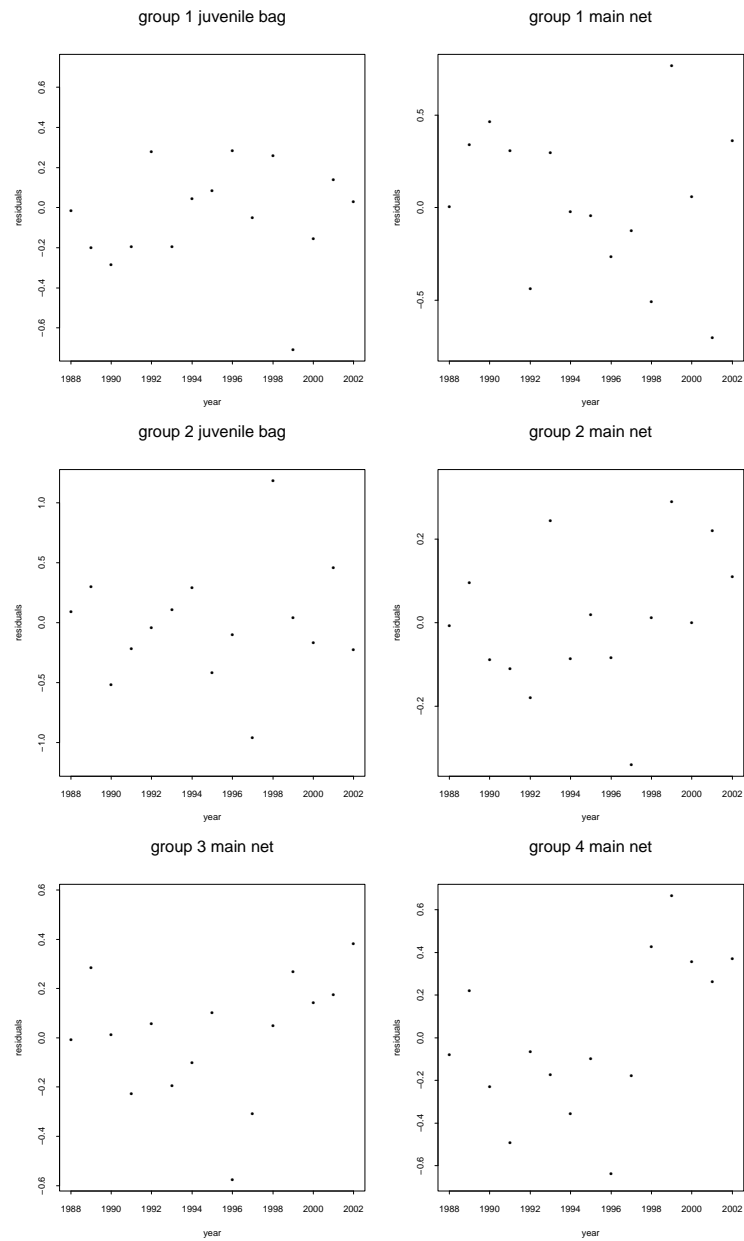


Figure 9.47: Plots of the residuals from the log-linear regression as estimated in Gadget, with one plot for each likelihood component.

2-area cod model

The following description focuses on aspects of the 2-area model which differ from the single area example in Section 9.3.

Data and likelihood functions

In a multi-area Gadget model most of the likelihood components can be aggregated over more than one area, area disaggregated within the same likelihood component or considered independent components. Survey indices are an exception to this and must be area disaggregated (although as with all likelihood data do not need to be provided for every area).

Data used in the case study are:

Input data:

- Landings data are obtained from the Directorate of Fisheries data base and are area disaggregated.

Likelihood data:

- Biological sampling likelihood data: length distributions, age-length keys and age distributions for the spring survey and commercial catch as for Section 9.3 but disaggregated by area.
- Stock composition likelihood data (i.e. proportion mature at length): disaggregated by area.
- Survey index likelihood data: three series of indices for each area for the spring survey (Palsson et al. 1989) for 1985–2002 and the autumn survey (Sigurdsson et al. 1997) for 1995–2002. For each year/area/survey/group one datum is available.
- Four tagging experiments: south 1993, south 1995, south 1996 and north 1993. The tagging likelihood data and components are described in Section 4.4 where a more extensive set of tagging likelihood data was used.

The relationship between the spring and autumn surveys can be seen in figure 9.48 & 9.49. The correlations between the surveys within the length groups are:

	South	North
group 1	0.759	0.579
group 2	0.654	0.703
group 3	0.659	-0.587

It can be seen that for length groups 1 and 2, the surveys provide similar information for the overlapping years (especially for length group 1 in the south) and that the conflicting information for the third length group is restricted to the northern area where the surveys are negatively correlated. It is also apparent from figures 9.48 & 9.50 that the distribution of fish at the time of the surveys is not constant between years. This is particularly true for length group 2 in the spring survey (correlation = 0.35).

When the length groups are compared within each survey (figure 9.51 for the spring survey and figure 9.52 for the autumn) there are strong correlations between length groups 1 and 2 for both surveys in both areas, indicating little migration of age 1 fish between these areas. The correlations are:

Spring

	South	North
group 1 : group 2	0.705	0.657

Autumn

	South	North
group 1 : group 2	0.670	0.857

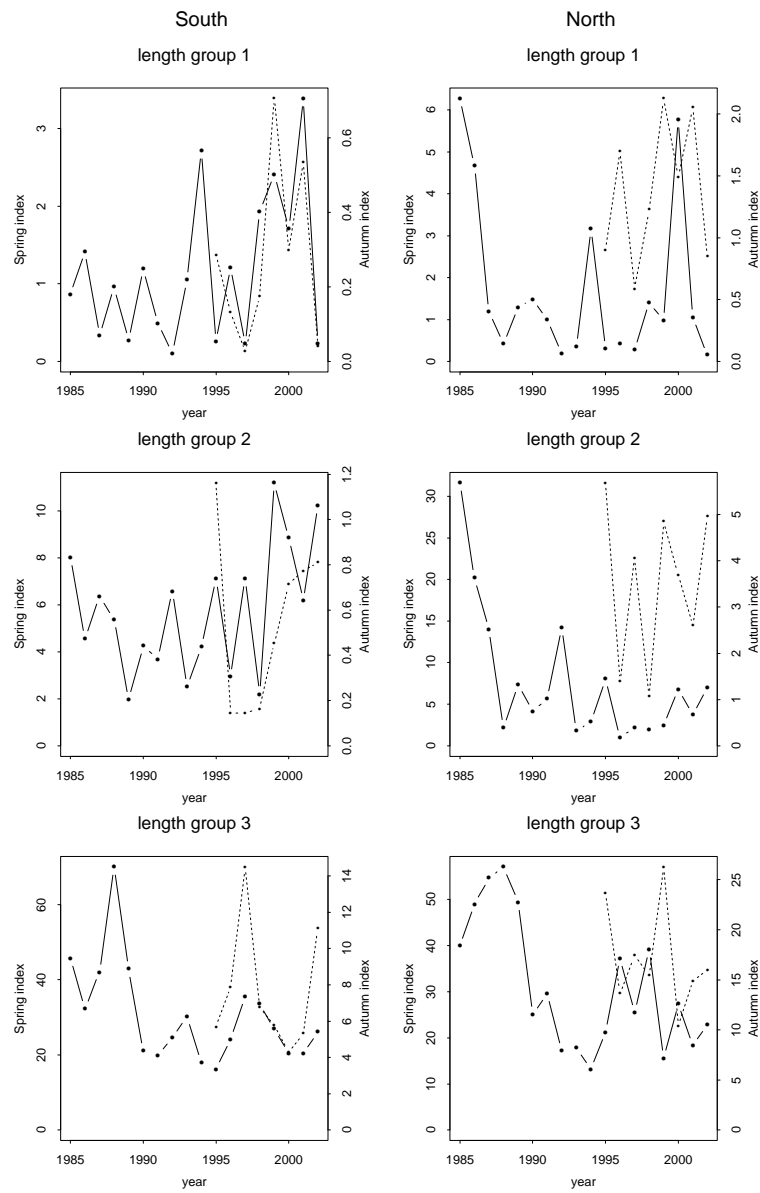


Figure 9.48: Survey indices for the spring and autumn surveys for each length group, with the y axis for the spring survey on the left and for the autumn survey on the right. Indices for the southern area are on the left in for the northern area on the right. The spring survey is represented by the solid line and the autumn index by the dashed line.

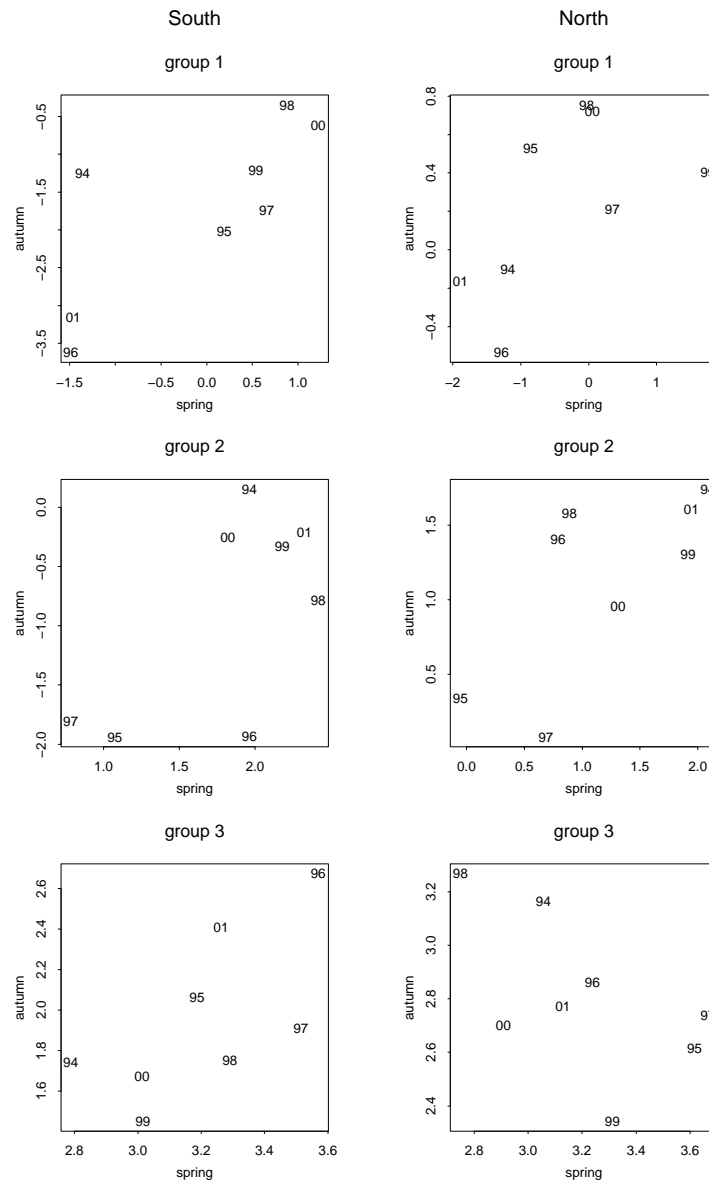


Figure 9.49: Scatter plots of the log transformed survey indices: autumn survey vs the spring survey for each length group.

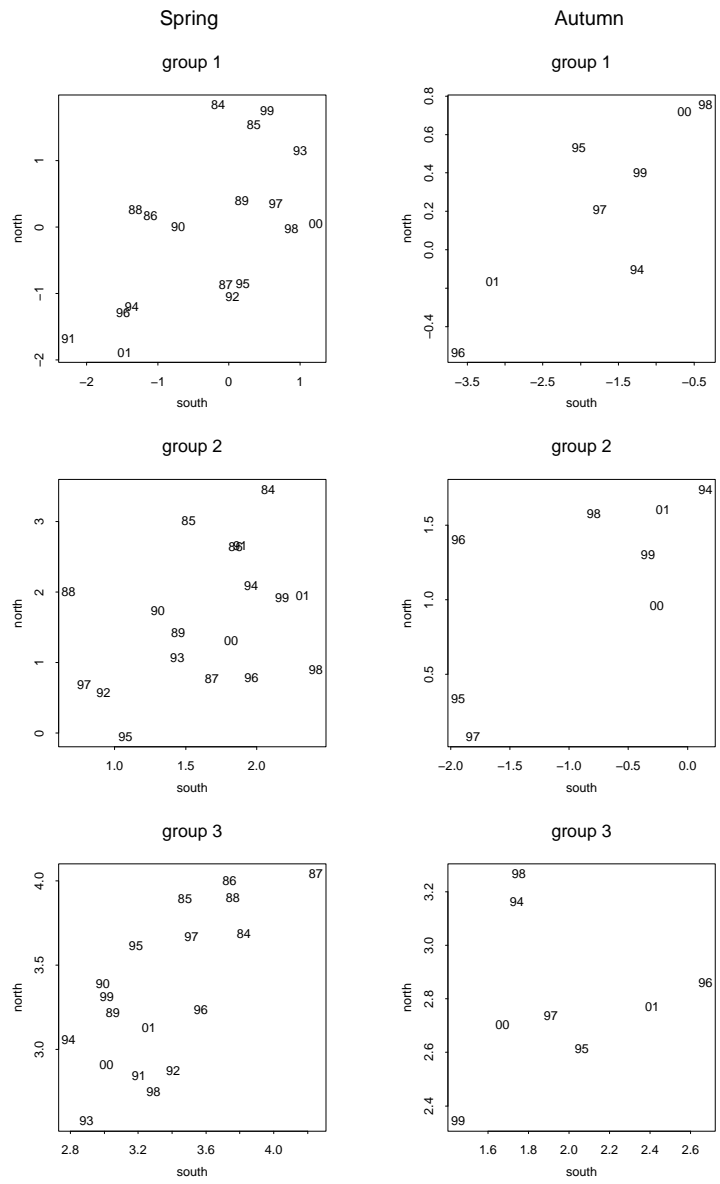


Figure 9.50: Scatter plots of the log transformed survey indices: for each survey and length group, plots of north vs south.

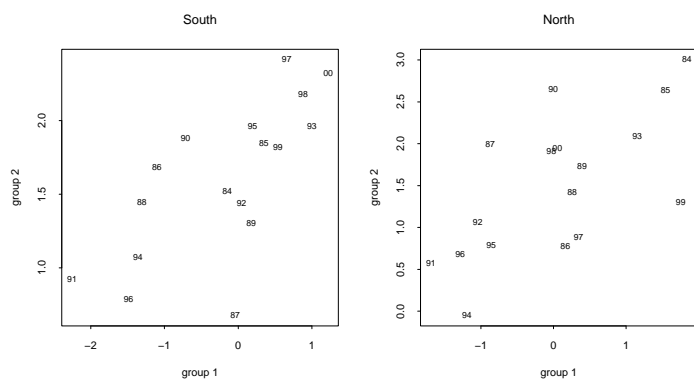


Figure 9.51: Spring survey: scatter plots of the length group 2 index against the length group 1 index for both areas on a log scale with each point labelled with the cohort year.

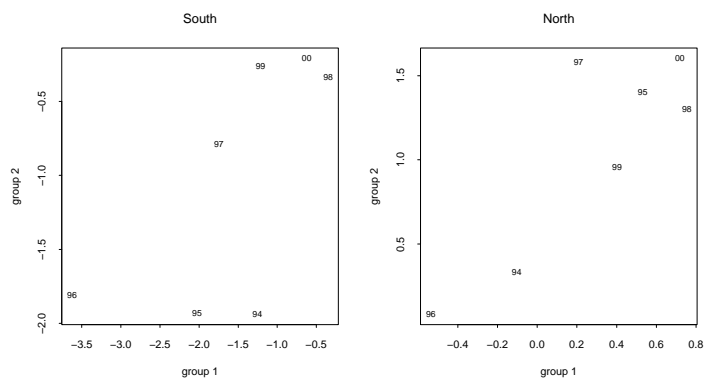


Figure 9.52: Autumn survey: scatter plots of the length group 2 index against the length group 1 index for both areas of the autumn survey on a log scale with each point labelled with the cohort year.

Model Implementation

As the model is similar to that described in Section 9.3 only issues pertaining to multi-area aspects of the model will be described here. Mature cod migrate, with a fixed migration pattern in every year and migration is not age dependent whereas immature cod do not migrate. To reduce computation time, in the development of the 2-area cod model there is no cannibalism. As the main interests of this model are to estimate migration and the distribution of the cod population between the two areas, growth, maturation and fleet suitabilities are fixed from values established from a single area cod model.

Distribution of recruits between the areas is not constant, as indicated in figure 9.48. To distribute the recruits in every year, either the proportion in each area for each year needs to be fixed or it is necessary to estimate two sets of recruitment parameters.

- The number at age of the initial population (ages 2 to 12) is estimated within the model. Separate parameters describe the initial population on each area i.e. 22 parameters describe the age structure of the initial population.
- The mean and standard deviation of length of the initial population on each area were calculated from survey data and output from the datawarehouse. The weight-length relationships used for weight growth were also used for the initial population in both areas.
- Mean and standard deviation of length of the age 1 recruits was estimated from the spring survey for each year, with separate values for each area.
- The number of age 1 recruits for each year (1984–2002) is estimated within the model, with separate recruitment parameters for each area.
- Migration is described by three matrices describing the movement of cod. Matrix 1 represents the spawning migration in January to April, matrix 2 any returns to the north from June to November, and matrix 3 describes no movement (May and December). This results in two migration parameters which need to be estimated.

Results

With the parameters for growth, selection and maturation fixed, only one optimisation run is required after the weights have been estimated. The weights on the age distribution and survey components are shown in table 9.31. As the tagging objective function is a Poisson distribution, rather than the sum of squares used for the other components, the appropriate weights for the tagging components cannot be estimated from the standard procedure. In this example the tagging weights were set arbitrarily, but, given the importance of the migration parameters this is an issue which needs to be considered more closely.

There is less difference between the weights of the survey indices for the 2-area model than for the single area case study (cf Section 9.3) with most indices of a similar order of magnitude. For the single area model, the weight on length group 2 was the highest for both surveys whereas length group 3 has the highest weight in the south for both surveys and in the north it is only for the autumn survey that length group 2 has a higher weight. This may reflect the relative importance of the north and south for juvenile and mature fish respectively. Alternatively, it may indicate the relative difficulty the model has in fitting the length group 2 indices for the 2-area model.

The estimated parameters are shown in figure 9.53 and they indicate that most of the population is in the larger southern area. Migration between the two areas is estimated to be very low with less than 2% of mature fish migrating in each timestep.

The fit of the indices to the model varies between indices (figures 9.54 & 9.55). Group 2 in the south is a poor fit for the spring survey and has a slope of 0.67. The equivalent slope for autumn is 3.4 and for the north the slopes are 2.3 and 2.2 for the spring and autumn respectively. In the north, the fit of the

Component	Weight	sse_f/sse_m
ADs	85.65	1.470
ADc	83.72	1.063
I_{1Ss}	7.63	1.989
I_{2Ss}	12.08	2.631
I_{3Ss}	42.99	4.115
I_{1As}	38.44	6.607
I_{2As}	65.20	4.482
I_{3As}	72.40	8.489
I_{1Sn}	6.00	3.513
I_{2Sn}	22.93	2.651
I_{3Sn}	22.42	2.051
I_{1An}	44.47	1.056
I_{2An}	56.42	1.305
I_{3An}	20.34	1.779

Table 9.31: Component weights calculated from the minimum sums of squares and sse_f/sse_m , the ratio of the sums of squares from the final model (sse_f) with the minimum sse (sse_m) from the iterative weighting. The components are: AD – age distributions with s and c denoting survey and catch and survey indices I_i , $i = 1, 2, 3$ are the length groups, the S, A subscripts indicate the spring and autumn surveys and the s, n subscripts the southern and northern areas.

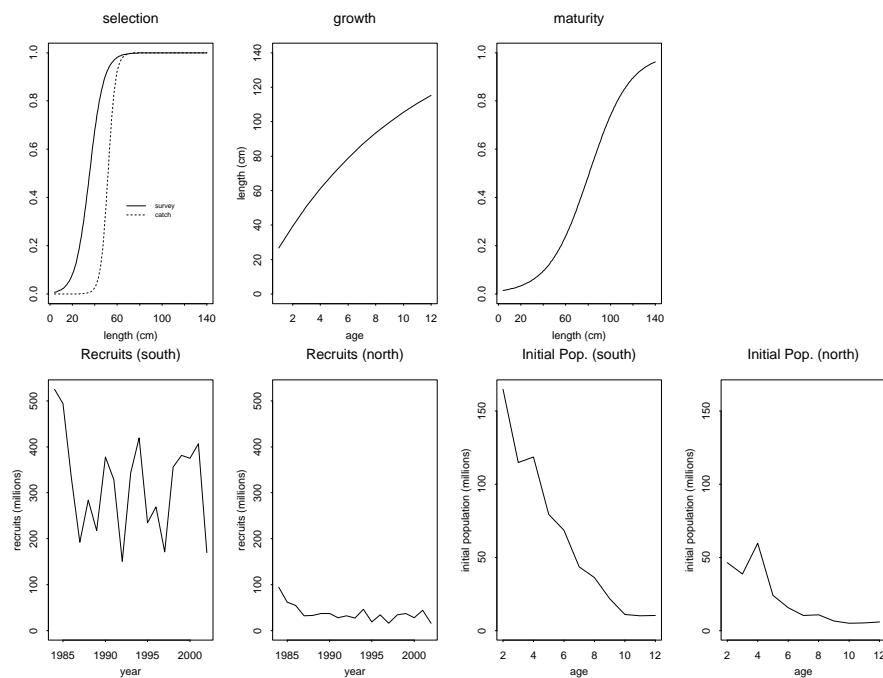


Figure 9.53: Parameter estimates from the final optimisation: selection patterns of the spring survey and catch (fixed), growth (fixed), maturation (fixed), number of age 1 recruiting into the model for the southern and northern areas and the initial population age 2–12 for the south and north.

model to the indices is worst for length group 3. For both surveys in the north, the slope fitted to the length group 1 indices is less than for the length group 2 indices which is contrary to expectations of catchability of these length groups.

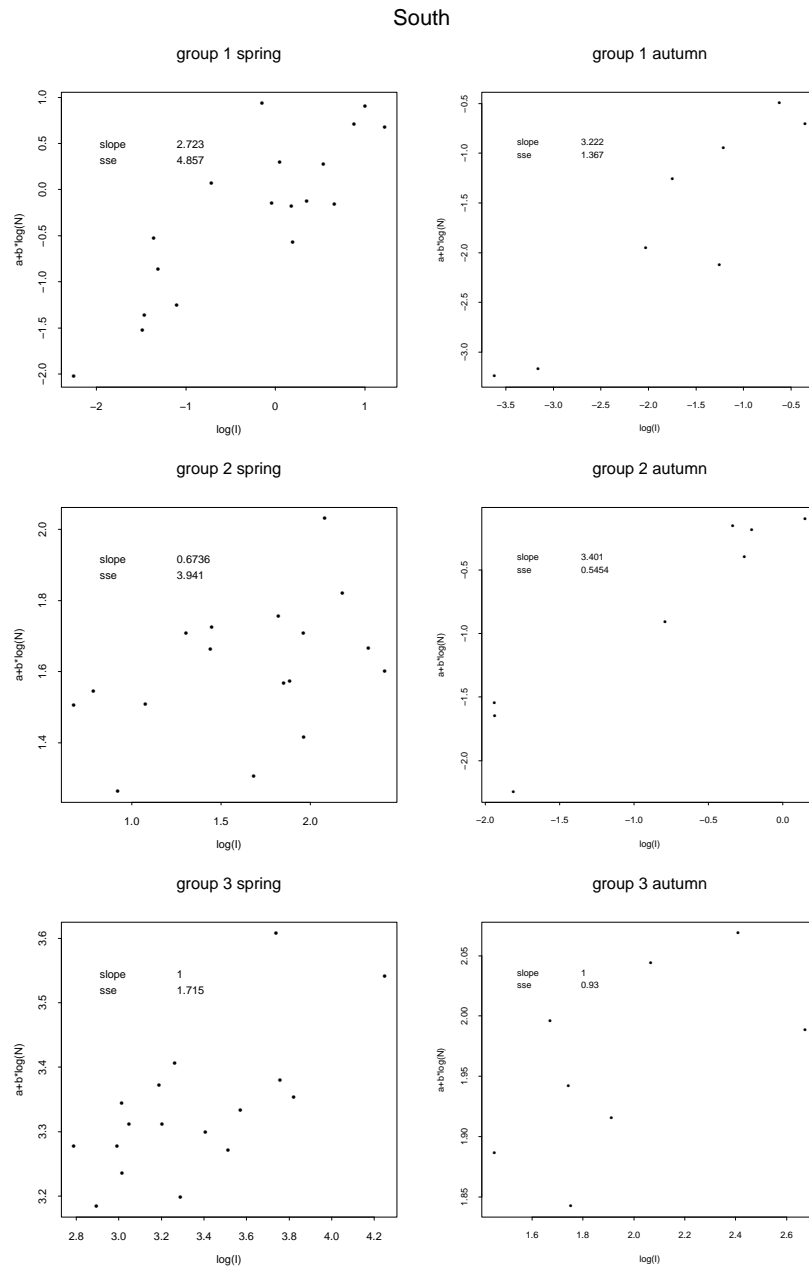


Figure 9.54: Plots of the log-linear regressions for the southern area as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b \cdot \log(N)$ the survey index estimated by the model.

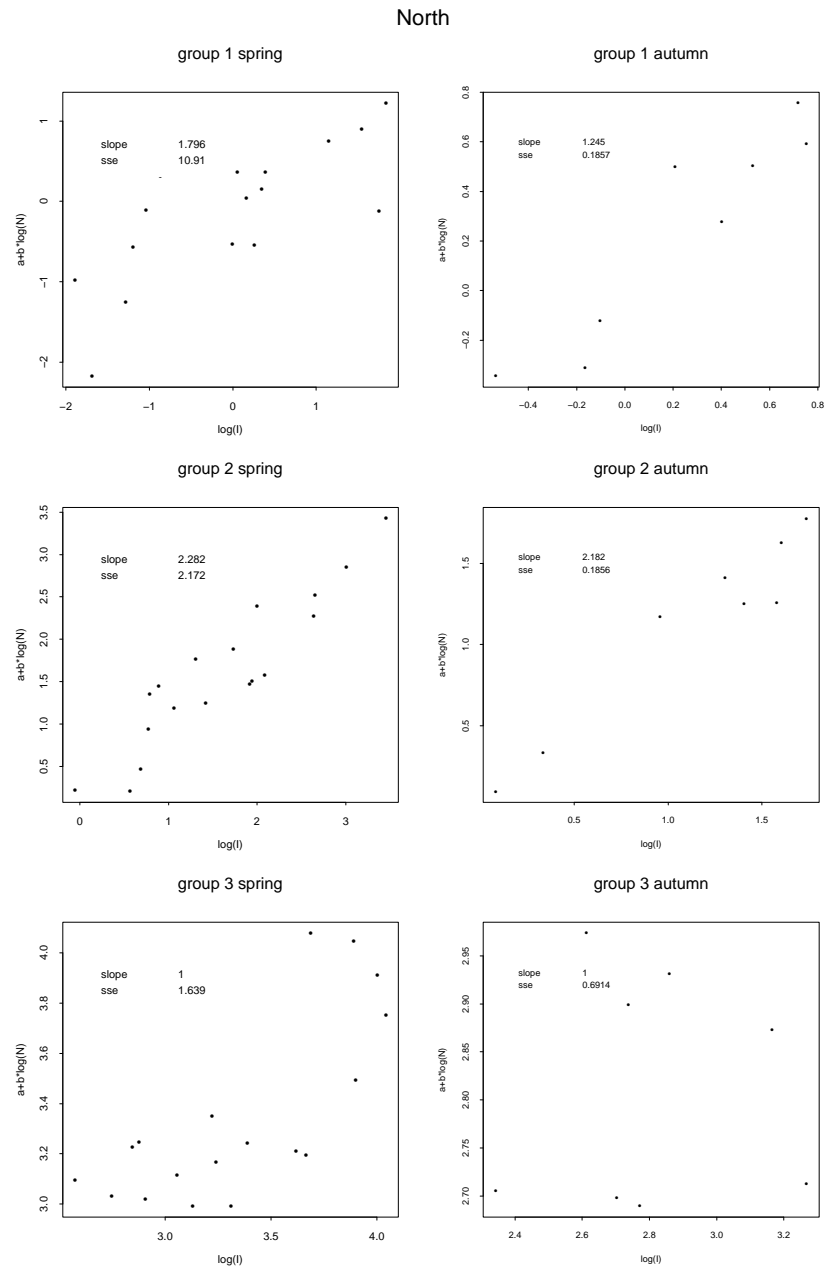


Figure 9.55: Plots of the log-linear regressions for the northern area as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b*\log(N)$ the survey index estimated by the model.

The area off the north of Iceland is an important nursery area for cod with the main spawning ground off the south-west coast (Marteinsdottir et al. 2000). This indicates that, at some time, migration must take place from the north to the south, even if only once. The tagging data used as likelihood data were from tagging experiments on the mature stock component, often during the spawning season. If migration, from north to south (given the spatial structure of this model), is primarily of first time spawners migrating from the nursery ground to the southern spawning grounds then these experiments will not provide any information on this pattern of migration. Without migration of this form represented in the model, the abundance of immature cod in the north will be underestimated and overestimated in the south. To include such a migration pattern involves a change in the way the stock is structured in the model and to estimate migration requires tagging experiments on juvenile cod. Tagging data on juvenile cod is limited for recent years but juvenile cod tagged in the north in 2002 have been recaptured off the north-west aged 4 and 5 (Saemundsson, pers. com.). This would represent migration between areas for the spatial structure in this model implementation.

Cod-shrimp interaction

The simplest manner in which to combine the cod and shrimp models is to have cod as predators of shrimp and other food, ignoring cod cannibalism. Cannibalism does not appear to have a large impact on the stock dynamics and with no cannibalism the cod parameters can be fixed to those from a single species 2-area model, reducing the number of parameters estimated. This is a temporary measure for the development of the model and ideally cannibalism would be included and more parameters estimated.

The preference for shrimp by cod, in Icelandic waters, decreases as predator length increases (Magnusson and Palsson 1991b) and as can be seen in figure 9.56. Magnusson and Palsson (1991b) also found that for small cod there is an increase in prey length as predator length increases. For some areas, predation on male shrimp is considered to exceed that on females as predation is largely by young cod Fu et al. (2001) and data from the north of Iceland indicate that most consumption of shrimp by small cod is on shrimp which are probably male.

Data indicate that shrimp constitute approximately 10% of the biomass in cod stomachs (figure 9.56) which is the same value found by Magnusson and Palsson (1991b). For both Icelandic waters (Magnusson and Palsson 1991b) and the Flemish Cap (Parsons et al. 1998) no significant relationship the stock biomass/CPUE of the shrimp fishery and the level of predation by cod.

In the stock production model of Stefansson et al. (1994) the consumption index was based on the abundance of the immature part of the cod stock. Two models are considered here, one with predation by all cod and the other with predation only by the immature stock component.

Data and likelihood functions

The only data required in addition to those described previously are stomach content likelihood data:

- Composition of stomach contents as ratios of prey biomass by species (i.e. shrimp or other) aggregated over all predator lengths from the spring groundfish survey for 1988–2002 and other data sources where available. These are combined into one likelihood component.
- Length distribution of prey by predator length groups as biomass ratios from the spring groundfish survey for 1988–2002. Predators are aggregated into 20cm length groups and prey into 4mm length groups.
- Length distribution of prey by predator length groups as biomass ratios from other stomach sampling projects. Predators are aggregated into 20cm length groups and prey into 4mm length groups.

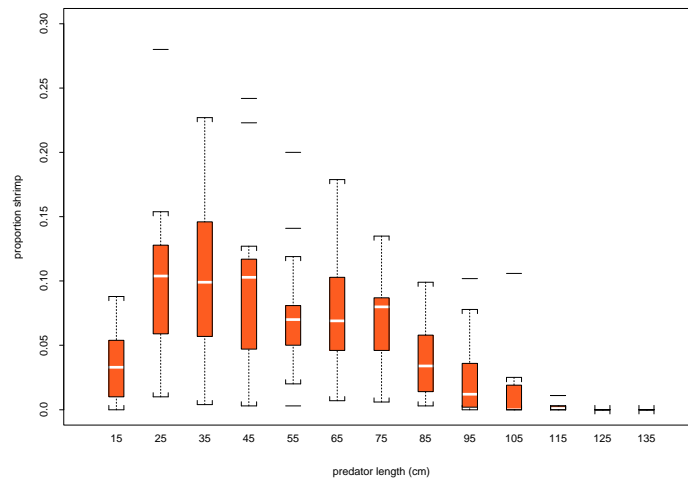


Figure 9.56: Box plots of the proportion of shrimp in cod stomachs by predator length from the Spring groundfish survey. The stomach contents are aggregated by year and area.

Model Implementation

The model runs from 1988 to 2002, with monthly timesteps, on two areas. There are two species, each with two stock components: immature and mature cod and male and female shrimp. Cod are present on both areas, with shrimp only on one area. The stocks are structured as for the single species models described earlier. There are four fleets, with two operating on each species and no fleet affects both species. The implementation of consumption is described in Section 9.3 for cod cannibalism and the approach is similar for the two species model.

Two models are considered, one with predation by both immature and mature cod and the other with predation only by immature cod. With predation by all cod a single set of prey suitability parameters is estimated.

Results

The prey selection patterns estimated within the models are shown in figure 9.57. The optimal predator length:prey length ratio was fixed to the same value (4) in both cases. Given the observed differences in the size preferences of juvenile and older cod the use of different selection parameters for immature and mature cod should be investigated. This would allow for an increasing size preference for smaller cod but also allow for larger cod being able to consume all length groups.

The annual consumption of shrimp greatly depends on the model specification as can be seen in figure 9.58. With predation only by immature cod, annual predation on shrimp by cod is less than the catch, whereas with the additional predation by mature cod, predation exceeds the catch in most years.

Stefansson et al. (1994) estimated cod consumption of the fishable shrimp stock to be 11 600 tonnes (approximately half that estimated here for immature alone), but only shrimp longer than 12mm and consumption by immature cod were considered. Magnusson and Palsson (1991b) estimated the annual consumption of shrimp by cod in Icelandic waters to be around 100 thousand tonnes but this estimate was for all *P. borealis* around Iceland and only the offshore stock is considered in this model.

The fit of both models to the shrimp survey indices is similar (figures 9.59 & 9.60) especially for the

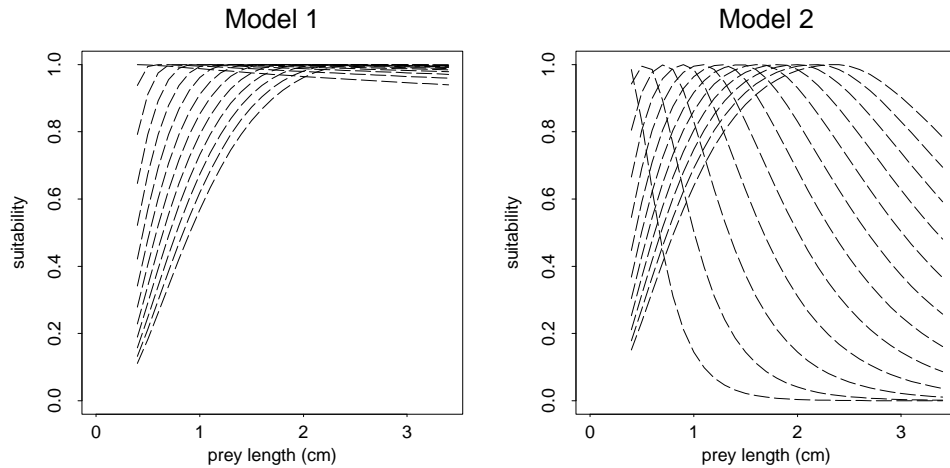


Figure 9.57: Estimated prey selection patterns with all cod as predators of shrimp (model 1) and with only immature cod as predators (model 2).

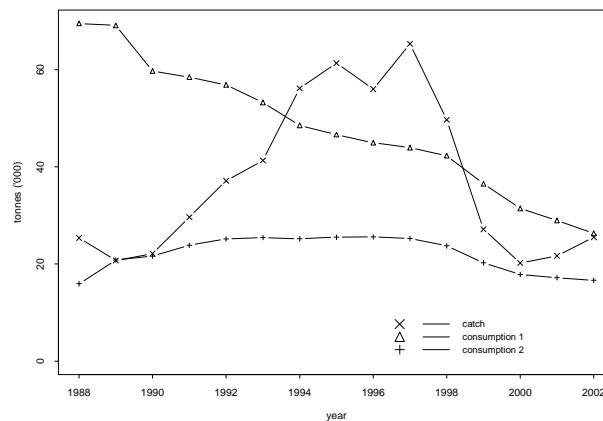


Figure 9.58: Catch and consumption of shrimp estimated from model 1 (consumption 1) and model 2 (consumption 2).

length group 2 indices. The stock biomass is very large in both cases and as with the single species model increases with time as the number of older shrimp continuously increases. The high biomass means that predation has little impact on the stock structure and dynamics.

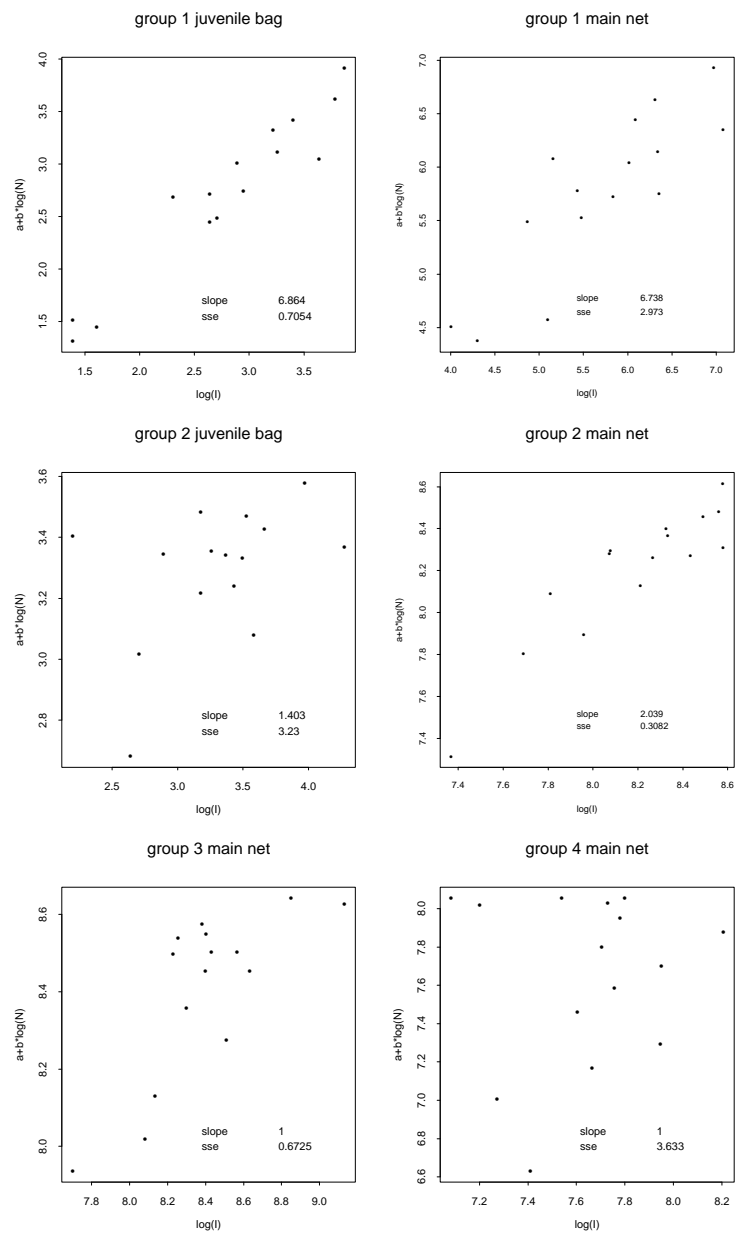


Figure 9.59: Shrimp survey indices from model with predation from immature and mature cod: plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b*\log(N)$ the model estimate of the survey index.

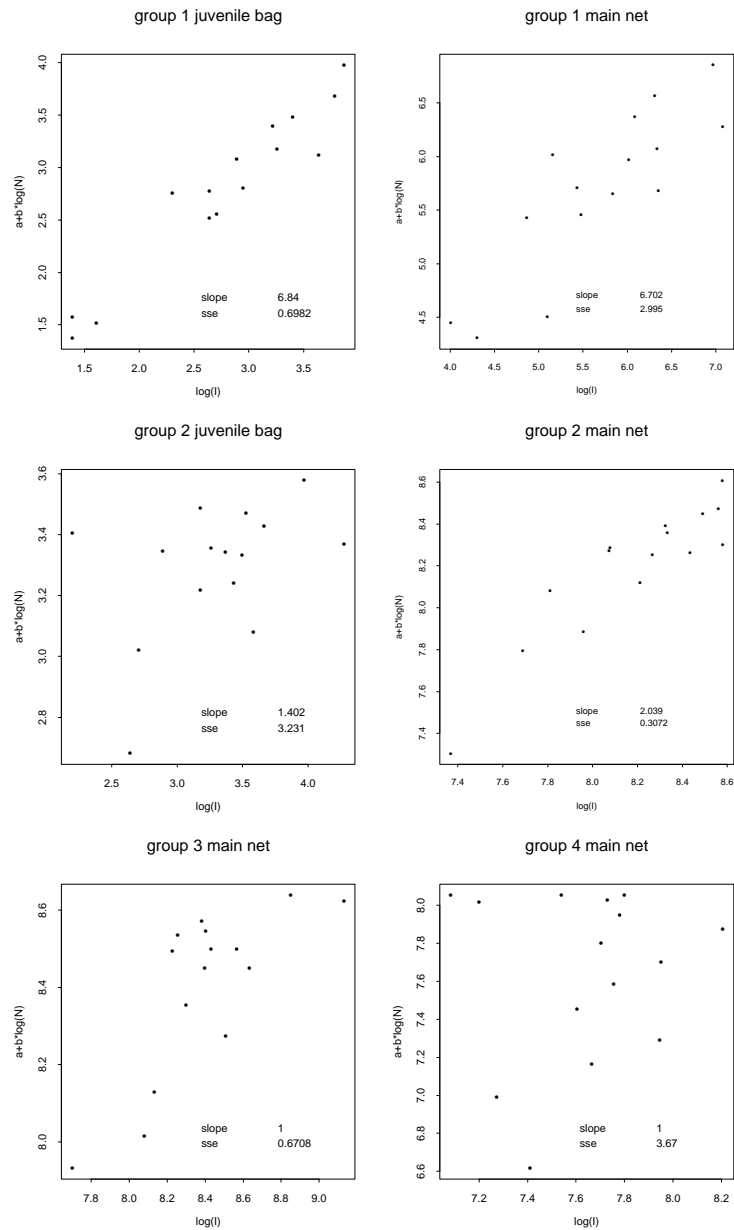


Figure 9.60: Shrimp survey indices from model with predation only by immature cod: plots of the log-linear regression as estimated in Gadget, with one plot for each likelihood component and the corresponding slope (estimated for length groups 1 and 2) and sse for each survey index. $\log(I)$ is the index and $a+b*\log(N)$ the model estimate of the survey index.

Discussion

Shrimp: There is clearly a problem in estimating the total biomass of the shrimp population and in determining the age structure. This is a common problem for shrimp due to the lack of age data and variable natural mortality. Given the ability of the model to fit the survey indices for the younger age groups, the mortality of the older shrimp, especially that of mature females, needs to be considered more closely. It would also be useful to find a way of creating more than one index for the older shrimp in order to be able to determine more appropriate weights for these likelihood components.

Cod: In a 2-area model, age data are required along with the survey to estimate the total population size as migration breaks the direct link between the oldest survey group (which in a single area model is an important determinant of the level of abundance) and recruitment. This means, however, that it is probably necessary to estimate the initial population abundance, recruitment and the migration parameters simultaneously. The possible importance of including more than one commercial fleet is discussed for the single area cod model in Section 9.3 and with more than one area, this would be expected to become a more important issue as the distribution of gear use on the different areas is not homogeneous.

To more accurately determine the distribution of cod between the areas, it is necessary to consider the migration of juveniles from the north to the south. This could be incorporated into the current implementation by including an additional cod component. It may also be useful to fix migration to externally estimated parameters and compare with tagging data rather than estimate migration directly from relatively limited mark-recapture data from juvenile cod. These areas are not of limited interest in terms of migration patterns of mature cod but migration of juveniles is expected to be significant.

Cod and shrimp: The predation of shrimp by cod needs to be considered in more detail. The decreasing preference for shrimp by cod should be incorporated into the model and the size preferences analysed more carefully. Length distributions from stomach contents indicate low consumption of shrimp of lengths 18–22mm for all but the largest cod. This is most probably due to spatial heterogeneity of the shrimp stock and shrimp are known to migrate in other area (e.g. the Gulf of Maine (Clark et al. 2000)). These bimodal length distributions, are expected to cause problems in parameter estimation. Given the problems in estimating migration the benefits of using more areas should be evaluated.

Predation of shrimp by cod is determined more by the abundance of cod than availability of shrimp and to accurately determine consumption the cod stock abundance and structure in the northern area needs to be modelled accurately. For any information on the impact of predation on the shrimp stock dynamics, more certainty is required on the biomass of the shrimp stock.

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9.5 Further published/in press papers

Assessment of golden redfish (*Sebastes marinus* L) in Icelandic waters

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Abstract: Assessment of redfish has traditionally suffered from the inability to age the fish. For golden redfish in Icelandic waters, length distributions and abundance indices are available both from commercial catch and from surveys, particularly a groundfish survey in March. This paper addresses the use of an age- and length-based cohort model for the assessment of redfish, where all selection curves depend on the length of the fish and information on age is not a prerequisite but can be utilised if available. In the last few years it appears that ageing of this species has been successful and in this paper we compare assessment results of a model that incorporates age information with those that do not. Finally, we calculate yield per recruit, F_{max} and $F_{0.1}$ for the stock. Stock size, catch and fishing mortality are then simulated 10 years ahead using different catch control laws.

Bjornsson, H and Sigurdsson, Th. 2003. Assessment of golden redfish (*Sebastes marinus* L) in Icelandic waters. *Scientia Marina*, 67(Suppl. 1): 301-314

Chapter 10

North Sea

10.1 A model of the North Sea herring fishery using GADGET

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Introduction

The North Sea herring is a natural resources that has been exploited for human consumption for centuries. In the past three decades, this fishery has gone through a wide range of exploitation situation (Nichols, 2000). Several over-exploitation periods (1970s and 1990s) were followed by a total ban on fishing (1977–1981) or a drastic reduction of the Total Allowable Catches (TAC). At present the stock is in good condition according to specialists. The TAC have been increased over the past 3 years and it is thought by experts that the stock is healthy enough to sustain a higher rate of exploitation.

Management decision on the NS herring stock are provided by the ICES committee management based on the Integrated Catch at Age (ICA) assessment method. This analytical method is used to describe the state of the stock during a particular period of time. It is based on the Virtual Population Analysis (VPA) method which was developed in the late seventies. During the last two decades, stock assessment methods have benefited from the improvements made in computer science. The increasing performances of the computer are giving the opportunity to deal with more complex stock assessment model that take the biological processes occurring in a fish population into account. Growth, sexual maturation, and reproduction are now commonly modelled together with the commercial fleet activity.

The Globally applicable Area Dis-aggregated General Ecosystem Toolbox (GADGET¹) is a computer program able to deal with different aspects of a fishery. It offers a flexible framework for the scientists to describe biological populations. In this paper we describe the methodology used to apply this framework to model the biological processes characterising the North Sea herring, the fishing industry harvesting it and the scientific surveys studying this species during the decade 1990–2000. The insights on the NS herring population dynamic are presented and compared to the information used currently for the assessment of the status of this stock.

Description of the model

This model of the NS herring deals with the North Sea (ICES divisions IVa, b, c and VIId) as an homogeneous area. The biological and fishery processes are assumed to be the same throughout the area. The model covers the time interval between 1977 and 2000 by quarters although the period used to compare its results with those from ICA is 1990–2000. The time span before this period (*i.e.* 14 years) is setup to let the simulation stabilise to a steady level (Kienzle and Gimona, 2003).

This parametric model of the North Sea herring fishery is composed by three components that specify

1. the herring population dynamic
2. the harvest processes characteristic of the fishing industry
3. the scientific methods used to survey the fishery

The herring population

Structure of the population The population of herring is structured into 9 age groups from age 1 to 9 (the latter being a plus group) and 23 length groups of width 1 cm between 8 and 32 cm. At the

¹This software and the related documentation are available at <http://www.hafro.is/gadget>

beginning of the simulation, the age structure is given by the vector of age group parameter ($age1 \dots 9$) multiplied by 10^5 . The length distribution for each age group, shown in Table 10.2, is calculated using the 1st quarter data for years between 1990 and 2000.

Natural mortality The instantaneous natural mortality rate (M) in the simulation is kept constant through time. But it decreases with age until the last age group as shown in Table 10.1. The high rate of natural mortality for the age group 9+ is used to avoid the accumulation of older individuals which can create an artificially high abundance of these individuals in the model. These settings are the same than those used for the Integrated Catch at Age (ICA) model as reported in (ICES, 2002a).

Recruitment Referring to the recruitment to the fishery, is set in the model to occur for 1 year old herring during the first quarter. The length of the recruit is fixed to 14.70 cm ($SD=1.74$) as it is the average observed length of 1 year old fishes in quarter 1 in the input data. The recruitment is set to be proportional to the Methots, Isaacs and Kidd (MIK) recruitment index by a factor (parameter rec) estimated during the optimization procedure.

Growth The average length increment by quarter is modelled using the Von Bertalanffy growth function with parameters L and k . The proportion of all individual growing a particular number of length bin at each time step is modelled by a beta-binomial distribution of parameter $bbeta$. The maximum length any individual can growth during a quarter is limited to 10 cm.

The length weight relationship The parameters of the length-weight (LW) relationship (Table 10.3) are estimated using the data of the North Sea (ICES division IVa,b and c) and East English Channel (ICES division VIId) stored in the data warehouse build for the dst^2 project (Kienzle, 2003) using a non-linear weighted least square regression.

The data were binned into 1 cm classes. The fit of the LW relationship was performed only on data between 8 and 34 cm, outside this size range the mean weight at length display large or an abnormally small variance (Fig. 10.1). Further inspection of the data should reveal that this is the result of a lack of data. But this investigation has not been carried out since the chosen range of data covers the range of length data used in the GADGET model of the NS herring.

According to the fit statistics ($DF^*=24$, $\chi^2 = 2.45$, $P \simeq 1$), the LW relationship gives a good description of the data. Therefore these parameters were used in the model of the NS herring.

Maturity NS herring maturity is not modelled. Nevertheless, maturity ogives are used to determine the spawning stock biomass (see section 10.1).

The fishing industry

The time series of the yearly landings (Fig. 10.2) shows a stable level of catches around 700.000 tons between 1985 and 1995. After 1995 the landings dropped by half to an average level around 350,000 tons. The time series of the landing by quarter (Fig. 10.3) gives more insight into the seasonality of the North Sea herring fishery. Before the year 1990, the bulk of the catches were made in the 3rd quarter. While the catches made during this quarter decreased steadily after 1990, the 4th quarter catches start to increase in importance. 1st and 2nd quarters catches have always been less important though some years they can account for up to a third of the whole catch.

*DF: degree of freedom

The model assumes that the NS herring is harvested by a single fleet that has an homogeneous pattern of exploitation throughout the area. The gear selectivity (S) (Eq. 10.1) is described with a logistic function².

$$S = \frac{1}{1 + \exp[-\alpha - \beta \times l - \gamma \times L]} \quad (10.1)$$

The value of the parameters α and β are chosen to constrain the selectivity of the gear to be an increasing function of the size of the fishes (more details in annexe 1 p. 422).

The scientific surveys

Data from 5 scientific surveys are used to determine specific aspect of the NS herring population:

- the Norwegian pelagic survey
- the International Bottom Trawl Survey (IBTS)
- the market sampling
- the index of herring abundance given by the summer acoustic survey
- the Methots, Isaacs and Kidd (MIK) recruitment index

The length frequency distribution (LFD) generated by GADGET are fitted to the LFD observed during the Norwegian pelagic, the IBTS and the market survey. The selectivity of the gear is modelled with a logistic function (Eq. 10.1) for both the market sampling data and pelagic survey. While a constant function of length is used to model the selectivity of the IBTS survey data.

The population abundance at age in the model is determined using the summer acoustic survey data. It is assumed that the logarithmic transformation of these 2 variables are linearly related for age group 2 to 8³.

The recruitment in the model is assumed to be proportional to the MIK index. The proportionality factor (variable *rec*) is estimated so as to minimize the difference between the estimation and the observation.

Data

GADGET's model of the North Sea herring uses the data stored in the database build during dst² project (Kienzle, 2003). This database provides several length frequency distributions (LFD), one age-length keys and the total herring landings in the concerned area.

During the modelling stage, it appears that some additional information would be required to fit the model (*e.g.* index of recruitment and number at age) and some would be required to process GADGET's predictions into variables commonly used by fishery biologist for stock assessment. These informations were taken from (ICES, 2002a) and are detailed in the following paragraphs.

Recruitment The Methots, Isaacs and Kidd (MIK) index of recruitment (ICES, 2002a) was used to determine the recruitment. Although it gives an index of the 0-group year class, it is used in the simulation as an index of the 1 year old age group, as it is the age of recruitment in the model. Therefore the values of the MIK index are shifted forward by 1 year.

²for more details, see ExpSuitFuncA at <http://www.hafro.is/gadget/userguide/userguide.html>

³Abundance of age group 1 is determined by the recruitment. Age group 9 being a + group accumulate all ages superior to 9 years therefore showing no relationship to the number at age 9 estimated by GADGET.

Index of abundance at age The number of herring at age estimated from the summer acoustic surveys between 1990 and 2000 (ICES, 2002a) are used to determine the number of individuals in the simulated stock.

Maturity ogive The maturity ogives were used to compute the time series of the spawning stock biomass (SSB) from the number at age estimated by the model. These ogives are calculated using sample collected during the summer acoustic survey. They are taken from (ICES, 2002a) and are reported in Table 10.4.

Weight at age These data were taken from (ICES, 2002a) and are used as an external constraint for fitting the model.

Estimation procedure

The parameters of the model are estimated by an iterative method using data collected between 1985 and 2000. Like every non-linear method, a starting value as well as the boundaries of investigation must be provided to the algorithm. The set of starting values together with the boundaries used by the NS herring model are presented in Table 10.5. The choice of these values was determined by previous studies when available. In some cases, as for the gear selectivity, the boundaries of investigation can be deduced from the shape of the desired function (more details in annexe 1 p. 422). But for most parameters of the model the starting value and the boundaries were fixed in an ad-hoc manner: by fitting repetitively the model with different values until a satisfying converged solution was reach.

The optimisation algorithm is designed to determine the set of parameter that minimise the overall likelihood value which is composed by the sum of each survey specific likelihood value. The model is fitted to the Norwegian pelagic, the IBTS and the market sampling survey data using the sum of the square of the differences between the proportion of individual in each age-length or length bin at each time step. While the abundance and recruitment are determined by fitting the survey indices using log-linear regression and minimising the square of the discrepancies.

GADGET's estimates are correct only if the optimiser meet its criterion of convergence (Table 10.6) and none of the parameter estimations are at the boundary of their range of investigation. Moreover the adequacy of the weight at age prediction was assess by plotting them together with the data. The settings of the model were modified when the agreement between these 2 sources of information was poor.

Results

The results of ten separate runs of the NS herring model are reported in Table 10.7. Eight of these runs converged to a solution according to the setting of the optimiser. The second row of Table 10.7 shows that every run finished with a different score of the likelihood suggesting that each of them has converged to a different solution.

Growth

The parameter were used to determine growth (L , k and $bbeta$). The estimate of the asymptotic length (L) of Von Bertalanffy growth function are between 32.2 and 38.2 cm are higher than those reported by (Beverton and Holt, 1959) ($L = 30$ cm) and (Blaxter, 1985) ($L = 31$ – 32 cm). The parameter of velocity of growth (k) is estimated to be between 0.29 and 0.46 years⁻¹ are similar to those reported by (Beverton and Holt, 1959) ($k = 0.38$) and (Blaxter, 1985) ($k = 0.35$ – 0.43). Of all the growth parameter, $bbeta$ is the most variable with estimates ranging from 13.7 to 9610.5.

Fig. 10.4 shows a representative example of the fit of the growth function to the data for each quarter of 1992. The growth model appears to be in good agreement with the data.

A comparison between weight at age data and those estimated using the model is shown in Fig. 10.5 for the years between 1991 and 2000. The estimated growth in weight is in good agreement with the data although if the model slightly underestimate the weight at age of the younger age classes.

Trend in spawning stock biomass

The trend in spawning stock biomass (SSB) shown by the different runs of GADGET are very similar to ICA (Fig. 10.6). They indicate that the SSB has decreased from 1990 to its lowest level in the mid 90s and increased again at the end of the decade. GADGET produces higher estimates of SSB than ICA at the higher level of SSB, while its estimate are lower than ICA when the SSB is at its lowest value.

The data between 2001 and 2003 have been added to Fig. 10.6 to compare the prediction of GADGET with ICA. Although the parameter were determine with data from 1985 to 2000, this parametrisation of the model allows to describe the variation of the SSB for the year following this period.

Trend in biomass of NS herring

The estimated trend in total biomass estimated by GADGET are shown together with ICA's estimation in Fig. 10.7. GADGET's estimates are 2–3 folds higher that ICA. The variation of the total biomass during the decade shown by GADGET is much greater than ICA.

Conclusion

The development of a statistically testable model to describe marine population and evaluate the sustainability of their exploitation is a highly desirable target as it will provide an objective method of evaluating the status of the exploited populations under study. The methods currently used in the field of stock assessment are often subjective and their prediction is often dependent on the experience of the scientist. In that respect GADGET's attempt to incorporate statistical criterion to guide the scientists through the description of a fish population, using a model that incorporate biological processes, is to be encourage.

The model gives a good description of the NS herring length and weight at age data. The L_{∞} parameter estimate are often higher than those found by previous studies. This is probably due to the implementation of growth within GADGET that constrain it to be higher than the highest length in the data. On the other hand the estimate of the velocity of growth parameter (k) is in agreement with estimate found in literature.

The trend in SSB produces by GADGET's model of the NS herring is similar to ICA. But GADGET estimates of the total biomass of the population are higher than those given by ICA. Since the SSB estimate are in good agreement between these 2 models, the difference in total biomass must be due to difference in the estimate size of the immature component of the stock with GADGET's model producing a much higher estimate than ICA.

The implementation of the framework of analysis is very efficient. The use of C++ as the coding language provides a fast software allowing us to investigate a large range of model to describe the NS herring fishery. The strategy of keeping the data independent from the formulation of the model was well appreciated as it keep separate the modelling of the population from the collection and the formatting of the data. The operating system (Linux/Unix) used for its implementation is also a major asset of the framework since it provides a powerful and flexible tool to use. The drawback may be that the dissemination of this tool is limited by size of the Linux user community as well as the amount of

computer literacy required to use it.

Acknowledgement

I am grateful to J. Simmonds for his supervision and advises he gave to enhance the model GADGET model for NS herring. I would like to thanks our Icelandic colleagues for the help they provide: in particular I am grateful to V. Kupča for all the information he provides on the datawarehouse issues. I am grateful to J. Begley and L. Taylor for their help in defining the model and finding errors in its definition. At FRS, I would like to thanks B. Edelsten to provide the computer facilities that reduce effectively the computation time.

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Annexe 1

Constraint on the parameter of the selectivity curve of the commercial fleet The selectivity function of the commercial fleet is model by the following logistic function ⁴

$$S = \frac{1}{1 + \exp[-\alpha - \beta \times l - \gamma \times L]} \quad (10.2)$$

It is parameterise such as the selectivity of the gear will increase as a function of the size of the fish for the range of herring length used in the model (*i.e.* 8–32) (*NB:* the influence of the predator size (L) is switched off by setting the parameter γ to zero). This constraint allows us to bound the space of search of the parameters of this function

$$\begin{cases} S < 0.01, & \text{for } l = 0 \\ S > 0.99, & \text{for } l = 40 \end{cases}$$

$$\begin{cases} \frac{1}{1+e^{-\alpha}} < 0.01 \\ \frac{1}{1+e^{-\alpha-\beta \times 40}} > 0.99 \end{cases}$$

$$\begin{cases} e^{-\alpha} > 99 \\ e^{-\alpha-\beta \times 40} > \frac{0.01}{0.99} \end{cases}$$

$$\begin{cases} \alpha < -4.6 \\ -\alpha - \beta \times 40 > \log\left(\frac{0.01}{0.99}\right) \end{cases}$$

$$\begin{cases} \alpha < -4.6 \\ -\beta \times 40 < -4.6 + \log\left(\frac{0.01}{0.99}\right) & \text{because } \alpha + \log\left(\frac{0.01}{0.99}\right) < -4.6 + \log\left(\frac{0.01}{0.99}\right) \end{cases}$$

$$\begin{cases} \alpha < -4.6 \\ \beta > \frac{1}{40} \times [\alpha - \log\left(\frac{0.01}{0.99}\right)] \end{cases}$$

Therefore, fixing the higher bound of α to -4 , we get the lower bound of β at 0.01 .

⁴See <http://www.hafro.is/gadget/userguide/userguide.html> for more details.

Tables

Age	M
0 – 1	1
2	0.3
3	0.2
4 – 8	0.1
9+	1

Table 10.1: Natural mortality rate (M) as a function of age of the fishes.

	mean	S.D.
age1	14.70	1.74
age2	22.40	2.61
age3	26.10	1.31
age4	27.20	1.20
age5	30.30	1.29
age6	29.80	1.41
age7	30.40	1.36
age8	30.70	1.42
age9	32.40	2.24

Table 10.2: Length at age distribution at the beginning of the simulation.

No data = 522878, DF=24, $\chi^2 = 2.45$, $P \approx 1$	
$\mathbf{p}_0 \pm \sigma$	$2.94\text{e-}06 \pm 6.63\text{e-}07$
$\mathbf{p}_1 \pm \sigma$	$3.32 \pm 7.19\text{e-}02$

Table 10.3: Summary statistics of the fit.

year	age 0	age 1	age 2	age 3	age 4	age 5	age 6	age 7	age 8	age 9
1990	0.00	0.00	0.73	0.97	1.00	1.00	1.00	1.00	1.00	1.00
1991	0.00	0.00	0.64	0.98	1.00	1.00	1.00	1.00	1.00	1.00
1992	0.00	0.00	0.51	1.00	1.00	1.00	1.00	1.00	1.00	1.00
1993	0.00	0.00	0.47	0.63	1.00	1.00	1.00	1.00	1.00	1.00
1994	0.00	0.00	0.72	0.86	1.00	1.00	1.00	1.00	1.00	1.00
1995	0.00	0.00	0.73	0.96	1.00	1.00	1.00	1.00	1.00	1.00
1996	0.00	0.00	0.60	0.97	1.00	1.00	1.00	1.00	1.00	1.00
1997	0.00	0.00	0.64	0.94	1.00	1.00	1.00	1.00	1.00	1.00
1998	0.00	0.00	0.64	0.89	1.00	1.00	1.00	1.00	1.00	1.00
1999	0.00	0.00	0.81	0.91	1.00	1.00	1.00	1.00	1.00	1.00
2000	0.00	0.00	0.66	0.96	1.00	1.00	1.00	1.00	1.00	1.00

Table 10.4: maturity ogives of the autumn spawning herring for the year ranging between 1990 and 2000.

	value	lower	upper
L	33.00	32.01	40.00
k	0.30	0.05	0.80
bbeta	10.00	0.01	10000.00
age1	10.00	0.01	100.00
age2	8.00	0.01	100.00
age3	6.00	0.01	100.00
age4	4.00	0.01	100.00
age5	3.00	0.01	100.00
age6	3.00	0.01	100.00
age7	2.00	0.01	100.00
age8	1.00	0.01	100.00
age9	1.00	0.01	100.00
rec	100.00	0.10	200.00
aCommercial	-6.50	-15.00	-4.00
bCommercial	0.30	0.10	0.99
apelagic	-6.50	-15.00	-4.00
bpelagic	0.30	0.10	0.99
aibts	0.50	0.00	1.00
;bibts	-0.30	-0.99	-0.10

Table 10.5: Starting values and boundaries of investigation of the parameters of the model.

Simulated annealing

iteration	5000
minimum epsilon	0.01
temperature (T)	100
T reduction factor	0.2
loops before T adjustment	2
loops before step length adjustment	5
step length	1
step length adjustment factor	2

Hooke and Jeeves

iteration	5000
minimum epsilon	1e-04
resizing multiplier	0.5
initial value for the step length	0

Table 10.6: The settings of the optimization algorithm.

	run 1	run 2	run 3	run 4	run 5	run 6	run 7	run 8	run 9	run 10
convergence	yes	no	yes	yes	yes	yes	yes	yes	yes	no
likelihood	23.54	25.57	24.97	23.70	25.77	25.13	24.13	24.89	24.74	24.28
L	32.20	33.58	38.22	34.01	33.36	32.91	33.89	33.94	35.38	35.17
k	0.42	0.30	0.23	0.36	0.30	0.46	0.33	0.31	0.29	0.31
bbeta	46.62	13.70	40.24	50.22	9.49	55.24	22.56	24.40	9610.52	54.09
age1	0.74	0.84	0.74	0.71	0.85	0.66	0.76	0.79	0.72	0.75
age2	50.24	4.78	74.31	36.62	5.92	14.29	12.18	36.47	33.80	31.53
age3	4.58	0.01	39.37	31.39	1.83	14.23	31.34	0.01	65.68	0.01
age4	18.04	30.42	0.01	2.93	0.63	15.80	52.23	0.01	64.39	34.07
age5	8.58	31.48	0.01	45.66	9.80	62.49	0.64	0.01	52.30	0.11
age6	31.09	0.01	0.01	3.78	36.43	0.01	0.17	0.01	41.72	0.90
age7	16.07	0.01	0.01	43.61	26.85	15.21	14.18	0.01	28.94	1.94
age8	0.23	0.01	0.01	35.97	14.35	11.86	64.39	0.01	61.35	0.77
age9	69.41	0.01	0.01	53.54	43.52	0.01	69.33	0.01	86.44	18.52
rec	84.58	98.15	85.28	81.95	99.58	78.48	87.89	91.90	84.69	86.78
aCommercial	-14.78	-7.24	-12.39	-9.99	-7.19	-12.90	-9.83	-7.21	-13.12	-12.21
bCommercial	0.64	0.29	0.52	0.40	0.29	0.15	0.41	0.28	0.53	0.52
apelagic	-13.92	-14.73	-11.57	-12.62	-15.00	-11.58	-14.53	-13.19	-13.31	-13.84
bpelagic	0.50	0.52	0.45	0.48	0.53	0.45	0.54	0.47	0.50	0.53
aibts	0.28	0.02	0.95	0.61	0.49	0.84	0.76	0.24	0.32	0.75

Table 10.7: Parameter estimations for 10 different runs.

Figures

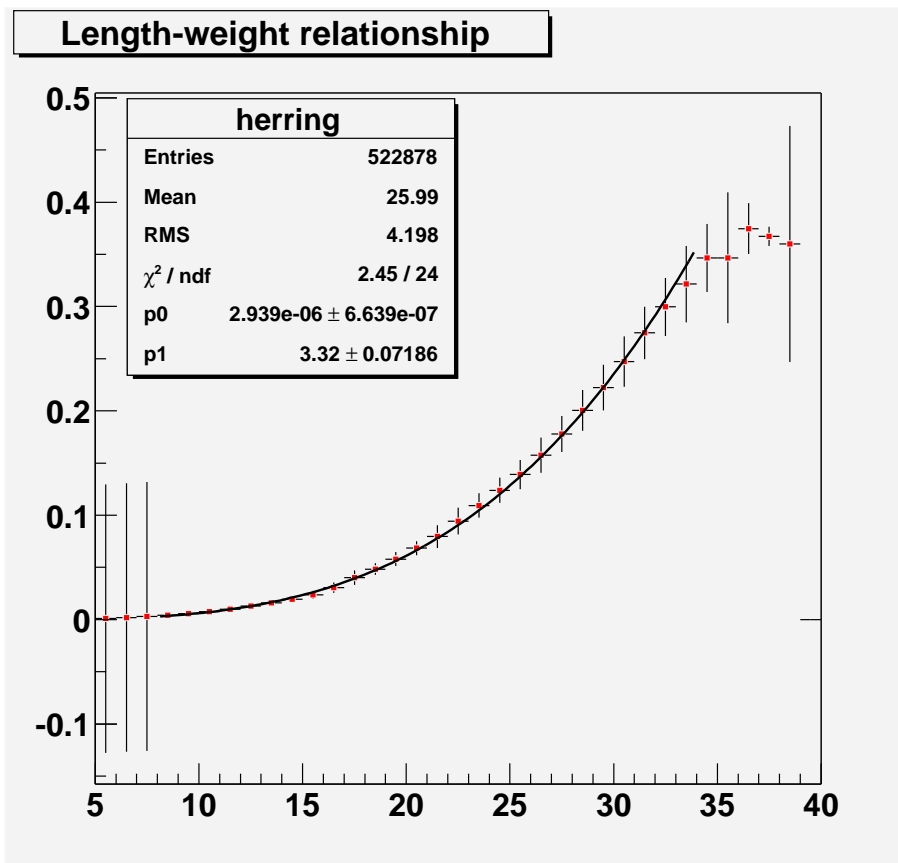


Figure 10.1: Fit of the length-weight relationship on the average weight at length of herring using data taken from the dst² database. The vertical bar represent the standard deviation of the data.

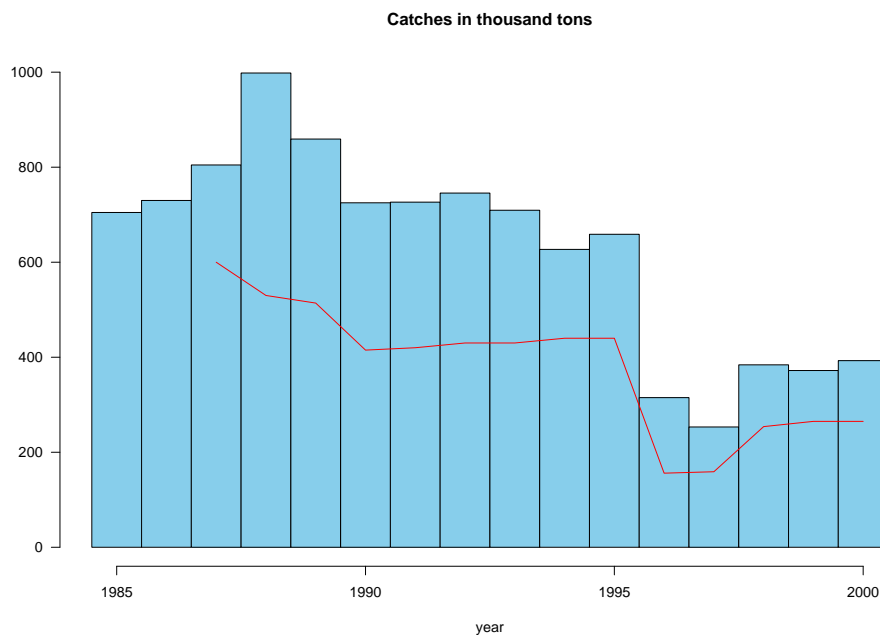


Figure 10.2: Yearly landings of autumn spawning herring from the North Sea fishery (bars) and total allowable catches (line) agreed by the Advisory Committee for Fishery Management (ICES, 2003)

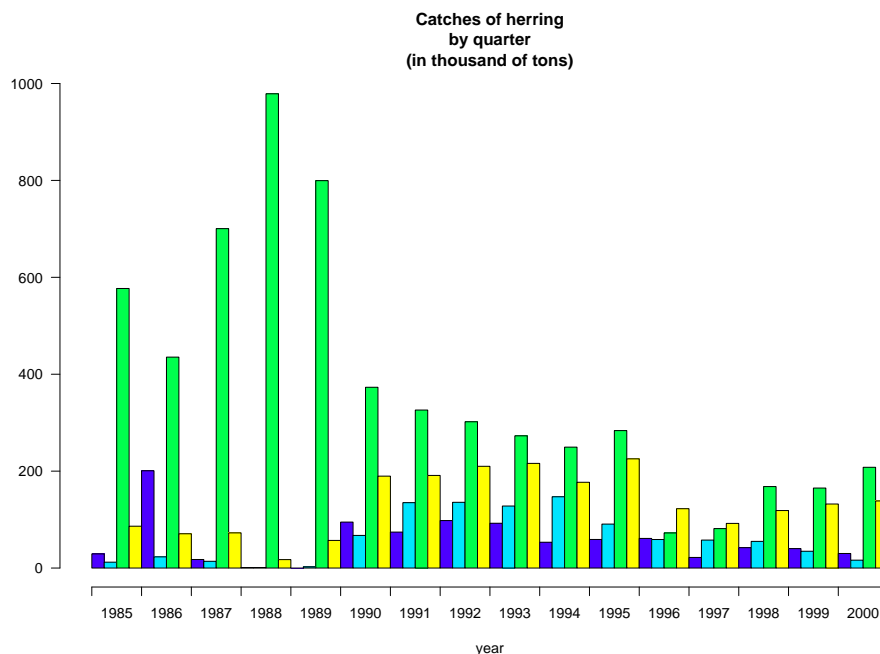


Figure 10.3: Quarterly landings of autumn spawning herring from the North Sea fishery.

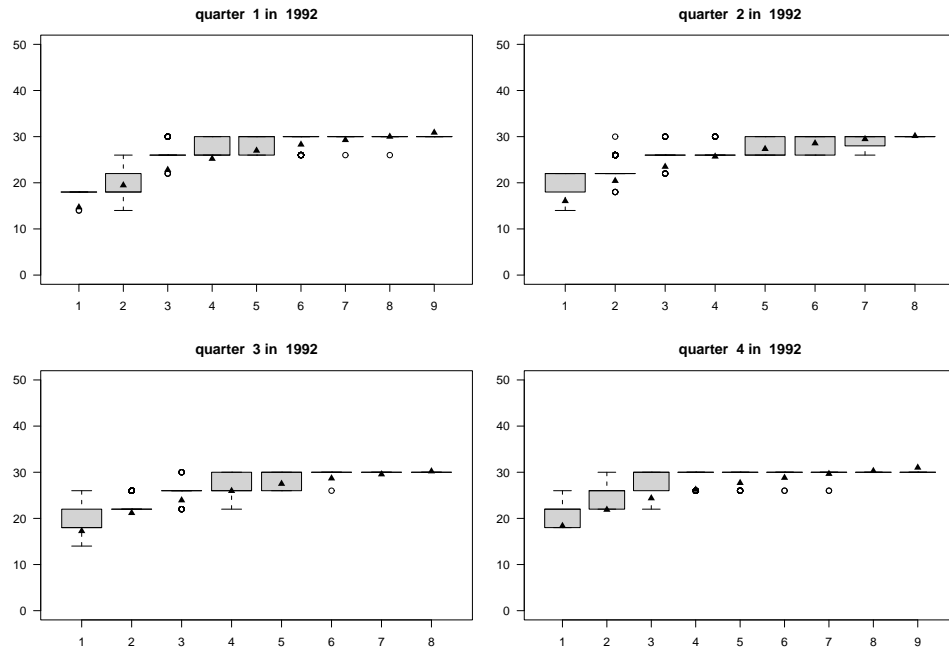


Figure 10.4: Comparison between length at age data and the description given by the model (triangles). The data are plotted using box-and-whisker plots for each age group (x axis): the grey box represent the spread of data lying in between the two quartiles, the horizontal line represent the extremes of the data and the very extreme points are shown by themselves using the open circles symbols.

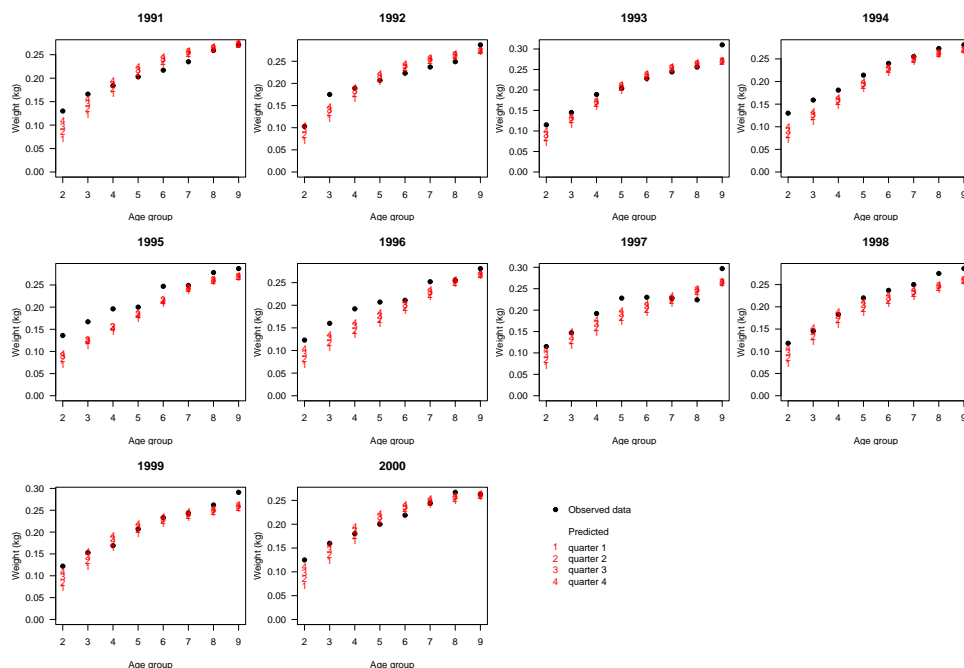


Figure 10.5: Yearly comparison between observed and modelled weight at age. The mean weight at age calculated from the model is represented with number ranging from 1 to 4 corresponding to every quarter of the year. The observations (dot) correspond to the annual average weight at age for the whole North Sea as reported in (ICES, 2002b).

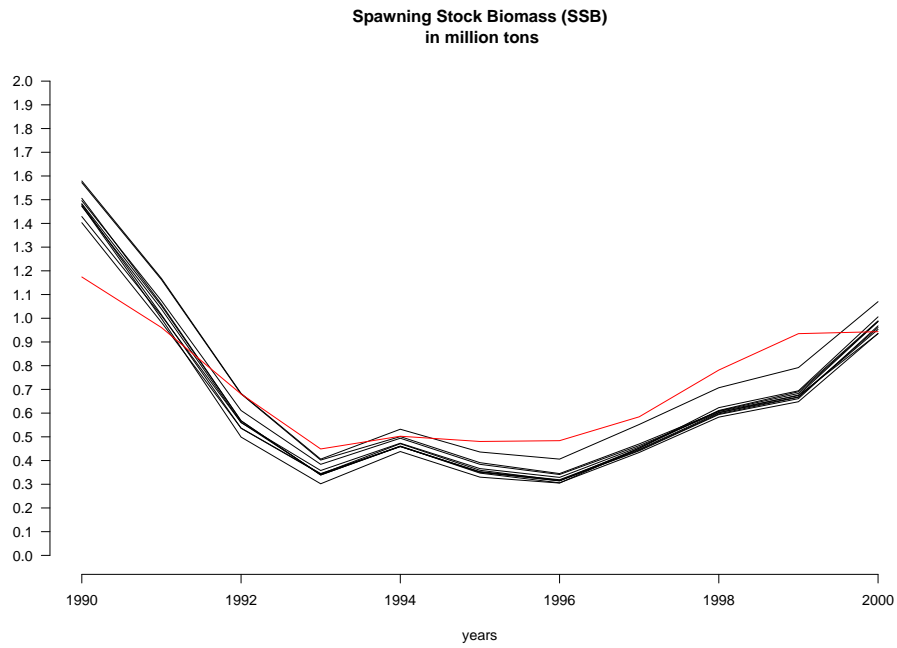


Figure 10.6: Comparison of the estimated Spawning Stock Biomass (SSB) given by GADGET (continuous line) and ICA (dotted line).

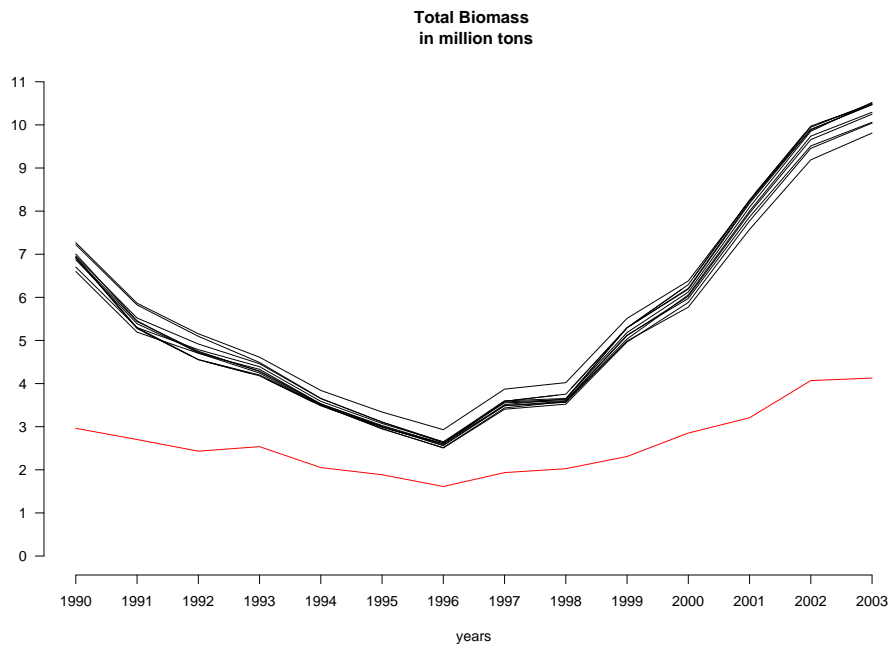


Figure 10.7: Comparison of the estimated total biomass in millions of tonnes given by GADGET (continuous line) and ICA (dotted line).

Chapter 11

Celtic Sea

11.1 Can multispecies models be expected to provide better assessments for Celtic sea groundfish stocks?

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Abstract: In the minds of many people, better stock assessment will require more complex models such as multispecies, multiarea and perhaps multifleet models. But is this always true? By considering a case-study based on Celtic Sea groundfish stocks, we review the biological processes and interactions and determine whether data and understanding of these processes is adequate for successful incorporation into a more complex management tool.

Our approach is to determine what such a multispecies model need look like in this situation, and then to consider the expected performance of such a model based on preliminary results from a simplified food-web and literature studies.

Keywords: multi-species, spatial, Celtic Sea, groundfish food web

Introduction

In many people's minds, more realistic stock assessments go hand in hand with more complex, multispecies, multiarea and perhaps multifleet models. But is this necessarily true? Mace (2004) has put forward strong arguments in defense of single species models in the context of the ecosystem approach to fisheries management. By reviewing the case of the Celtic Sea, we attempt to elucidate whether, for this system, a multi-species, multi-area stock assessment model would be expected to lead to more precise, unbiased stock assessments, (i.e. more accurate population abundance estimates) and, hence to more reliable predictions for informing management choices.

The Celtic Sea is a continental shelf sea situated between France, Ireland and Great Britain. It supports an international fishery and the main commercial species are assessed by International Council for the Exploration of the Sea (ICES) working groups. Total international landings have increased steadily since the 1950s from about 70,000 t to around 300,000 t in the late 1990s (Pinnegar et al 2002).

The Celtic sea groundfish community consists of over a hundred species and the most abundant 25 make up 99 percent of the total estimated biomass and around 93 percent of total estimated numbers (Trenkel and Rochet 2003). Population and community analyses have shown that fishing has impacted a number of commercial species, primarily because individuals of too small a size have been killed in the past (Trenkel and Rochet 2003). This over-exploitation of small fish may have resulted from too small mesh sizes used by bottom trawlers and fishing on nursery grounds, a hypothesis supported by the large amounts of small fish observed to have been discarded by French bottom trawlers (Rochet et al. 2002).

Identifying species interactions

Fish species of commercial interest are predators of fish and other organisms but also prey themselves. Both predators and preys influence each other in various ways (top down and bottom up control). In addition, there are intra- and inter species competition. Preys have an impact on predators through their numbers, energy content and spatio-temporal distribution. The strength of this impact for a given predator-prey couple will depend on the size of the prey portfolio (feeding diversity), the overlap of this portfolio with that of other predators (competition) and the preference for this prey species (functional response type). Three classes of functional response models have been proposed: prey dependent

response also known as Hollings three functional response models, ratio-dependent functional response which is a function of the ratio between prey and predator population sizes; thirdly there are also multi-species functional responses (see review by (Abrams and Ginzburg 2000)). The relationship between the per capita predator population growth rate and prey ingestion, predator density etc. is described by the numerical response (see also Abrams and Ginzburg 2000). A general lack of suitable prey might lead to poor body condition but also reduced offspring production. Empirically years with low prey availability might be identified through low body condition and size at age for piscivore predators. For example, it is believed that low availability of energy-rich prey sources such as capelin and herring have negatively influenced the condition of cod in the Barents and Baltic Seas (Marshall et al. 2003). Conversely, predators with a mixed and flexible diet, which consume many prey species between which they often switch (functional response type III) should be less sensitive to the fate of any given prey species or competition from other predators. For example, Greenstreet et al. (1998) found that the proportion of fish in the diet of older (> 30 cm) North Sea haddock (*Melanogrammus aeglefinus*) ranged from 30 to 80% depending on season and year. This might be caused by an adaptation to varying prey availability. Similarly, fish prey only contribute a minor part to the diet of cod in the Celtic sea as compared to a much greater proportion elsewhere (Pinnegar et al. 2003).

Predator species might themselves be preys of predators during their whole life or only as juveniles. Density dependent juvenile mortality has often been found to be a result of cannibalism. Cannibalism in North East Arctic cod has been identified as a minor source of mortality overall, but the frequency of occurrence of cannibalism seems to increase with juvenile cod abundance (Bogstad et al. 1994).

Predator-prey relationships

There are many ways to measure interaction strength between predators and their prey (see recent review by Berlow et al. 2004). Estimation of some of these indicators such as the interaction coefficients in a Lotka-Volterra predator-prey model require manipulation of prey and predator densities and can therefore only be carried out in the laboratory. Using stomach field samples, we can try to evaluate the type of functional response, i.e. the relationship between prey density and consumption, relative prey preferences and spatial and temporal predation patterns.

For the Celtic Sea, two sources of stomach data were available which are described in Pinnegar et al. (2003) and Trenkel et al. (submitted). In summary, UK researchers collected stomachs for 66 of species during routine annual groundfish surveys in 1986 and 1987 and between 1991 to 1994. By contrast, Du Buit (du Buit 1982; du Buit and Merlinat 1987; du Buit 1995; du Buit 1996) sampled stomachs of seven species aboard commercial fishing vessels, throughout the years 1977 to 1992 (in all seasons). Based on these data it was possible to propose a food web for the main fish predators and their principal prey species (Figure 1). Non-fish prey are not shown here, although data exist. The general impression is one of a highly interlinked food web, where several predators feed on the same prey species (i.e. their trophic niches overlap) and on several trophic levels simultaneously. Note that *Trisopterus* spp consists primarily of poor cod (*Trisopterus minutus*) and Norway pout (*Trisopterus esmarkii*) but also some bib (*Trisopterus luscus*), whilst dragonets include *Callionymus lyra*, *C. maculatus* and *C. reticulatus*.

Several predators share the pelagic prey species blue whiting, horse mackerel, mackerel and *Trisopterus* spp. In addition, some of these same predators consume gobies, dragonets and argentines. Apart from the two monkfish species, hake appears to be the most piscivorous, consuming nearly all species in this partial food web, including the predators whiting and megrim.

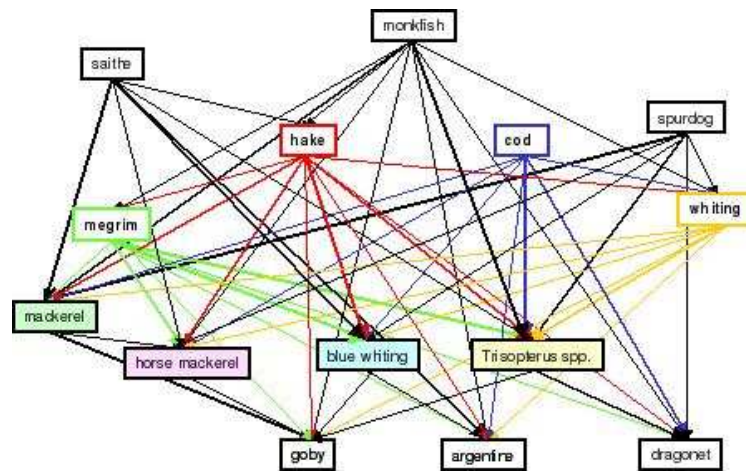


Figure 1. Partial food web for Celtic Sea. In bold important predator-prey relationships (prey appeared in at least 10% of sampled predator stomachs).

The body mass of many piscivorous fish species can increase by five orders of magnitude during their lives, and a fast-growing animal may begin life as a prey item, only to become the main predator on the same group of species within one year (Jennings et al.). Clearly size is an important determinant of fish diets (see Pinnegar et al 2003 for Celtic Sea predators). The actual body size after which the proportion of fish in the diet becomes stable ranges from around 30 cm for whiting to 50 cm for cod (Table 1). The proportion of individuals above this size in spring groundfish varies from around 20% for hake to 100% for saithe (Table 1). Adult cod in the Celtic sea continue to consume large quantities of crustaceans even at very large sizes. Analyses of relative predator lengths and prey lengths has shown, that cod, megrim, hake, dogfish and whiting have similar selection patterns (Pinnegar et al. 2003). The median ratio between predator length and prey length was found to be around 1/4.5 with an upper ratio of $\sim 1/3$ and a lower of $\sim 1/6$.

Table 1. Predator length after which the percentage of fish in the diet becomes stable (derived from Pinnegar et al 2003), average proportion of fish in the diet for predators above this minimum length and average (1982 to 2003) proportion of fish above minimum length in UK spring groundfish surveys (standard error in brackets, see survey description in Trenkel et al 2004).

Species	Predator size (cm)	% fish in diet (% numbers)	Prop fish >min size
Cod	50	<30	0.62 (0.20)
Hake	35	<98	0.19 (0.09)
Megrim	25	<40	0.41 (0.08)
Saithe	40	<80	0.99 (0.01)
Whiting	30	<90	0.84 (0.15)

Certain species, in particular cod (see Bogstad et al. 1994) and hake (Pillar and Wilkinson 1995) are known to feed on their own young. For the Celtic Sea stocks however, there was little sign of cannibalism in the stomachs examined (Table 2).

Table 2. Cannibalism in Celtic Sea. Percentage of stomachs with presence of individuals of same species or fish larvae (N sample size).

Species	N	% cannibals	% fish larvae
cod	3068	0	0.1
hake	1968	0.9	0
mackerel	3833	0.03	0
megrim	4053	0.3	0
whiting	1742	0.4	0

Functional response types

Pinnegar et al (2003) found that cod, hake and megrim in the Celtic Sea consumed more blue-whiting when stock abundance was high. The same study revealed a significant correlation between horse-mackerel consumption by hake and horse mackerel abundance over time. This would point towards a type III functional response, and indicate relatively unselective feeding by predators, which consume whatever is most available at the current time. In contrast, standardized forage ratios for the same data showed that hake, megrim, saithe and whiting preferred argentinines by selecting them more often than would correspond to their proportion in the survey data (Pinnegar et al. 2003). Whiting did not preferentially select *Trisopterus* spp. at the wider Celtic Sea level, however, a high index of spatial collocation between whiting (the predator) in the environment and *Trisopterus* spp (a key prey) in the stomach of whiting, may indicate preferential selection at a more localised scale (Trenkel et al. submitted).

Overall, there was general agreement between higher densities in the environment and higher occurrences of blue-whiting, horse-mackerel, mackerel and *Trisopterus* spp. in predator stomachs (cod, hake, lesser-spotted dogfish, megrim, saithe and whiting) providing further evidence for local density dependent feeding. Hence this again provides evidence for functional response type III which implies some prey switching as predators move around the Celtic Sea and adapt to local conditions. It is important to note that, sigmoidal type III functional responses are rarely used in complex multispecies models since they are very difficult to implement and parameterise (Liermann and Hilborn 2001).

Population trends

Survey based stock assessments have shown that many fish populations in the Celtic Sea have been stable in recent years, with the exception of argentinines that have been decreasing (Table 3). However, despite this recent stability in population abundance, a number of species seem to be 'reproduction overfished' in the sense that total mortality (fishing and natural mortality together) is greater than the limit reference point estimated based on total length and length at maturity. For non-commercial species such as greater argentine, fishing mortality is entirely due to caught but discarded fish. 'Length overfishing' means that mean length in the catch (landings + discards) is smaller than average length at maturity. ICES stock assessments show that most commercial species are outside safe biological limits with the exceptions of megrim, whiting and black anglerfish.

Table 3. Survey based stock assessments for Celtic Sea species using French survey data (1997 – 2000) (adapted from Trenkel et al 2003). Length overexploited: $L_{catch} < L_{maturity}$; reproduction overexploited $Z < Z^*$. ICES assessments from 2003. + Stock area larger than Celtic Sea.

Species	English name	Population size	Total mortality	Mean length of catch	ICES assessments
<i>Argentina silus</i>	Greater argentine	decreasing	reproduction overexploited	length overexploited	–
<i>A.sphyraena</i>	argentine	decreasing			–
<i>Callionymus lyra</i>	Dragonet	no trend			–
<i>Gadus morhua</i>	Cod	no trend		length overexploited	outside limits
<i>Lepidorhombus whiffigonis</i>	megrim	no trend		length overexploited	safe +
<i>Lophius budegassa</i>	Black anglerfi sh	no trend		length overexploited	safe +
<i>L. piscatorius</i>	White anglerfi sh	no trend			outside limits +
<i>Merlangius merlangus</i>	Whiting	no trend			safe
<i>Merluccius merluccius</i>	Hake	no trend		length overexploited	outside limits +
<i>Micromesistius poutassou</i>	Blue whiting	no trend	reproduction overexploited	length overexploited	outside limits +
<i>Scomber scombrus</i>	Mackerel	no trend	reproduction overexploited	length overexploited	outside limits +
<i>Trachurus trachurus</i>	Horse mackerel	no trend		length overexploited	unknown
<i>Trisopterus esmarkii</i>	Norway pout	no trend			–
<i>T. minutus</i>	Poor cod	no trend			–

Joint fisheries exploitation

Individuals of different species are often caught by the same fishing gear (technical interactions) and this represents a second way that species interactions can be created. Three métiers are commonly distinguished for the French Celtic Sea bottom trawlers: gadoid trawlers, benthic trawlers and Nephrops trawlers (Biseau and Gondeaux 1988; Péroudou 1988; Charuau and Biseau 1989). Similar métiers were proposed by ICES for fishing fleets in the Celtic Sea more generally (see (Anonymous 1992)). Each métier targets a distinct group of species usually in distinct areas (see Fishing section below). Table 4 provides the targets, landed species and discards for the three French métiers (based on Rochet et al 2003). Although the target species vary, all three métiers catch the whole suite of species included in the partial food web (figure 1) and broadly the same species are discarded by all métiers. Both Marchal and Horwood (1996) and Laurec et al. (1991) have attempted to model multispecies fisheries interactions in the Celtic Sea.

Vessels from many countries exploit Celtic Sea fish resources. For a certain number of demersal species, such as hake and megrim, the French and English landings make up the majority of landings. In contrast, small pelagics, e.g. blue whiting are dominantly fished by other nations. All main fish predators such as saithe, monkfishes, megrim, hake, cod and whiting are sought after commercial species. In contrast, the prey species mackerel, horse mackerel and blue-whiting are only exploited by pelagic fleets, none of which land in France or the UK. Similarly the *Trisopterus* species have little commercial value in these countries.

Table 4. Target, landed and discarded species of the three French bottom trawler métiers in the Celtic Sea based on a study carried out in 1997 (Rochet et al 2003). Only species in partial food web are shown. T= targets; L=landed; D=discarded. Discards of commercial species are usually undersized fish.

Species	Gadoid trawlers	Benthic trawlers	Nephrops trawlers
Anglerfishes	L	T	L
Argentine	D	D	D
Blue whiting	D	D	D
Cod	T	L	L D
Dragonet	D	D	D
Hake	T D	T D	T D
Horse mackerel	D	D	D
Mackerel	D	D	D
Megrim	L D	T D	T D
Norway pout	D	D	D
Poor cod	D	D	D
Saithe	L	L	L
Whiting	T D	L D	T D

Discard monitoring programmes also exist for UK and Irish fishing fleets, and these conduct regular sampling campaigns in the Celtic Sea.

Selecting species

The criteria used for selecting species to be included in a multispecies assessment model are: (1) commercial importance, i.e. need for assessment, (2) important role as predator or prey, (3) data availability. Based on these criteria, nine species were selected, including the commercially important hake, mackerel and megrim and the two non-commercial *Trisopterus* species Norway pout and poor cod (Figure 3). All of the predators selected consume all of the preys selected although to a varying degree (bold links in Figure 3 indicate larger consumption). In addition cod and hake occasionally prey on the predator whiting; hake also prey on megrim.

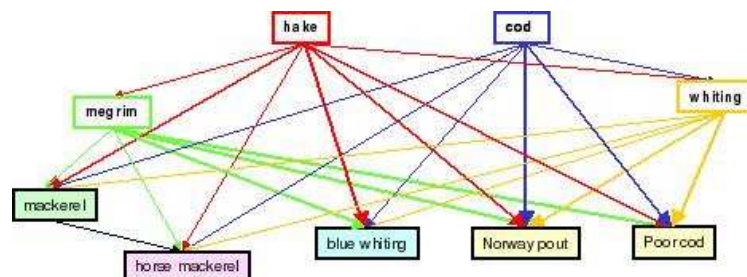


Figure 3. Food web of selected species for Celtic Sea multispecies assessment model. Strong links are in bold (more than 10% of sampled stomach contained the prey species).

Together these species represent around 71% of international landings from the Celtic Sea and around 43% in value (Table 4 and Figure 4). Valuable species not included here are Norway lobster (*Nephrops*), monkfish, plaice and sole.

Table 4. Ecological and economical importance of species proposed to be included in a multispecies assessment model for the Celtic Sea. Biomass from UK spring survey; international landings from ICES; value of UK landings from the UK Department for Environment, Food & Rural Affairs (Defra).

Species	Biomass (Survey 1999) %	Landings (ICES 1999) %	Value (UK 1999) %
Blue whiting	0.93	0.87	0.003
Cod	0.22	1.08	2.62
Hake	0.95	5.66	17.77
Horse mackerel	12.41	42.21	2.30
Mackerel	56.61	15.07	6.77
Megrim	0.24	3.37	13.30
Norway pout	0.54	0	–
Poor cod	0.17	–	–
Bib	0.05	0.05	0.03
Whiting	0.72	2.61	0.67
Monkfish	0.14	2.11	14.24
Haddock	0.28	0.75	0.98
Sole	0.001	0.51	7.19
Plaice	0.04	0.43	1.24
Other	26.70	25.28	32.89

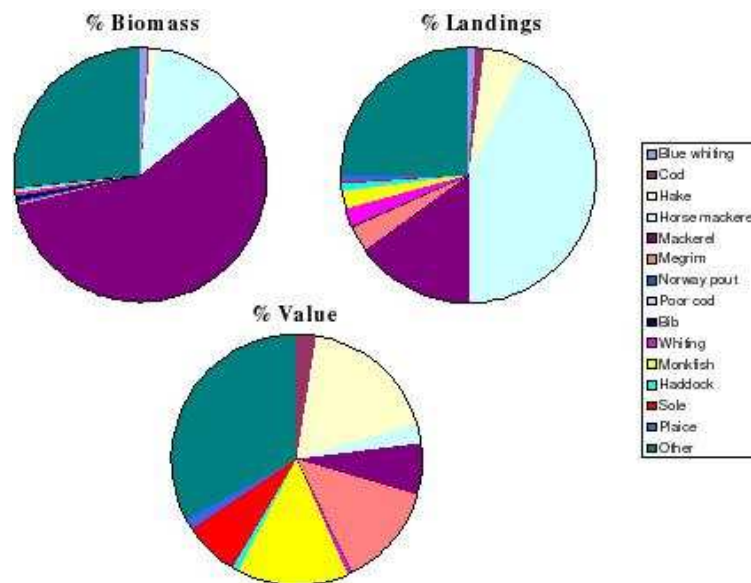


Figure 4. The importance of various fish species in the Celtic Sea in terms of biomass in trawl surveys, commercial landings and commercial value.

Identifying spatial structures

Spatial ecological patterns

Many species in the Celtic Sea have particular spawning and feeding grounds which are determined by bottom depth (Figure 5). Four species assemblages can be distinguished, (1) coastal spawners (South-East Ireland and Cornwall), (2) continental shelf spawners, (3) shelf edge spawners (deep water) and (4) those that spawn outside the area (Table 5) (also see section 3.5 on ‘eggs and larvae’).

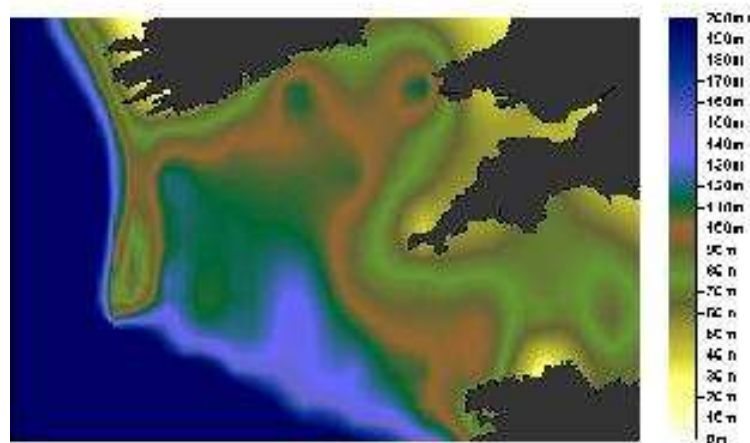


Figure 5. Depth contour map of the Celtic Sea.

Table 5. Stock and spawning grounds of fish populations occurring in the Celtic Sea. Stock areas as in ICES stock assessments.

Species	Stock area	ICES Areas	Spawning
Blue whiting	Spain to Norway	I-IX, XII, and XIV	outside area
Cod	Celtic Sea	VIIe-k	coastal
Hake	Bay of Biscay to Norway	IIIa, IV, VI, VII, VI-IIa,b,d	shelf edge
Horse mackerel	Bay of Biscay to Norway	IIa, IVa, Vb, VIa, VIIa-c,e-k, VIIIa,b,d,e)	shelf edge
Mackerel	Bay of Biscay to Norway	IIa, IIIa, IV, Vb, VI, VII, VIII and IXa	central shelf & coast
Megrim	Celtic Sea & Bay of Biscay	VIIb,c,e-k and VI-IIa,b,d	shelf edge
Norway pout	Not assessed	-	central shelf & coast
Poor cod	Not assessed	-	unknown
Whiting	Celtic Sea	VIIe-k	coastal outside area

Detailed analyses of stomach content data has allowed us to characterise spatial predation patterns in the Celtic Sea (Trenkel et al submitted). Trenkel et al found that blue-whiting were consumed more often at the shelf edge while mackerel, horse mackerel and *Trisopterus* spp. were eaten more often on the continental shelf (Figure 6). These spatial feeding patterns have a strong seasonal component. Blue-whiting was more often found in stomachs during the summer, whilst mackerel and *Trisopterus* spp. were present more often during the winter half year.

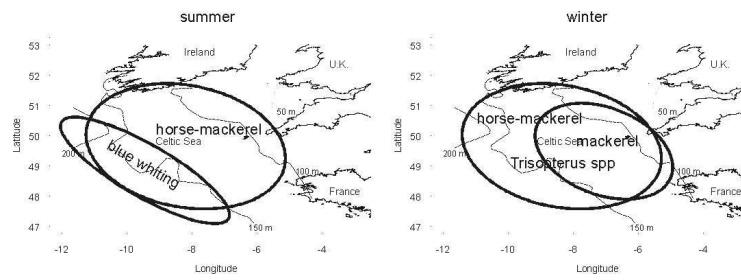


Figure 6. Dominant feeding locations in the Celtic Sea in the spring and winter half year for the prey species blue whiting, horse mackerel, mackerel and *Trisopterus* spp. by the predators cod, hake, megrim, lesser-spotted dogfish, saithe and whiting (reproduced from Trenkel et al submitted).

Spatio-temporal mapping and statistical analyses were carried out for adults and juveniles of several fish species present in the Celtic Sea (Anonymous 2002). The demersal species (cod, haddock whiting megrim and monkfish) were divided into two size groups (above and below length at 50% maturity (L_{50})) whereas the pelagic species were not divided. Data from annual Celtic Sea groundfish surveys in spring were used to map the presence and absence in each given year.

Haddock, cod and whiting appeared to be present at both the shelf edge and central areas of the Celtic Sea whilst megrim tended to occur closer to the shelf edge as compared to the other species. Mature fish were nearly always present at fewer stations than immature fish, reflecting the more frequent occurrence of smaller fish in the area. This was particularly the case for cod.

Monkfish (*Lophius piscatorius*) were present at both shelf-edge and shelf areas but white anglerfish (*Lophius budegassa*) were more prevalent on the shelf edge. Four-spotted megrim also was prominently a shelf-edge species as were the pelagic species, mackerel, horse mackerel and blue-whiting.

GAMs (Generalised additive models) were used to evaluate the probability of occurrence (Anon 2002). According to these models, there appear to be clear shelf edge species (megrim, four spotted megrim, white anglerfish, mackerel, horse mackerel and blue whiting) compared to those more frequently found throughout the Celtic Sea and particularly towards the northeastern area (haddock, cod, whiting, monkfish) (e.g. Figures 7a–c).

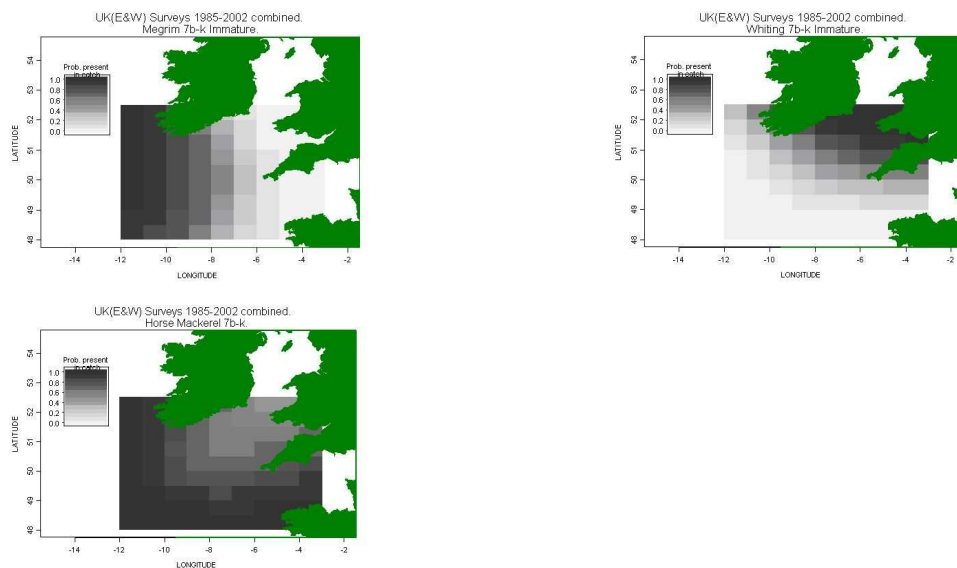


Figure 7a–c Predictive GAM surfaces

Spatial fishing patterns

Different fishing métiers concentrate their operations in particular areas (e.g. (Pelletier and Ferraris 2000)). The result is that overall fishing effort deployed in the Celtic Sea varies spatially and seasonally (Mahevas and Trenkel submitted). Hierarchical cluster analysis with imposed spatial contiguity has provided a rather heterogenous picture of total fishing effort distribution (Figure 8a). Nevertheless, the global pattern is that coastal areas, the central Celtic Sea and the shelf edge have each been fished at different intensities. This is also borne out by an analysis of fishing vessel sightings from UK fishery-protection spotter aircraft and ships (Figure 8b) (Blanchard et al submitted).

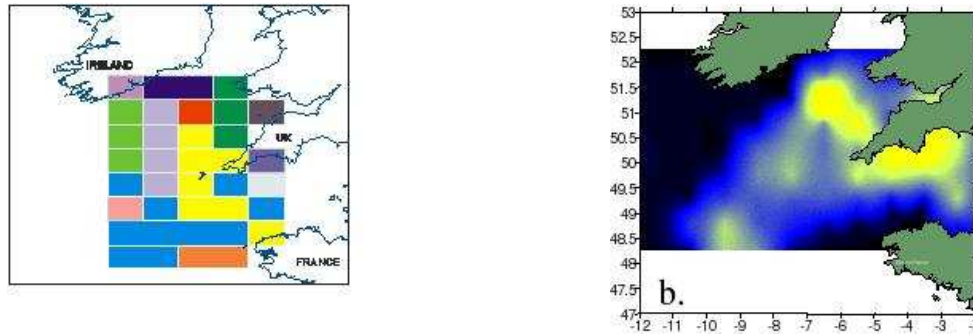


Figure 8(a) Map of homogenous fishing effort (number of hours fished per month) for French trawler fleet based on French effort data for the period 1991 to 1998 (reproduced from Mahevas and Trenkel submitted). Colours indicate similar effort levels **Figure 8(b)** Standardised sightings (from surveillance aeroplanes) of UK fishing vessels in the Celtic Sea (pooled data for 1985–2002). Surveillance area does not extend past bright blue contour and light yellow indicates highest level of sightings (reproduced from Blanchard et al submitted).

Defining spatial areas

Based on the spatial patterns of fish populations, spawning areas and fisheries operations, the Celtic Sea can be broadly be divided into four areas: the coastal zones around Cornwall, the Southern Irish coast, the central Celtic sea and the shelf edge. This proposed division is shown in figure 9.

Defining fish movements

In order to parameterise a spatial assessment model it is necessary to understand the nature and seasonality of fish movements from one spatial unit to another (i.e. to construct migration matrices). The most common method for obtaining such information involves tagging fish and recording the position where they were released and recaptured. Unfortunately there have been very few tagging studies for relevant species (i.e. those in figure 3) conducted in the Celtic Sea, and hence construction of a multiarea model for this region would be very difficult.

Studies by Norwegian researchers in the 1970s focussed on mackerel released off southern Ireland (see Bakken and Westgaard 1996), although most of these were recaptured in areas north of Scotland, around the Shetland Islands or off the Norwegian coast, rather than remaining in the Celtic Sea.

Studies on cod were carried out by Irish researchers during the 1970s and also more recently. From 1997 to 2000, over 2200 cod were tagged in the Celtic and Irish Seas (Connolly and Officer 2001), and these data indicated that there is some movement of cod over the boundaries of existing management units (area VIIa to VIIg). Although several cod tagged in the Irish Sea were recaptured in the Celtic Sea, no cod released in the Celtic Sea were recaptured in the Irish Sea.

Cod were also tagged and released by UK scientists in ICES rectangles 28E4 and 29E4, known cod

spawning areas either side of the Cornish peninsula (see (Anonymous 2001)). Most of these animals were recaptured within the same rectangle as where they were originally released, thus providing limited scope for modelling migration and drift.

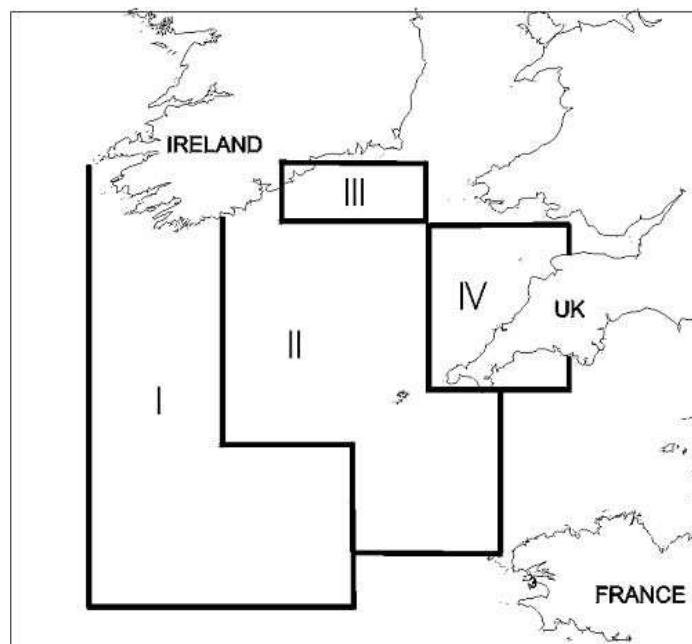


Figure 9. Proposed division of Celtic Sea into four model areas.

Fish Eggs & Larvae

Estimates of ichthyoplankton (eggs and larvae) distribution and abundance can be very useful when constructing spatially disaggregated assessment models. Such data can indicate the location of spawning or nursery grounds and the timing of spawning events.

Fortunately, from 1977 to the present, a triennial series of international egg surveys, co-ordinated by ICES has been carried out from north-west Ireland to Bay of Biscay; including the Celtic Sea. Although focussing primarily on mackerel and horse mackerel, these surveys have enabled mapping of ichthyoplankton for 79 species (see (Horstman and Fives 1994; Fives et al. 2001; Acevedo et al. 2002), including important commercial fish such as megrim, cod, whiting and hake.

Mackerel has accounted for approximately 72% of all fish eggs and larvae recorded, and only seven of the 79 types were recorded in numbers which represented more than 1%, notably: horse-mackerel (8.9%), sardine (2.3%), dragonets (1.9%) and megrim (1.09%) (Horstman and Fives 1994). Hake larvae were never widespread or abundant, similarly the presence of blue-whiting larvae was sporadic and abundances were low, with most larvae being recorded in early April. Blue-whiting spawn mainly over the Porcupine Bank west of Ireland, the larvae of this species found in the Celtic Sea were always >5.1mm (i.e. relatively large), confirming their distant centre of spawning (Fives, Acevedo, Lloves, Whitaker, Robinson and King 2001).

Discussion

Multispecies vs single species models

The simplest "multispecies" models are those involving only one species, but which prey upon their own young. Models including cannibalism have been constructed for Cape hake (*Merluccius capensis*) by Punt and Hilborn (1994) who found that including or excluding cannibalism in the model generally led to similar medium term predictions. Given that only weak evidence was found for the existence of cannibalism for Celtic Sea cod, hake, whiting and megrim, it is probably safe to assume that models with cannibalism would not make much difference for stock assessment or forecast of these species.

The next step is to include a predator (top down) or a prey (bottom up) in addition to the species of interest. First consider including a predator in the model who would substantially impact the mortality of the species of interest. Not much is known about the main predators of the adult megrim, hake or cod. Marine mammals might play a role but unfortunately little information is available for this region. In the MSVPA model of the North Sea, grey seals are the only major predator of adult cod and haddock (Anonymous 2003). If anything can be learned from other systems, the study by Mohn and Bowen (1996) of grey seal predation on eastern Scotian shelf cod (*Gadus morhua*) might provide some insights. These authors found that grey seal predation mortality was about 10-20% of fishing mortality depending on model assumptions, implying that it was more important to obtain a good estimate of fishing mortality rather than carry out expensive studies to count grey seals. Of course this might not be true for the Celtic Sea, and it has been estimated (SCOS 2003) that around 5000 grey seals exist off south-west England and Wales, as well as 2000 or so around Ireland.

Predation on prerecruits by fish, mammals and cephalopods has been found to be particularly important in some systems, and habitat structure in terms of providing refuge can play an important mediation role (Bax 1998). Unfortunately information about predation of prerecruits is all-but non-existent for Celtic Sea species, hence it would be utopic to include this stage in a model. By contrast, the predators of adult and juvenile mackerel, horse mackerel, blue-whiting and *Trisopterus* spp are well known. Choosing a particular predator-prey couple which would be strongly linked, is however difficult. In the ideal couple, a substantial proportion of the non-fishing mortality of the prey would be caused by the particular predator. This is not guaranteed, for example, blue-whiting in the Celtic Sea is only the southern most extent of a very large stock (similarly for horse-mackerel), hence it seems unlikely that any single Celtic sea predator species in a localised area will have a big impact on the total stock of prey. As none of the *Trisopterus* species are of commercial importance building a model focussed on these species seems less pressing and also less information is available.

For cases where only parts of the prey stock overlap with a particular predator stock, it would be possible to create a model where the true dynamics of a large proportion of the prey population are not modelled, and the animals simply migrate into or out of the model area. A more coherent approach would of course be to model all predator stocks that prey on the species considered throughout the animal's large range. For blue-whiting and any of its predators this would be a massive undertaking and require large amounts of additional data.

Due to life history omnivory, a sequence of preys might have to be considered (Rice 1995). Murdoch (2002) suggested in a theoretical study, confirmed by empirical evidence, that for generalist predators, long term population dynamics are independent of the availability of particular prey, i.e. prey population cycles have a period of $4 T_C$ (time to maturity) whilst strongly linked predator species have consumer-resource cycles of longer period ($>4T_C + 4T_R$ (maturation time of resource)). Thus Murdoch argues that single species models are justified for generalist predators. Using a predator-prey model (differential equations; partially coupled predator-prey interactions) with alternative food and red noise Spencer and Collie (1995) found that adding alternative food, adds stability to high predator abundance at low prey level supporting the argument of generalist predators having population dynamics independent of prey species. The evidence presented suggests that most predators are generalists in the Celtic Sea hence this argument might apply here.

Many authors have studied the properties of food webs. If top predators compete, as cod, hake, megrim

and to some degree whiting do in the Celtic Sea, food web and ideal free distribution models show that both the abundance of top predators and intermediate foragers will largely depend on the underlying habitat productivity (Mittelbach 1992). Furthermore, multiprey-predator systems and non-linear food-webs, i.e. predators feeding on several levels as for example hake or cod or monkfish in the Celtic Sea, are expected to have long reaction times and react in an unknown direction to the removal of top predators by fishing (Yodzis 2001). Christensen (1996) comes to the same conclusion based on empirical evidence. He compiled many case studies where top predator removal has led to increases or decreases in yield, thus no coherent effects were observed. Indeed given the complex spatial and temporal feeding patterns observed in the Celtic Sea, it is rather unclear how for example the blue-whiting might react to further reductions of hake or even cod. Changes in fish community structure of the Georges Bank (Canada/USA) due largely to over-fishing (gadids and flounders replaced by elasmobranchs) might be an indication for the existence of 'competitive release' in this system (Fogarty and Murawski 1998).

One of the longest studied multispecies assessment models is MSVPA, Multi-Species Virtual Population Analysis (Gislason and Helgason 1985). The main contribution of MSVPA for the North Sea has been improved natural mortality rate estimates for use in single-species fish stock assessments. However, Magnússon (1995) in his review of MSVPA stressed the importance of the assumption within this modelling framework of a type II functional response, and the difficulty associated with implementing a type III (prey switching), since multiple model solutions are likely. Livingston (1985) has come to similar conclusions for the bulk biomass model; biomass estimates were most sensitive to the assumptions on diet composition and body growth. The available evidence suggests that Celtic Sea predators are indeed switching prey on a seasonal basis linked to spatial movements. Hence a functional type III would have to be considered. This agrees with the opinion of Murdoch and Oates (1975) cited by Spencer and Collie (1995) who thought that most marine fish exhibit a type III functional response due to spatial patchiness.

Long term predictions needed for making management choices require the modelling of recruitment processes (Shepherd 1988). Unfortunately we still lack thorough understanding of recruitment processes for most marine fish species. In a multispecies context, 'numerical response' becomes a crucial but little understood process which is needed for forecasting long term predator population dynamics. Taking account of the impact of predation and cannibalism on recruitment is also essential.

Using an MSVPA model for the Georges Bank fish community, Tsou and Collie (2001) found evidence that predation mortality increased with stock abundance for cod and silver hake largely due to cannibalism. Similarly predation mortality of age-1 walleye pollock was almost exclusively caused by cannibalism and hence dependent on population density (Livingston and Methot 1998). Given that there was little evidence for cannibalism in the Celtic Sea predators, recruitment processes are more likely to depend on the 'numerical response' of the predator i.e. the transformation of ingested prey into offsprings. However, detailed studies would need to be carried out in order to really understand the recruitment processes as well as the driving forces for the Celtic Sea species. Environmental factors, in particular temperature have been found to partly determine the recruitment of certain species. In a comparative study Brander (2000) found that cod (*Gadus morhua*) recruitment was highest in the temperature range 5–7 °C. As the temperature in the Celtic Sea is generally above this optimum range, cod recruitment might be expected to be extremely sensitive to any temperature variations experienced. A practical drawback for including recruitment process in a multi-species assessment model is that currently neither MSVPA nor the multispecies modelling framework Gadget (Begley 2004) allow for the inclusion of multi-or even single-species recruitment functions.

Given the lack of knowledge on fundamental processes such as predation and recruitment, multiple models types and formulations need to be explored, in order to come up with robust management recommendations (Whipple et al. 2000). In addition, overparameterization is an inherent problem in many multispecies models but by no means unique to this class of models. Hollowed et al. (2000) developed a range of assessment models for walleye pollock including predation by three predators. The models had over 200 parameters many of which were strongly confounded. Hence these authors conclude that independent estimates for a range of parameters (survey catchability, alternative food, feeding response, etc) would be required to obtain reliable parameter estimates.

Multi-area vs single area model

Spatial stock assessment models have been developed primarily for predicting changes in the distribution of fishing effort as a consequence of closing areas to fishing (Walters and Bonfil 1999). They have also been used to better account for the spatial structure of fish stocks and their large scale annual migrations for example around Iceland (e.g. Stefánsson and Pálsson 1998).

Authors have proposed spatial simulation modelling tools intended to support management choices, in particular closed area management (e.g. Mahévas and Pelletier 2004). But since it is the spatial pattern of the fishing operation that is typically of interest, only technical interactions are taken into account and not biological interactions. As soon as populations are assumed to exist in spatially distinct units, modelling the movement between those units becomes a crucial point. These movements can be on a small time scale, for example redistribution after local depletion by fishing, or on a seasonal basis such as large-scale spawning migrations. Unfortunately, as stated in section 3.4, very limited data exist for estimating large scale migrations in the Celtic Sea.

Although data from two independent bottom trawl surveys in spring (UK) and autumn (France) exist, they use different gears and consequently the coherence of abundance estimates is doubtful (Trenkel et al. 2004). Furthermore, the age and length structure of the French landings obtained from port sampling schemes is not spatially dis-aggregated for the Celtic Sea. Thus the feasibility of fitting a spatial assessment model for any species in the Celtic Sea food web seems unlikely.

A Three species test model for the Celtic Sea

GADGET is a flexible, length-based, modelling framework (see Begley 2004) which can be used for multi-species, multi-area and multi-fleet simulations. In essence, it evolved from an earlier approach developed by Stefánsson and Pálsson (1998).

The single-species version of Gadget (whether under the name of Bormicon or Fleksibest) has been 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) or where there are large inter-annual variations in growth and thus size at age, (e.g. North-East Arctic cod, Frøysa et al. 2002). As part of an EU Framework V project (dst² — Development of Structurally detailed, Statistically Testable models of marine populations), a preliminary 3 species multispecies Gadget model was constructed for the Celtic Sea. In this model cod and whiting feed on blue-whiting, and cod also feeds on whiting (i.e. 3 predator-prey links). Until work began on the 'Celtic Sea case study', multi-species Gadget models had only been created for fish stocks around Iceland.

In the first instance three independent single-species models were developed in parallel (cod, whiting, blue-whiting), and then these were later combined into a single multi-species context. The models spanned 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. The resulting models operate on a quarterly (seasonal) time-scale and cover ICES areas VIIe–k, the geographical unit used in most demersal stock assessments (see Table 5).

One major problem which became apparent was the lack of detail in commercial catch data. ICES collate data for all counties only on an annual basis. These annual international catches were therefore 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 2004). Subsequent analyses (in August 2003) suggested that additional survey indices might be beneficial to improve the whiting model (which otherwise gave non-sensible results). Data were obtained from the 2002 ICES stock assessment report. A time-series (1984–1992) of age-based LPUE data for Lorient Trawlers was used, as well as the non age-based index based on UK spring-survey data (1984–1994).

For cod and whiting models the following variables were estimated:

11.1 A multispecies model for the Celtic Sea

- 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 were only interested in the southernmost extremity of this stock, for which very limited data were 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 through ICES. For the blue-whiting model, growth parameters were fixed (at W_{∞} 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.

The function which describes a predator’s consumption in Gadget has been outlined by Stefánsson & Pálsson (1997), and closely resembles the way that predation by cod was characterised in MULTSPEC (Bogstad et al. 1997), but is dissimilar to that in MSVPA.

Consumption is given by equation 1 below:

$$C = \frac{M\psi F}{\sum_{prey} F} \quad (1)$$

The parameter F gives the amount of a given prey that is consumed by the predator, which is obtained by multiplying the biomass of the prey by the suitability (see below). The summation over prey is over all length groups of all prey types (including non-modelled prey, given as “otherfood”). M represents the maximum possible consumption for the predator and ψ gives the “feeding level” which is the fraction of the available food that the predator is consuming. M is defined by

$$M_L = m_0 e^{(m_1 T - m_2 T^3)} L^{m_3} \quad (2)$$

where:

L is the length of the predator, H is the half feeding value and T is the temperature.

$$\psi = \frac{\sum_{prey} F}{H + \sum_{prey} F} \quad (3)$$

Equation 3 defines the “feeding level”, ψ . This is governed by the total amount of prey available and the ‘half feeding value’ H . The value of H is the density of prey required to allow the predator to consume prey at half the maximum consumption level.

For cod the maximum consumption (M) as a function of predator length was based on the values reported by Bogstad et al. (1997). We adjusted this upwards slightly to account for warmer temperatures, - thus 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. In our current multispecies model the same value was also assumed for whiting.

m_0 was calculated as $a^{(1/1.25)}$ because it was necessary to convert the maximum feeding rate into a value based on length (as opposed to weight, as in Bogstad et al. 1997), whereby ‘a’ is the alpha from the length-weight relationship (6.32E-06 for cod).

m_3 was taken as 2.4, based on an exponent of 0.8 from (Bogstad et al. 1997) multiplied by 3 (assuming b in the length-weight equation to be approx. 3).

The ‘half-value’ (the food abundance at which cod or whiting eats half of maximum consumption) was set at zero, hence food consumption was treated as being independent of food availability in the environment. 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 utilised values reported in the ICES southern-shelf working group reports. It was assumed that cod ‘otherfood’ would be about 20 times more abundant than whiting (i.e. whiting is 5% of the diet), and hence the density of ‘otherfood’ was set at 5×10^9 kg for cod and 8×10^9 kg for whiting ‘otherfood’.

Currently there are 5 ‘suitability’ functions possible within Gadget: (1) a constant suitability function, where there is no dependence on either the length of the predator or the length of the prey; (2) ‘straight-line suitability’ where there is no dependence on the length of the predator, and a linear dependence on the length of the prey [used to model fishing vessels]; (3) a suitability function that has no dependence on the length of the predator, and a logarithmic dependence on the length of the prey; (4) a suitability function that has a logarithmic dependence on both the length of the predator and the length of the prey; and (5) The ‘Andersen and Ursin suitability function’; a more general suitability function that is dependant on the ratio of the predator length to the prey length. In the three species Celtic Sea model, we chose to use the Andersen and Ursin suitability function, which can be defined as in equation 4.

$$S(l, L) = \begin{cases} p_0 + p_2 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_4}} & \text{if } \ln \frac{L}{l} \leq p_1 \\ p_0 + p_2 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_3}} & \text{if } \ln \frac{L}{l} > p_1 \end{cases} \quad (4)$$

Using plots of mean predator length vs mean prey length (published in Pinnegar *et al.* 2003) together with quantile regression estimates (e.g figure 10) it was possible to manually shift the suitability function (figure 11) back and forth (by manipulating the p_1 parameter) until the predator size matched with the median prey size, as determined from observational data. The ‘spread’ of the suitability function was then manipulated (using the p_3 and p_4 parameters), until the ‘tails’ of the distribution coincided with the observed 10% and 90% quantiles. Parameter p_2 is simply a scalar which determines the maximum suitability for the particular prey, this may be lower than 1 for a non-preferred prey type. In the present model, because we have little data on species-specific suitabilities, we have assumed that predators will consume any prey within a given preferred size range, irrespective of species. One notable feature of the Andersen and Ursin (1977) suitability function is that the range of suitable sizes becomes greater for larger animals, and this seems to agree with our observations using real stomach data (Pinnegar et al. 2003), that large animals continue to eat small prey.

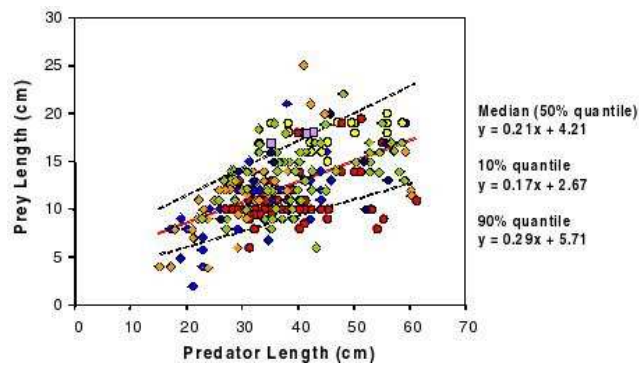


Figure 10. Prey length vs predator length for whiting *Merlangius merlangus* in the Celtic Sea. Solid (red) line indicates the median (50% quantile) regression, dashed lines represent the 10 and 90% quantile regression lines (after Pinnegar et al 2003).

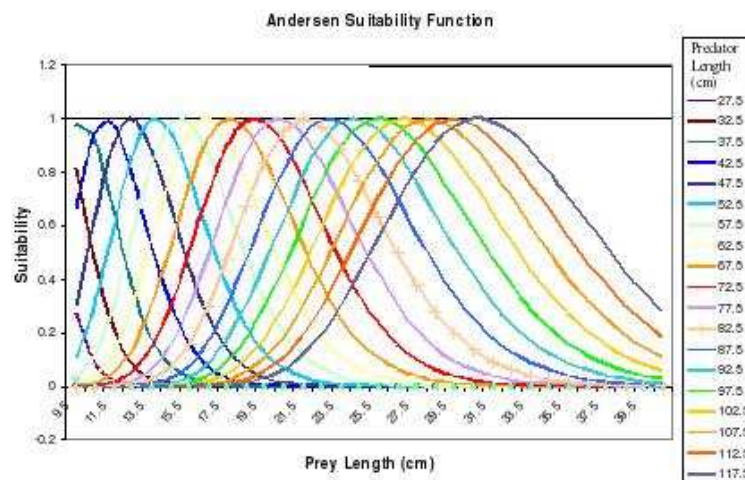


Figure 11. Andersen & Ursin (1977) suitability function, expressing the suitability of prey in terms of length, for different predator lengths. This example is for whiting *Merlangius merlangus* based on the observed data above.

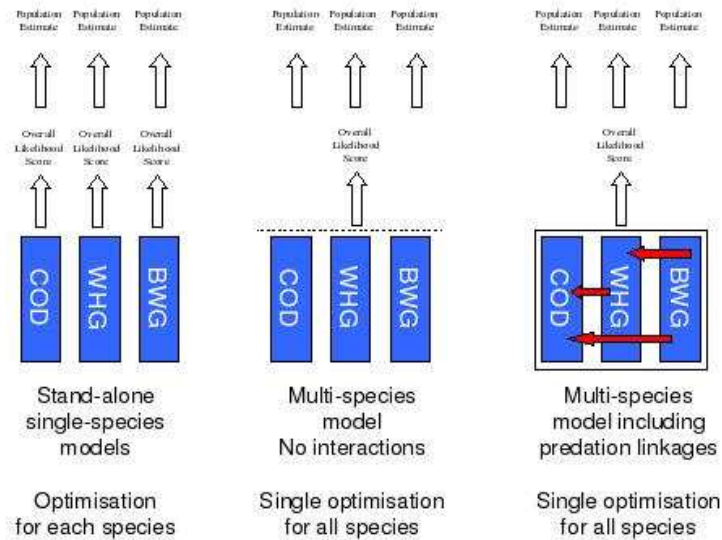
Table 6. Feeding Parameters used in the 3 species Celtic Sea model:

Species	Suitability P1	Suitability P2	Suitability P3	Suitability P4	Half-value	m0	m3
Cod	1.25	1	0.05	0.05	0	6.93e-05	2.5
Whiting	1.34	1	0.06	0.06	0	6.93e-05	2.5

Sensitivity analyses were performed on each model 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. Three model formulations (figure 12) were tested and the results compared: a) single-species models, optimized independently ('stand-alone'); b) multispecies model with a single optimization, but with no interactions ('unconnected'); c) multispecies model with single optimization and predator-prey interactions ('multispecies').

In general, the addition or removal of predator-prey interactions (although admittedly small in magnitude) resulted in negligible change to population estimates (see figure 13-15, compare 'multispecies' with 'unconnected'). Of much greater importance was whether or not the stock models (cod, whiting and blue-whiting) were optimized independently or within a single multispecies framework. It appears

Fig. 12



that by combining the three single-species models (even without implementing predator-prey linkages), the optimizer is forced to find a consensus overall-likelihood score, and this can greatly affect the outputted population estimates. Cod population estimates were little affected by this phenomenon and parameter estimates remained similar in the multispecies model formulation to those in the single-species ('stand-alone') model (see figure 13). By contrast, blue-whiting population estimates were particularly adversely affected (see figure 15) since much less data were available for the optimizer to fit to (7 likelihood components compared to 9 each for cod and whiting as well as fewer years of data). Thus, in a multispecies context the optimizer tended towards values more consistent with the cod and whiting data, at the expense of the rather sketchy blue-whiting stock data.

Biomass and abundance time-series from the single-species ('stand-alone') and multispecies ('unconnected') Gadget models were very similar in terms of trends (with a massive peak in 1998), although the estimated stock size in 1998 differed by 31 thousand tonnes (72,247 tonnes in the multispecies model, compared to 41,410 tonnes in the single-species model).

Population estimates were also compared and contrasted with values reported by ICES working groups (WGSSDS and WGNPBW). In general, age-based (ICES) and Gadget estimates of stock numbers, biomass and recruitment, coincided surprisingly well. In particular, there was close correspondence between ICES estimates for cod and those obtained from Gadget (see figures 13a–c). For whiting, ICES estimates were higher than those from Gadget during the modelled period (figures 14a–c), with a peak stock size during quarter 1 of 1995 of 238 million individuals estimated by ICES compared to 173 million individuals using Gadget (or 80 thousand tonnes compared to 37 thousand tonnes).

There are no spatially-resolved ICES data which would allow us to ascertain if blue-whiting numbers for the Celtic Sea sub-stock were sensible or not. However, time-series trends in the ICES blue-whiting stock (covering much of the NE Atlantic) and our Gadget estimates for the Celtic Sea sub-stock did generally agree.

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.

Fig. 13a

Cod numbers, age 1+ (quarter 1)

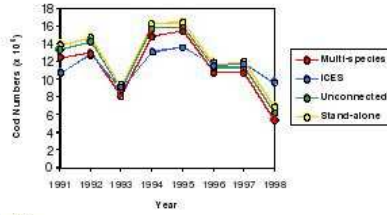


Fig. 13b

Cod biomass, age 1+ (quarter 1)

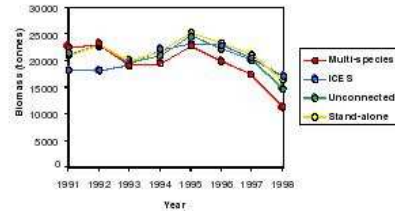


Fig. 13c

Cod recruitment (quarter 1)

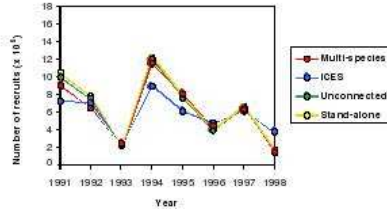


Fig. 14a

Whiting numbers, age 2+ (quarter 1)

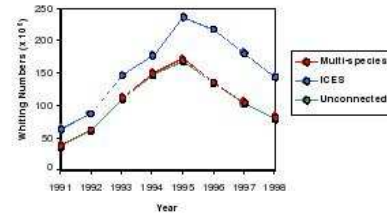


Fig. 14b

Whiting biomass, ages 2+ (quarter 1)

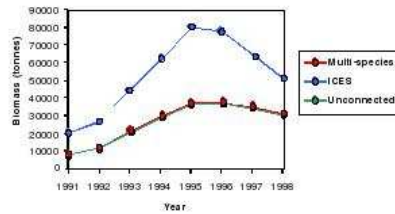


Fig. 14c

Whiting recruitment, age 2 (quarter 1)

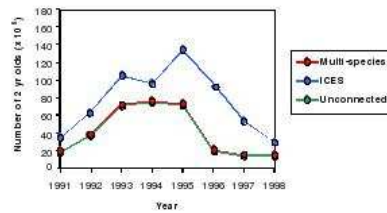


Fig. 15a

Blue-whiting numbers, age 1+ (quarter 1)

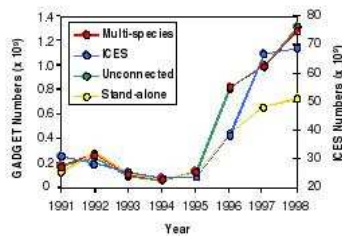
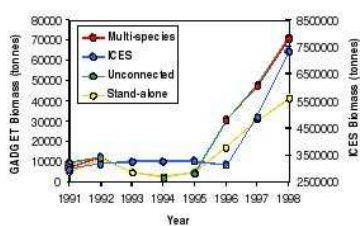


Fig. 15b

Blue-whiting biomass, age 1+ (quarter 1)



Conclusions

1. Most Celtic Sea predators are generalist feeders, changing their preferences to reflect local prey availability. Links between particular predator-prey pairs are weak and many prey stocks extend far beyond the Celtic Sea, out of range of localised predators. Hence multispecies models may be of limited utility for improved stock assessments, even though sufficient data probably exist.

2. Predators of pre-recruits (larval and young fish) would be difficult to characterise in the Celtic Sea. There is also limited understanding of the 'numerical response', i.e. how a predator population converts ingested prey (or a lack of them) into future offspring.
3. Insufficient fish tagging data and spatially-resolved fishery catch data would probably preclude the construction of a complex, multi-area, multi-season model for the Celtic Sea.
4. Care must be taken when combining datasets into a multispecies context. Sensitivity tests should be performed in order to ensure that observed differences between single-species and multi-species formulations are the result of predator-prey interactions and not simply an artifact of the optimization process.

Acknowledgements

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11.2 Further published/in press papers

Censored catch data in fisheries stock assessment.

Hammond, T. R. and Trenkel, V. M.

Abstract: Landings statistics can be lower than true catches because many fish are discarded or landed illegally. Since many discards do not survive, treating landings as true catches can lead to biased stock assessments. This paper proposes treating catch as censored by bounding it below by the landings, L , and above by cL (for scalar $c > 1$). We demonstrate the approach with a simulation study, using a Schaefer surplus production model. Parameters were estimated in a Bayesian framework with BUGS software using two sets of priors. Both the traditional true-catch method and a survey-and-effort method (which was landings free) performed worse on average than the censored approach, as measured by the bias and mean square error of estimates of MSY and of an index of depletion (X). Recursive partitioning (regression trees) was used to associate simulation parameters to best-performing methods, showing that higher commercial fish catchability favoured the censored method at estimating X . In conclusion, censored methods provide a means of dealing with discarding and misreporting that can outperform some traditional alternatives.

Hammond, T. R. and Trenkel, V. M. Censored catch data in fisheries stock assessment. ICES Journal of Marine Science, submitted.

Utilisation de modèles mixtes pour décrire la distribution spatio-temporelle du temps de pêche e la flottille française en mer Celtique

Mahévas, S. and Trenkel, V.

Abstract: The spatial and temporal allocation of fishing effort of the French fleet operating in the Celtic sea was modelled using spatially explicit fishing trip data for the years 1991 to 1998. Generalised linear mixed models with and without random effects taking account of spatial and temporal correlations were used. The available explanatory variables were the spatial unit, the month and the year. This paper presents the exploratory data analysis and the choice of the model best describing the heterogeneity of the data in order to define homogeneous fishing seasons and fishing areas. This final model revealed both a temporal correlation of order one and a spatial correlation of the fishing time. It also showed that the fishing activity was stable over the study period.

Mahévas, S. and Trenkel, V. 2002. Utilisation de modèles mixtes pour décrire la distribution spatio-temporelle du temps de pêche e la flottille française en mer Celtique. Journal de la Socityté Française de Statistique 143: 177–186.

Using generalized linear mixed models to describe the spatio-temporal distribution of fishing time: application to the Celtic sea.

Mahévas, S. and Trenkel, V. M.

Abstract: The spatio-temporal fishing activity patterns of the French trawler fleet in the Celtic sea were analysed by modelling fishing time with generalised linear mixed models (GLMM). Spatial and temporal correlations of fishing time were explicitly taken into account in the models and the explanatory variables required for the analysis are the spatial unit, the month and the year. The final selected model indicated that the spatio-temporal

allocation of fleet fishing time has been stable over the study period (1991–1998). A temporal fleet habit behavior process was revealed by a significant autoregressive time series effect of order one. In addition, a significant decreasing exponential spatial autocorrelation of fishing time indicated similarities between fishing times allocated to neighbouring areas. Cluster analysis on the estimated model coefficients of the best fitting model allowed to construct homogeneous spatial areas and periods of fishing activity. The winter months stood out as being more diverse than the other periods. The spatial clusters were of varying size, and generally larger offshore than closer to the coasts. The proposed method is general and could also be used to analyse temporal and spatial patterns in catch or catch per unit of effort (CPUE) data.

Mahévas, S. and Trenkel, V. M. Using generalized linear mixed models to describe the spatio-temporal distribution of fishing time: application to the Celtic sea. *Canadian Journal of Fisheries and Aquatic Sciences*, submitted.

Does diet in Celtic Sea fishes reflect prey availability?

Pinnegar, J. K., Trenkel, V. M., Tidd, A. N., Dawson, W. A. and du Buit, M.-H.

Abstract: Feeding preferences of Celtic Sea fishes were investigated using a database of stomach content records, collected between 1977 and 1994. The diet of cod *Gadus morhua*, hake *Merluccius merluccius*, megrim *Lepidorhombus whiffiagonis*, whiting *Merlangius merlangus* and saithe *Pollachius virens* changed markedly as the animals grew larger, and although large predators generally chose larger bodied prey, the variability of prey sizes consumed also increased. Large predators continued to select small, low value, benthic prey (e.g. *Callionymus* spp. and *Trisopterus* spp.) which were easier to catch, rather than larger, more energy lucrative pelagic prey (e.g. mackerel *Scomber scombrus*), even though these pelagic prey-fishes were nearly always available and were often very abundant. Stock estimates of the International Council for the Exploration of the Sea and U.K. groundfish survey catches were used as indices of prey abundance. Blue-whiting *Micromesistius poutassou* and other small pelagic fishes (*Argentina* spp. and clupeoids) were identified as being particularly important, and were consumed by some predators more often than would be expected given the abundance of these prey in the environment. There was no evidence for density-dependent feeding by predators on mackerel and only hake exhibited density-dependent feeding on horse-mackerel. Hake, cod and megrim consumed more blue-whiting when this prey was at higher abundance in the environment. In choosing what prey to consume, predators must balance costs and benefits, considering the quality of prey and the energy expended during search, capture and handling.

Pinnegar, J. K., Trenkel, V. M., Tidd, A. N., Dawson, W. A. and du Buit, M.-H. 2003. Does diet in Celtic Sea fishes reflect prey availability? *Journal of Fish Biology* 63 (Supplement A): 197–212.

Different survey designs provide similar pictures of community structure but not of individual fish populations.

Trenkel, V. M., Pinnegar, J. K., Rochet, M.-J. and Rackham, B.

Abstract: Choice of sampling method and survey period can have an important impact on the perception of the structure and dynamics of an ecological community. For the Celtic Sea fish assemblage we compared data obtained by three different trawl surveys: an autumn ground trawl survey with a GOV trawl, and a spring and an autumn ground trawl survey, both carried out with a Portuguese high-headline trawl. Time-series of abundance estimates were not consistent among surveys for all species and were generally very noisy. An analysis of

variance components showed that the sampling method contributed more to the variance in abundance estimates compared to survey period, interannual variability, or even sampling variance. Overall community assessments based on indicators such as proportions of non-commercial and piscivorous species, and the proportion of benthic species showed similar trends for all data series. The shape of the size spectrum based on abundances per length class summed over all fish species, although stable over time, was highly sensitive to the sampling method. With the exception of size spectra, community indicators for marine fish assemblages monitored by surveys seem to be robust to survey period and trawling gear, but species abundance trends are method dependent.

Trenkel, V. M., Pinnegar, J. K., Rochet, M.-J. and Rackham, B. 2004. Different survey designs provide similar pictures of community structure but not of individual fish populations. *ICES Journal of Marine Science* 61: 351–362.

Performance of indicators derived from abundance estimates for detecting the impact of fishing on a fish community.

Trenkel, V. M. and Rochet, M.-J.

Abstract: Population and community indicators for the impact of fishing are often estimated using abundance estimates instead of raw sampling observations. Methods are presented for testing null hypotheses of non-significant impacts and where possible, for calculating the statistical power. The indicators considered concern populations (intrinsic growth rate, total mortality, exploitation rate, and a new indicator, the change in fishing mortality required to reverse population growth) and communities (k- and partial dominance curves, a biodiversity index, size spectrum and proportions of various population groups). The performance of these indicators is compared for the Celtic sea groundfish community based on achieved precision, statistical power and availability and estimation method of reference points. Among population indicators, mean length in the catch was most precisely estimated and the corresponding hypotheses tests had consistently large powers. Total mortality performed reasonably well. In contrast, both the intrinsic population growth rate and the exploitation rate gave unreliable results. All tested community indicators performed similarly well. Indicators for which the direction of change caused by fishing is predictable, such as the proportion of non-commercial species or piscivores in the community, are promising indicators at the community level.

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Spatial and temporal structure of predator-prey relationships in the Celtic Sea fish community.

V.M. Trenkel, J.K. Pinnegar, W.A. Dawson, M.H. du Buit and A.N. Tidd

Abstract: The spatial and temporal structure of predator-prey relationships in the Celtic Sea was investigated for four commercially-important predator species: cod (*Gadus morhua*), hake (*Merluccius merluccius*), megrim (*Lepidorhombus whiffiagonis*), and whiting (*Merlangius merlangus*) using stomach content and bottom-trawl survey data for the period 1982 to 1995. Blue-whiting (*Micromesistius poutassou*) were consumed more often during the summer months whereas mackerel (*Scomber scombrus*) and *Trisopterus* spp. were found more often in predator stomachs during the winter half year. On a spatial scale, blue-whiting was consumed over the shelf edge, in accordance with their higher densities in the

environment, while mackerel, horse-mackerel and *Trisopterus* spp. were eaten more often on the continental shelf, again in agreement with their depth-related density distribution patterns. The spatial distribution of whiting closely matched that of a key prey, *Trisopterus* spp. This might indicate an 'aggregative response' by the predator. This study suggests seasonal and spatial prey switching behaviour by hake, cod and whiting. Overall the Celtic Sea fish community is characterised by opportunistic predators and general independence between predator and prey distributions. Inter-specific predator interactions are reduced by size-, space and time-dependent feeding behaviours.

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Chapter 12

NE Arctic Cod

12.1 A model for size preferences in cannibalism in Northeast Arctic cod (*Gadus morhua* L.)

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Introduction

Cannibalism in Northeast Arctic cod (*Gadus morhua* L.), which is an important cause of mortality of young cod, is highly variable from year to year (Bogstad *et al.*, 1994; Bogstad and Mehl, 1997; ICES, 2001). In models for assessment of current stock size and for prediction of stock development for Northeast Arctic cod, cannibalism has been included (ICES, 2001; Frøysa *et al.*, 2001). Cannibalism is there modelled as a function of predator abundance, prey length and capelin (*Mallotus villosus*) abundance. The model formulations for cannibalism have not been thoroughly discussed, however. In this paper we attempt to develop a model of size preferences in cod cannibalism, based on data on cod stomach content and estimates of abundance of cod by size. The model can be utilized by the new assessment tool for Northeast Arctic cod - Fleksibest (Frøysa *et al.*, 2001).

Material and methods

According to Bogstad *et al.* (1994), cod is able to prey on cod which is half its own length or shorter. The prey (cod) length distribution for given predator length is rather wide, and thus it is not obvious which prey (cod) length groups is preferred by a predator cod of a given length. This size preference is what we attempt to model here.

In order to describe the size preference of cod preying on cod, data on stomach content as well as data on abundance of cod are needed. Annual data on cod stomach content of Northeast Arctic cod are available from the period 1984-2000. They were extracted from the joint Norwegian-Russian stomach content data base (Mehl and Yaragina, 1992). The stomachs were analysed individually. Predator length was recorded to the nearest cm. In the period 1984-1992, the prey length was recorded in the following groups within the range relevant for cod as prey: 5.0-6.9 cm, 7.0-9.9 cm, 10.0-14.9 cm, 15.0-19.9 cm, 20.0-24.9 cm, 25.0-29.9 cm, 30.0-39.9 cm, 40.0-49.9 cm, 50.0-69.9 cm. From 1993 onwards, prey length was recorded to the nearest cm. In order to transform the data to 5cm prey length groups used in the analysis, the cod in the 30.0-39.9 cm and 40.0-49.9 cm length groups was assumed to be evenly distributed on the two 5 cm groups within those intervals. Cod in the 50.0-69.9 cm group was assumed to belong to the 50.0-54.9 cm group, as cod longer than 55 cm has not been found in cod stomachs.

Abundance at age estimates from the assessment made for Northeast Arctic cod for the period 1984-1999 (ICES, 2001) were averaged to give an estimate of the average age distribution. This age distribution was combined with length at age data (5 cm length groups) from the Norwegian bottom trawl survey in the Barents Sea in February (Jakobsen *et al.*, 1997) and the Lofoten acoustic survey (Korsbrekke, 1997) to give an average length distribution of the stock.

Cod prey < 10 cm were excluded from the analysis because cod of this length is mainly found pelagic, and our sampling of cod stomachs is mainly from bottom trawl hauls. Cod = 110 cm were excluded from the analysis because few stomach samples are available for cod of this length. Also, the abundance of cod of this size is very low. No cod was found in stomachs of cod < 20 cm, and these (predator) length groups were excluded from the analysis.

Modelled consumption

We assume that the consumption of cod by cod can be calculated as total consumption by cod multiplied by the proportion of cod in the diet of cod. Further, this has to be divided on cod (prey) length groups. The modelled consumption rate (kg/quarter) by one (predator) cod of length L of cod (prey) of length l , $C_{mod}(l, L)$, can then be formulated as:

$$C_{mod}(l, L) = C_{max}(L)P_{cod}(L) \frac{f(l, L)N(l)W(l)}{\sum_l f(l, L)N(l)W(l)} \quad (12.1)$$

$N(l)$ is the number of cod of length l and $W(l)$ is the weight of cod of length l . $C_{max}(L)$ describes the maximum consumption rate by cod of length L , $P_{cod}(L)$ is the proportion (in weight) of cod in the diet of cod of length L and $f(l, L)$ describes the preference of cod of length l by cod of length L . Below, we discuss how the various components in (12.1) should be formulated.

$C_{max}(L)$ is assumed to depend on fish weight $W(L)$ in the same way as described by Jobling (1988), i.e.

$$C_{max}(L) = \alpha(W(L))^{0.802}$$

A length-weight relationship for cod was estimated from all predators in the stomach content data base for which length (L-cm) and weight (W-kg) was recorded, giving

$$W(L) = 0.0000068L^{3.06}, R^2 = 0.99, p < 0.0001 \quad (12.2)$$

This gives

$$C_{max}(L) = \alpha L^{2.45} \quad (12.3)$$

$P_{cod}(L)$ increases with increasing L (Bogstad *et al.* 1994). The proportion of cod in the stomach content (here assumed to be equivalent to the proportion in the diet) of cod for each 5 cm length group was calculated from the stomach content data base. Assuming $P_{cod}(L)$ to be a function of L , the following parameters were obtained by fitting data for the interval 20-110 cm:

$$P_{cod}(L) = 0.0145 + 5.1 \cdot 10^{-7}(L - 20)^3 \quad (12.4)$$

The fit is shown in Fig. 12.1.

In order to formulate $f(l, L)$, it seems reasonable to start by plotting predator length vs. prey length for cod preying on cod (Fig. 12.2).

Only stomachs where the length of the cod prey was recorded are included. The prey and predator sizes are represented by the midpoint of the recorded size interval. A linear regression line is included:

$$l_{prey} = 0.42 + 0.24L_{pred}, R^2 = 0.27, p < 0.0001, N = 3853 \quad (12.5)$$

Since the data show that prey length generally is less than about half the predator length (Fig. 12.2), a simple assumption describing the length preference would be (r_1 close to 2)

$$\begin{aligned} f(l, L) &= 1, L > r_1 l \\ f(l, L) &= 0, L < r_1 l \end{aligned} \quad (12.6)$$

An alternative is an asymmetric bell-shaped function for $f(l, L)$:

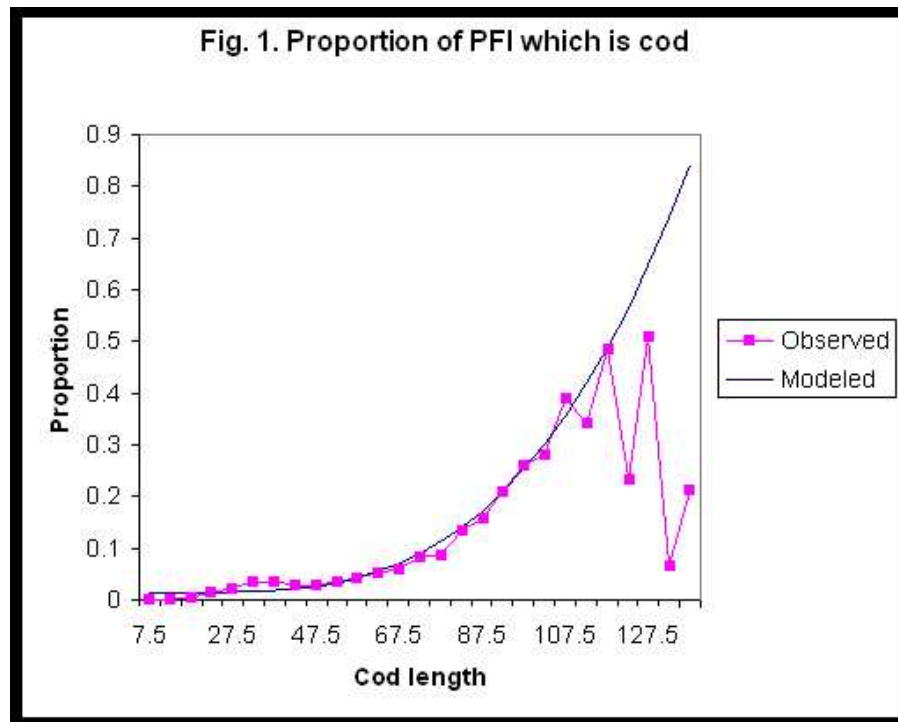


Figure 12.1: Observed and modelled proportion of cod in the cod, by predator length group

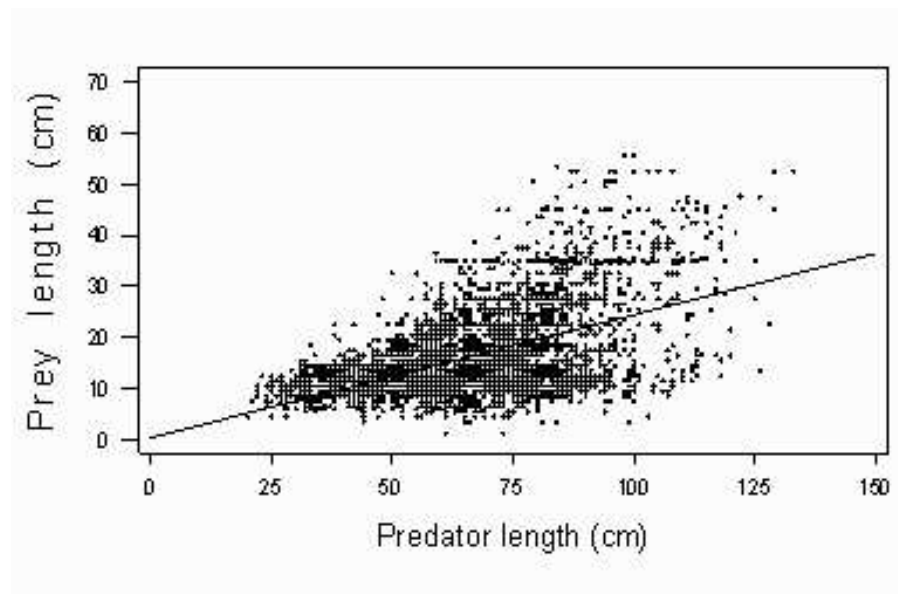


Figure 12.2: Prey size vs. predator size for cod preying on cod, for the period 1984-2000.

$$f(l, L) = e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_2}} \text{ if } \ln \frac{L}{l} \leq p_1 \text{ and } f(l, L) = e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_3}} \text{ if } \ln \frac{L}{l} > p_1 \quad (12.7)$$

This is one of the functions implemented in BORMICON (Stefánsson and Pálsson, 1997) to describe prey suitability. With $p_2=p_3$, it becomes symmetrical and equivalent to the size selection model suggested by Andersen and Ursin (1977). Andersen and Ursin used weights instead of lengths in their model, but if the exponent in the weight-length relationship for predator and prey is the same, the formulations are equivalent. The Andersen and Ursin size selection model has been used in the Mul-

species Virtual Population Analysis (MSVPA) model (Gislason and Sparre, 1987), which has been applied e.g. to the North Sea and the Baltic.

It should be noted that the function $f(l,L)$ describes cannibalism on the population level, and thus incorporates both actual prey size preferences as well as geographical overlap between predator and prey. The smallest cod is distributed farther east and north than the larger cod (Ottersen *et al.*, 1998).

Calculation of length distribution in the stock

In the calculations of cod abundance by age made by the ICES Arctic Fisheries Working Group (ICES, 2001), cod cannibalism is accounted for. Using these data in the calculations in the present paper thus introduces circularity in the reasoning, but as we do not consider it possible to use survey abundance indices directly in the calculations, no better approach seems to be available at present.

The average proportion of the cod stock which has age a and maturity stage (immature/mature) s is given by

$$P_{vpa}(a, s) = \frac{1}{16} \sum_{y=1984}^{1999} \frac{N_{vpa}(y, a, s)}{N_{vpa}(y)} \quad (12.8)$$

where $N_{vpa}(y, a, s)$ is the abundance in year y of fish of age a and maturity stage s , as estimated by the VPA (ICES, 2001) and $N_{vpa}(y)$ is the total abundance of cod in year y . Abundance estimates for ages 3-13+ are taken directly from ICES (2001). They are extended down to ages 1 and 2 in the same way as done by ICES (2000) ($M=0.2+\text{cannibalism}$).

The length distribution from the winter survey, $N_{winter}(y, a, l)$ is applied for immature cod. The proportion of fish in a given length group for a given age is averaged over the time period:

$$P_{imm}(l|a) = \frac{1}{16} \sum_{y=1984}^{1999} \frac{N_{winter}(y, a, l)}{N_{winter}(y, a)} \quad (12.9)$$

where

$$N_{winter}(y, a) = \sum_l N_{winter}(y, a, l) \quad (12.10)$$

For the mature cod, the length distribution from the Lofoten survey, $N_{Lofoten}(y, a, l)$ (available for 1985-1999) is applied:

$$P_{mat}(l|a) = \frac{1}{15} \sum_{y=1985}^{1999} \frac{N_{Lofoten}(y, a, l)}{N_{Lofoten}(y, a)} \quad (12.11)$$

where

$$N_{Lofoten}(y, a) = \sum_l N_{Lofoten}(y, a, l) \quad (12.12)$$

The resulting average length distribution in the stock is then given by:

$$N(l) = \sum_{s=imm}^{mat} \sum_{a=a_{min}}^{a_{max}} P_{vpa}(a, s) P_s(l|a) \quad (12.13)$$

Observed consumption

The observed consumption is calculated based on the stomach content data and the evacuation rate model developed by dos Santos and Jobling (1995). Essentially the same methodology as in Bogstad and Mehl (1997) is used, but the calculations are made based on individual stomachs.

The average consumption rate of cod of length l by cod of length L (kg/year) is given by:

$$C_{obs}(l, L) = \frac{1}{NS(L)} \sum_{k=1}^{NS(L)} R_{cod,l,k} \quad (12.14)$$

where $NS(L)$ is the number of cod stomach samples from length class L for the period 1984-2000. No weighting by catch rate in trawl hauls is applied.

The consumption rate (kg/quarter) by an individual cod of weight W of cod prey in length group l is calculated in the same way as Bogstad and Gjørseter (2001) calculated the consumption of capelin (*Mallotus villosus*) by cod:

$$R_{cod,l,k} = \begin{cases} \frac{2.19 \ln 2 e^{\gamma T_k} W_k^{\delta} S_{cod,l,k}}{\alpha_{cod} (1.42 S_k)^{\beta}}, & S_{cod,l,k} > 0 \\ 0, & S_{cod,l,k} = 0 \end{cases} \quad (12.15)$$

where $S_{cod,l,k}$ is the stomach content (g) of cod of length l in cod no. k (in length group L), S_k is the total stomach content (g) of cod no. k , T_k is the ambient temperature (°C), W_k is body weight (g) and α_{cod} is a prey-specific half-life constant. The values of the constants are $\beta = 0.52$, $\delta = 0.26$, $\gamma = 0.13$ and α_{cod} (α for cod as prey) = 84. In this working document, a constant temperature of 5° C was used for all stations. The factor 2.19 is included to obtain the consumption in kg/quarter (Fleksibest unit for consumption) rather than in g/h.

The following quantity is then minimized:

$$\sum_{L=L_{min}}^{L_{max}} NS(L) \sum_{l=l_{min}}^{l_{max}} (C_{obs}(l, L) - C_{mod}(l, L))^2 \quad (12.16)$$

5 cm length groups are used both for predators and preys, and the mid-point is used to represent the length groups: $l_{min}=12.5$ cm, $l_{max}=52.5$ cm, $L_{min}=22.5$ cm, $L_{max}=107.5$ cm.

Results

The fit is described in the table below, as well as in Figs. 12.3 & 12.4 (Linear and bell-shaped length preference, respectively)

Model	SSQ	%
F(l,L)=1 (L>r _l)	7.25	100
Bell-shaped	2.04	28

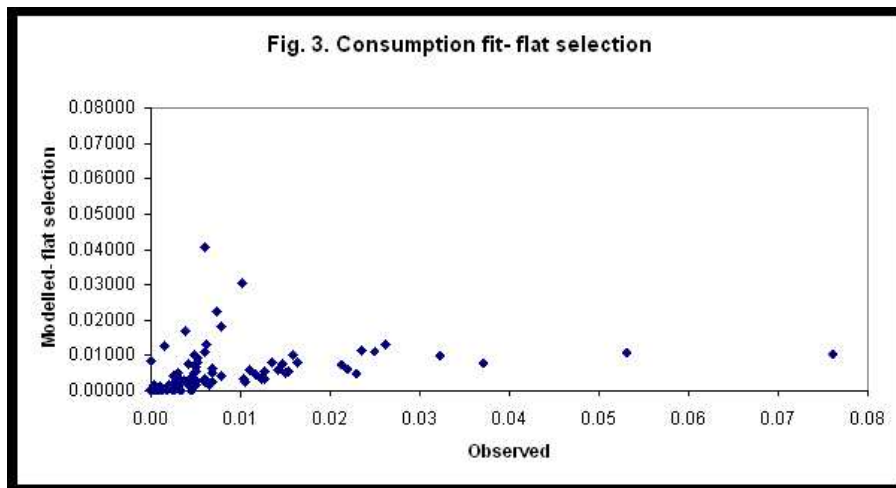


Figure 12.3: Observed and modelled consumption using $f(l,L)$ described by equation (12.6).

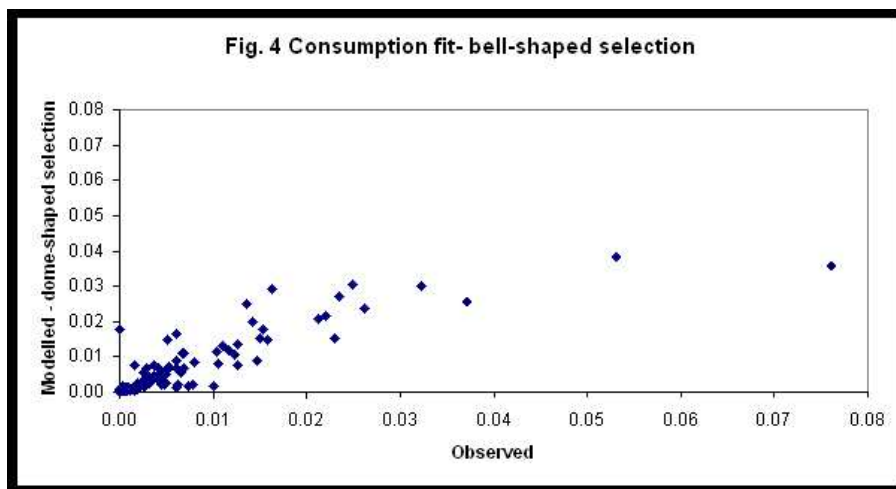


Figure 12.4: Observed and modelled consumption using $f(l,L)$ described by equation 12.7.

When fitting the predation model (Eq. 12.1) to the data using Eq. 12.16, the following parameter estimates were obtained:

$f(l,L)$ described by (12.6):

Parameter	Value
α	8.72E-06
r_1	1.8

$f(l,L)$ described by (12.7):

α	1.66E-06
p_1	1.12
p_2	0.015
p_3	0.228

This indicates that the preferred predator length/prey length ratio is $e^{1.12} = 3.06$.

$f(l,L)$ from (12.7) is shown in Fig. 12.5.

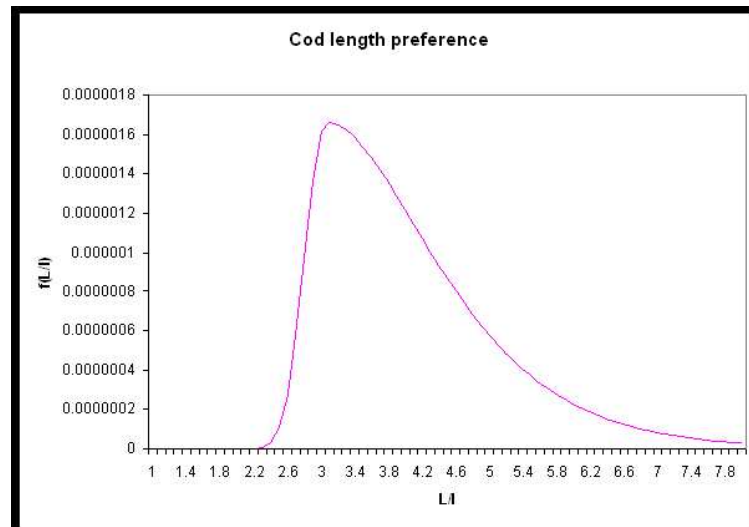


Figure 12.5: The function $f(l,L)$ as estimated by the predation model (12.7).

A similar analysis (using weight instead of length in the suitability function) was carried out by the ICES Multispecies Assessment Group (ICES, 1996). Several prey, among those cod, were analysed. Generally, a wider spread of prey lengths was found for Northeast Arctic cod than for North Sea cod.

Discussion

A model for prey size selection in cod cannibalism has been established. An asymmetric bell-shaped curve gave a much better fit to the data than assuming that the cod prey equally on all cod smaller than given size (close to half its own size). For application in assessment and prediction of cannibalism mortality for the Northeast Arctic cod stock, the year-to-year variation in cannibalism also need to be explained. One likely reason for the variation is fluctuations in the abundance of the capelin (*Mallotus villosus*) stock in the Barents Sea. A first approach to this could be to make the parameter α dependent on capelin abundance.

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12.2 Comparison of the effects of forced errors in survey data between an age and an age-and-length structured model of Northeast Arctic Cod

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Abstract: It is known that many fisheries data sets contain several different sources of error. It is likely that models with different structures will, in general, be affected in different ways by these errors. It is therefore important to examine what those differences are, both in order to select models of “appropriate” complexity, and to interpret discrepancies in situations where multiple models are run on the same datasets.

This paper examines the Northeast Arctic Cod (*Gadus morhua*). A series of experiments have been conducted introducing additional, known, errors into some of the survey data sets. These errors have been selected in order to mimic problems known to occur in practice. The modified data sets have then been used as inputs into two different models. The two models are currently both run as part of the assessment process for Northeast Arctic Cod. One is a relatively simple, XSA age-structured model, and one a more complex biologically-detailed age-length based model constructed using Gadget. The effects on the model results of these known forced errors are then compared.

Keywords: Northeast Arctic Cod, appropriate complexity, population model, Gadget, XSA.

Introduction

It is increasingly the case that multiple different models, of different design and complexity, are available for application to a given problem. It may be that a single model must be selected, in which case it becomes a question of selecting the “appropriate” complexity for the situation at hand (e.g. Costanza and Sklar, 1985, Håkanson 1995). In other situations the approach taken is to run more than one model on the same fish stock, and compare the results. In both cases it is useful to know how the different possible models would react to different known, or anticipated, sources of error in the data. It can be expected that the response of different models will depend on the interaction between the fish stock dynamics, the type and magnitude of error involved, and the structure of the model employed. This paper represents an attempt to examine the response of models from two different classes, one age based (XSA) and one age-and-length based (Gadget). The level of complexity is different in the two models, with the age-and-length model employing a higher degree of complexity and biological realism (Anon 2003, Begley and Howell 2004). Gadget is also a much newer model, and it is therefore useful to compare the response of a Gadget model to known errors to that of the better known XSA model.

Data

The ideal approach to a problem of this kind would be to use simulated data sets. Error free, biologically realistic data, of known structure and properties, could be used as input into both models, producing an optimised reference solution. Specified errors could then be added to the data and the modelling repeated for each different, known, error. The differences between the models produced could then be studied, and related to the induced errors. However no such data set currently exists that can be used in this way. One could be generated using Gadget, but using this as input into a new Gadget model gives a situation where the model is well specified to the data, and this situation is unlikely to arise in

practice. Furthermore having one model, but not the other, well specified to the data would undermine any comparisons that might be made.

The approach chosen here is therefore to use existing real-world data and induce additional errors. This approach has the disadvantage that the ‘truth’ in the population is never known. Thus it is only possible to analyse the difference between several different error prone situations, where only a part error structure is known. However it allows for experiments to be conducted in such a way that they correspond to real world situations and problems. For instance a situation where additional error is introduced into a single data series (e.g. discarding affecting the reported catch in length), or a single or small number of years (e.g. an anomalously high survey index in one year) is known to occur in real-world data. The existence of this error is often well known, even if the details are not always understood. It is possible to replicate this situation, and analyse and contrast the effects of different possible errors on several different models.

The case study chosen here is that for the Northeast Arctic cod. A large, detailed collection of data sets is available covering this stock, some of them covering a long time period. The current practice is for the Arctic Fisheries Working Group covering this stock to run several different models during the assessment process. This therefore makes an ideal setting to compare the differing responses of the different models, as well as ensuring that the results of such an investigation will be relevant in practice.

Models

The experiments have been conducted using two different models for the Northeast Arctic cod. The XSA model used during the AFWG (ICES 2004b), and a variant of the Gadget closed life-cycle cod model described in this volume (Fræysa et. al. 2002, Bogstad et. al. 2004). Both of these models were used at the Arctic Fisheries Working Group in 2004 (ICES 2004b). The two models employ very different methodologies. Gadget conducts a forward simulation of the population dynamics of a stock, and then uses all available data sets to optimize the parameters of the simulation model. XSA is a variant of the Virtual Population Analysis (VPA) model (Darby and Flatman, 1994), and is a backwards simulation. The XSA program “tunes” (optimizes) the solution to fit the supplied fleet data sets. The level of complexity in the two models is also different, with Gadget being more complex, and including a higher degree of biological realism than XSA. Both models use a range of data sets, but the current work concentrates on only one. In this preliminary analysis a single survey has been selected for these experiments. The survey chosen is Joint Norwegian-Russian winter survey on the Northeast Arctic cod (Jakobsen et. al. 1997). The survey is conducted in January-March (mostly in February) of each year, and is targeted at immature fish. Although there have been changes in gear and area coverage over time, the survey has remained unchanged since 1994, the start of the time period examined in this paper. This survey is used in the AFWG XSA cod model as a tuning fleet, and as one of the data sets used during optimisation of the Gadget model. In both cases the survey is an important, but not overwhelming, source of data to the model.

The Gadget cod model employed here is that presented at the AFWG in 2004 (ICES 2004b), and the same as the closed life cycle model (Bogstad et. al. 2004) except that a value for recruitment of age one fish is estimated for each year rather than a spawning relationship being used. This was done for simplicity, and to avoid using a new, experimental, model for the comparisons undertaken here. The model was run from 1985 to 2004, with the period 1994-2003 examined here. The model considers immature and mature cod, with length-based growth, maturation and cannibalism-induced mortality. Residual natural mortality is modelled as an age based process. Fishing is conducted by two different aggregated commercial fleets (one trawl and one gill net), each with it’s own length selectivity. The following data sets from the Barents Sea are used by the model; joint winter bottom trawl survey; joint winter acoustic survey; Lofoten acoustic survey; Russian bottom trawl survey; International 0-group cod survey; commercial catch in numbers, tons, and by length; Capelin abundance estimate. The model deals with the change in gear size in the Joint winter survey by splitting the affected surveys into two separate components, and fitting to each separately. XSA is the main assessment model used for Northeast Arctic Cod at the Arctic Fisheries Working Group (ICES 2004b), and is largely based on the

same data sets. The model does not correct for the changes in mesh size in the Joint Winter survey in 1994, but the period with a larger mesh size is before that examined here.

Experiments

A general investigation of the responses of different classes of models to different possible data errors is needed. This study represents a start on this work, and concentrates on a single source of errors. The error considered here is that of a single year with an anomalously high survey index result. Such an occurrence is relatively common in real-world data series (e.g. ICES 2003), and may have a significant effect on the modelled population. It is not clear what the exact effects in a Gadget model would be, or how these would compare to the effects of errors on a VPA/XSA type model. In particular it would be useful to know if errors in some years would produce a more serious effect on the modelled population than others, and what the dynamics of the response are. An experiment was therefore conducted in which the survey index for a single year was artificially inflated by 50% and the model optimised. This was repeated for each year in the model separately, and the results analysed. The whole process was conducted on two both models, and the results compared.

Diagnostics

Within the Gadget model a weighted likelihood score is produced, and is used during optimisation. However this is not a suitable measure to use to compare the experiments conducted here. Introducing an error in the data will result in an increased likelihood score. Because some years have more data than others this increase will vary between years, as a result of the data structure, even before the effects on the modelled population are considered. Equally a variety of residuals in the XSA model can be studied, or residual plots produced, but not all of these can be directly compared with the results of the Gadget model. Correlations between the XSA results and various survey indices can be investigated, but the induced change in the main survey makes interpreting these results difficult. The two models produce different levels of detail and complexity in their outputs. As a result of its greater structural complexity Gadget is capable of outputting a higher level of detail than the XSA model. However both models produce directly comparable outputs on the overall stock trends in numbers, biomass, and fishing pressure. It has therefore been decided to concentrate on the effects on the final modelled population, and in particular the biomass of the spawning and total stocks. This ensures a realistic comparison of the key outputs of the two models, and investigates the effects of the induced errors on the most important model output from a practical fisheries management perspective. For an error in the survey in a given year the biomass throughout the simulation can be examined. Graphs can be produced for data errors in different years, allowing for comparisons between the different experiments conducted here. It should be noted that the aim here is not to identify the added errors in the data and adjust for them; rather it is to see how the two models respond to those errors.

Results

The reference runs for the gadget and XSA models are shown in Figures 1 and 2. The numbers of the spawning stock and the 3+ cod (Figure 2) and the biomass of spawning and 3+ fish (Figure 3) at January 1st of each year are shown for the duration of the simulation. Both models show the same population trends, and have similar sized stocks in both numbers and biomass. Total and spawning stock biomass and numbers are high for most of the 1990s under both models, declining to a low in 1999 and 2000, followed by a rise in the present decade. It can be seen that the two models are in good agreement for biomass (Figure 3), with the exception that the current model suggests that the high stock levels in the mid 1990s resulted in an even higher spawning stock biomass than that predicted by the XSA. The models are also in good agreement for stock numbers through time (Figure 2).

The results of the experiments are presented in Figures 3-6. Each line represents a complete model simulation conducted with a 50% increase in the winter survey values in the relevant year. The variation in results due to the induced extra errors is smaller than the year-to-year variation in stock size during

the simulation. The results of the experiments are therefore presented as deviations from the standard reference runs for each model.

XSA results

The biomass of the total stock and spawning stock through time for each of the experiments are shown in Figures 3 and 4. Both the spawning stock and the total stock biomass show the same trends, though with slightly different percentage changes from the reference run. In all cases the maximum discrepancy, positive or negative, is highest in the last year of the model run (2003). The addition of errors in any years of the winter survey tuning fleet produces very little effect on the population size in the early part of the model (prior to 1998-1999). This is a result of the nature of VPA/XSA models, which have strong convergence in the early part of the time series, with the greatest potential for variation in the later years. It can be seen that increasing the magnitude of the winter survey in 2001, 2002 and 2003 produce increased stock biomasses in the later part of the run (1999-2003). Higher values in the survey for years before 1999 produce a slight decrease in the modelled biomass in the latter part of the model. This is due to the fact that the survey is acting as a survey index, where an increase in one year is the same as a decrease in all other years. An increase in an early year therefore produces an apparent downward trend in population size in later years.

Gadget results

The response of the gadget cod model to the data errors is markedly different to that in the XSA model. Adjusting the 1994 survey produces significantly different results from all the other years. This is the first year of the winter survey, and it is clear from Figures 5 and 6 that adjustments in this first year can have a noticeable impact on the overall population model.

For the total stock a clear pattern can be seen in the period 1994-1999. The modelled population is increased in the year of the data error, and this increase may persist at a lower level the following year. This is compensated for with a slight decrease in the stock prior to, and following the increase. However this trend breaks down in 2000, when stock levels reached a low value (Figure 5). It is likely that other information (from the other surveys and the catch) indicated at a stock size any higher than that predicted by the reference run would not be realistic, and this was therefore rejected during the optimisation procedure.

As with the XSA model and increase in the survey index in an early year results in a downward trend in stock sizes in the final years of the survey. An increase in the later years (2001, 2002 and 2003) produces a rise in stock numbers in the final years of the simulation, although they do not have any clear effect on the stock in the early part of the simulation.

The impact on the spawning stock is much less obvious and clear cut (Figure 7). The Joint Norwegian Russian Winter survey focuses on the immature portion of the stock. Where the error occurs in a year with a relatively large year class (1995, 1996, 1997) the increase in the recruitment for that year produces a higher number of mature fish overall. It is likely that the model is seeking a compromise in the proportion of larger fish between the year of the induced error, and the unaltered years.

Comparison

Although the two models examined here have very different structure and levels of complexity, they show similar responses in the terminal years of a simulation. An artificial increase in the survey value in the last few years produces higher predicted total stock biomasses in the last years of the model run. In both models an increase of 50% in the single survey studied here produced increases of up to 8% in the estimates for the last year of the model run. Conversely an increase in an early year produced a reduction in the predicted total biomass for the most recent years. This decrease was more marked in

gadget (up to 9%) than in the XSA model (2%). The XSA model produces almost identical responses for total and spawning stock biomass, even though the affected survey is targeted at immature fish. The Gadget model, with its ability to model the maturation process, gives different responses for immature and mature fish. The Gadget model also shows a dynamic process throughout the simulation, with the greatest response being concentrated around the year of the induced error. The XSA model, in contrast, shows the greatest response in the last year of model time.

Mitigating data errors in a Gadget model

In this paper the effects of data errors on model results have been examined. In practice some of these errors will be identified and dealt with during the development and testing of the models. Because Gadget provides a great deal of flexibility in how data is used during optimisation, there are more possibilities for handling suspect data than simply excluding it.

An erroneous year in the survey index data can have an impact on the simulated population produced from a Gadget model. Because of the way Gadget creates a simulation through time the data error can effect the whole simulation, not just the years around the error. In general the effects on the model are fairly small, although they can be large enough to distort or obscure the actual trends occurring in the modelled stock. Using multiple surveys can reduce the errors introduced into the modelled population, as the model will attempt to find a solution best fitting the whole suite of data sets used. However there are situations in which a number of different survey indices can all give anomalous results in a single year (ICES 2002), in such a case having multiple surveys will not reduce the effects of the error.

If it is suspected that a problem has occurred with collection of survey data there are several possible remedies. The data may be used "as is", especially if there are other data sources unaffected by the error, and the affected data source contributes only a small amount to the overall likelihood score. The year of data may simply be excluded if it is suspected that the relative frequency of different classes has been affected. However if the problem is with the level, but not the length structure, of the data then placing that year's data in a separate likelihood component may remove the problem. The distribution of length classes within the year will be preserved, but the year will make no direct impact on any long-term trends within the model.

Summary and Conclusions

The preliminary work conducted here indicates that different categories of models currently used in fisheries assessments respond to data errors in fundamentally different ways. A VPA/XSA type model produces responses in the last part of the time series, and responds to increased survey index values by increasing the terminal population for increases in later survey years, and slightly decreasing it for high survey index values in early years. Altering a single tuning survey in this way has almost no effect on the predicted population in the earlier part of the model run. Gadget responds to a single year error by increasing the population size in that year, if the overall stock dynamics permit such an increase. The increase persists, at lower levels, for several years after the errors. Earlier and later years show a slight compensatory reduction in stock biomass.

In a number of situations more than one model, or class of models, is run on a stock. It is therefore useful to know the likely response of each class of model to different known or suspected errors in the data.

Further work

The most obvious extension of this work is to examine random errors in the data. By using multiple replicate data sets, each with an additional random error component, the differing response of the two models to such situations can be examined. The errors could be purely random and unbiased in nature,

or they could add bias to reflect processes such as discarding or misreporting of catches. Only one of the data sets has been modelled here. The work should be extended to examine different surveys and the commercial catch data. It may be that the different models exhibit different degrees of sensitivity to errors in different data sets. Other classes of models exist (e.g. Huse and Ottersen 2003), and where these are used in an assessment context it would be valuable to extend the methodology described here to incorporate as many different models as possible.

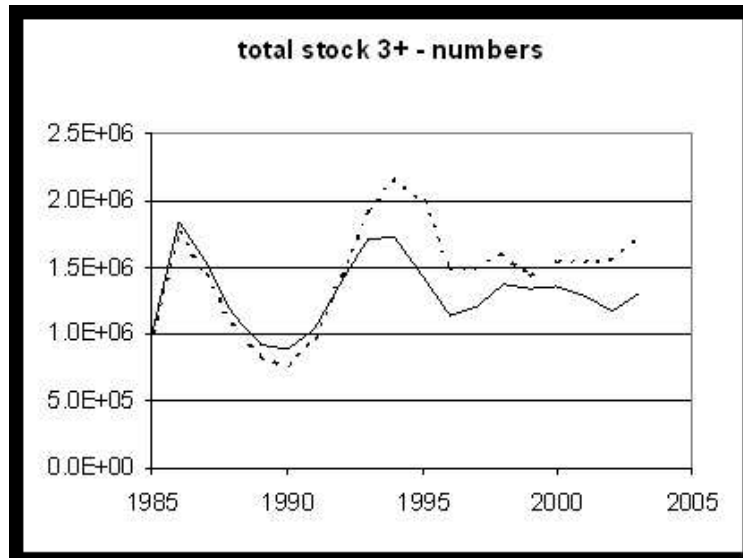
The gadget model employed here considers cod of age 1+, but does not include a closed life cycle. Instead a recruitment value is estimated for each year. A comparison between the closed and non-closed life cycle gadget models could be run to examine the effects of the different dynamics of the two model formulations.

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Figures

a)



b)

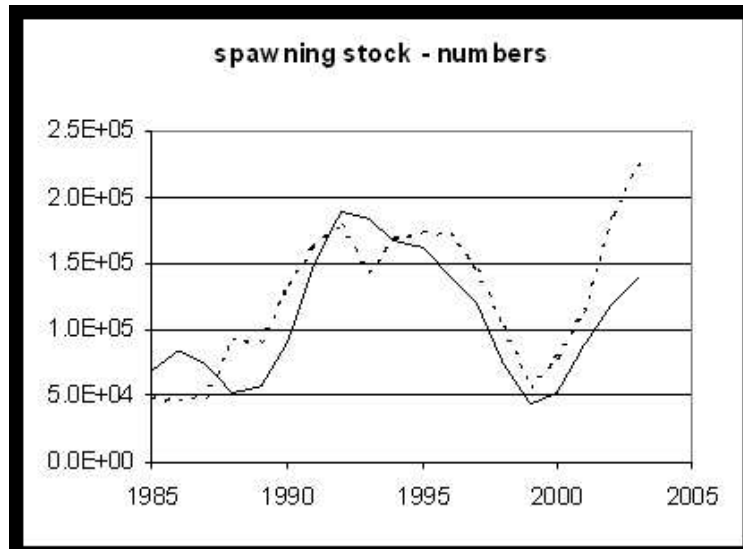
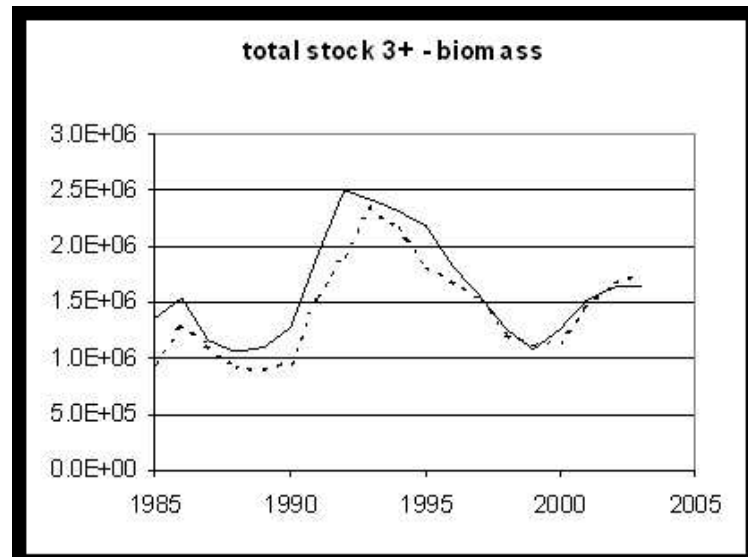


Figure 1. Number of fish of age 3+ (a) and in the spawning stock (b), in million fish for the references (unaltered) runs. Solid line indicates the Gadget model, dotted line is the 2004 AFWG XSA assessment.

a)



b)

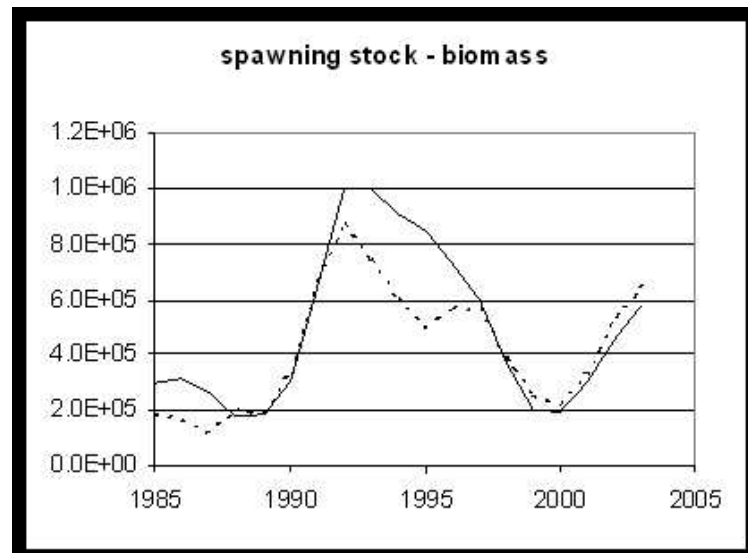


Figure 2. Total biomass fish of age 3+ (a) and in the spawning stock (b), in tonnes for the reference runs, with no added errors. Solid line indicates the Gadget model, dotted line is the XSA model.

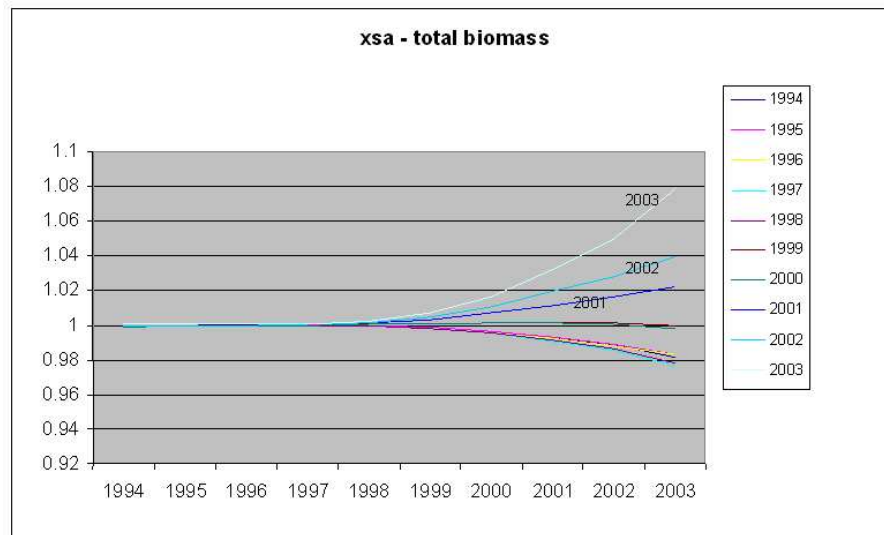


Figure 3. Variation from reference run biomass for the total stock through time for the XSA model. Each line represents a separate simulation, with a 50% increase in the Joint winter survey in the year stated.

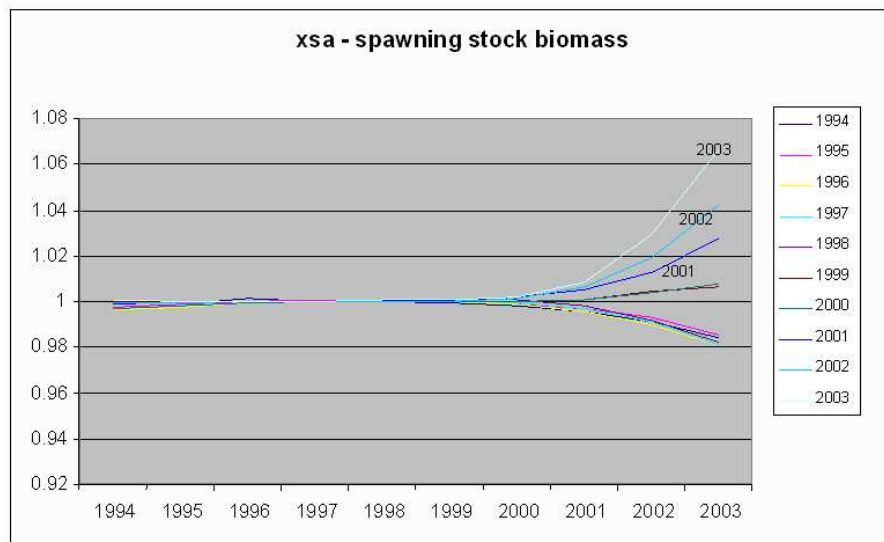


Figure 4. Variation from reference run biomass for the spawning stock through time for the XSA model. Each line represents a separate simulation, with a 50% increase in the Joint winter survey in the year stated.

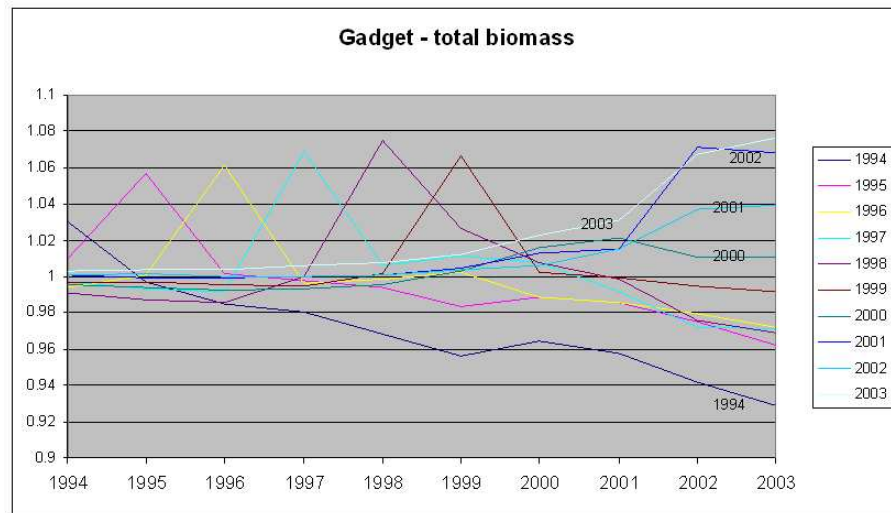


Figure 5. Variation from reference run biomass for the spawning stock through time for the Gadget model. Each line represents a separate simulation, with a 50% increase in the Joint winter survey in the year stated.

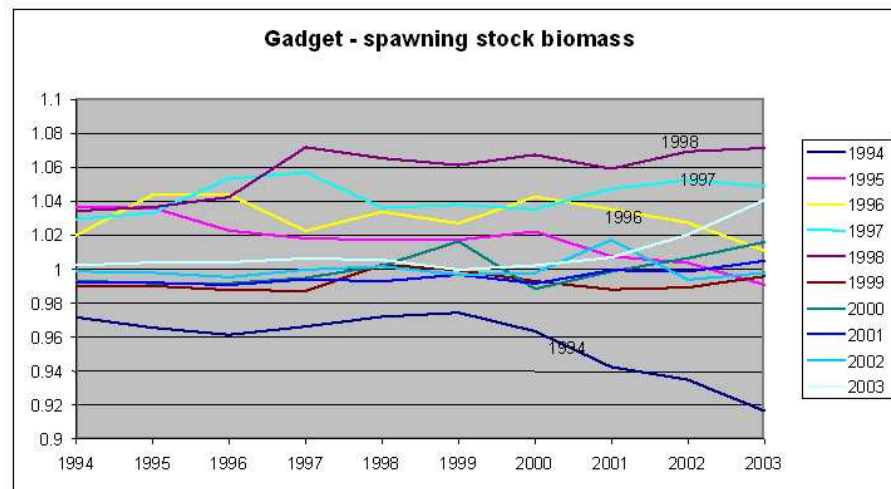


Figure 6. Variation from reference run biomass for the spawning stock through time for the Gadget model. Each line represents a separate simulation, with a 50% increase in the Joint winter survey in the year stated.

12.3 A closed life-cycle model for Northeast Arctic cod

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Abstract: For Northeast Arctic cod (*Gadus morhua*), there is much knowledge available concerning the main population dynamics processes (growth, maturation, fecundity, recruitment, natural mortality, fishing mortality). This knowledge is incorporated into a biologically detailed age-length structured population model. The model contains four population groups: EggsandLarvae, 0-group, immatures (age 1-10) and matures (age 4-12+). Recruitment to EggsandLarvae is modelled as a function of the number of mature fish and their population characteristics (length and weight), giving a fully closed life cycle. The model is implemented using the Gadget framework for population models, and the details of the implementation are described here. Results of fitting the population model to observations are presented. The utility of such a model in the assessment of current stock status and the exploration of harvest control rules is discussed.

Introduction

At IMR, Bergen, Norway, work on the Fleksibest model for Northeast Arctic cod has been going on for some years (Frøysa et al., 2002; ICES, 2004b). This is a biologically-detailed age-and-length structured model, where mortality, growth and maturation are modelled as functions of length and weight, and possibly age. The cod stock is divided into mature and immature components. In order to incorporate more of the biological knowledge available for this stock, the model is being extended to include a closed life-cycle. This WD outlines how this can be done using the Gadget model framework (Anon., 2003a; www.hafro.is/gadget). Such a model will be able to incorporate research presented to SGPRISM (ICES, 2002) and SGGROMAT (ICES, 2003a; 2004a) in recent years, and provide a framework to incorporate future developments into an existing population model.

In this paper we first describe the division of cod into population groups, and how the movement between population groups takes place. Then we describe the model structure (time step, length groups, age groups, which kind of mortality applies to each population group, spawning time etc.) This is followed by a review of the equations describing the population dynamics processes maturation, fecundity, mortality and growth. Finally we present results of fitting the model to the available data.

This paper shows how the Gadget framework can be used to incorporate such models, using Northeast Arctic cod as an example. A discussion of how and why more biological knowledge should be included in stock assessment is given by Ulltang (1996).

Model structure

Figure 1 illustrates the division into population groups. All individuals within a single population group share the same equations governing their biological processes.

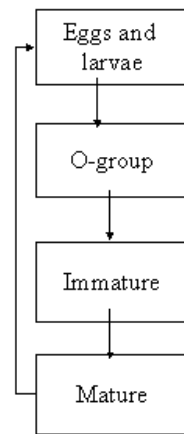


Figure 1. Movement between population groups in closed life-cycle model for Northeast Arctic cod

Time step: quarter (could be changed to month later)

Time period: 1985-2004, last time step in model is quarter 1 in 2004.

Population group descriptions

Movement of fish between population groups is either by the *Move* or the *Maturation* function. *Move* means that all individuals move to the new stock at a specific time, while a *Maturation* function allows the transition between population groups to be based on age and/or length.

Eggs and larvae

Spawned at end of quarter 1 (31 March). Hatched in quarter 2.

Age: 0

Length group width: 0.5 cm

Length range: 1-15 cm

Mortality: Very high, year-dependent residual natural mortality in quarter 2, otherwise no mortality.

Moves: to 0-group at 30 June (end of quarter 2)

Length distribution (mean length, standard deviation) given.

Growth: None. Mean length and standard deviation are model parameters (these are in reality the corresponding parameters for 0-group).

Except for the mortality, this stock is a dummy stock to which nothing happens. It is introduced to allow for a delay between spawning and time of recruitment as 0-group fish. Having *Eggs and larvae* as a separate stock also allows for the effects of larval drift in future multi-area models.

0-group

Age: 0

Length group width: 0.5cm

Length range: 1-20cm

Mortality: Cannibalism (quarter 4 only), residual natural mortality (possibly year-dependent)

Moves: to immatures at end of quarter 4 (December 31)

Growth: See section 4.4

Immature

Age range: 1-10

Length group width: 1 cm

Length range: 5-105 cm

Mortality: Fishing, Cannibalism, residual

Predator: Cannibal on immatures and 0-group

Growth: See section 4.4

Maturation function: See section 4.1. Applied at end of quarter 4 (31 December). Immature fish mature into mature fish

Mature

Age range: 4-12+

Length group width: 1 cm

Length range: 45-135cm

Mortality: Fishing, Cannibalism, spawning, residual

Predator: Cannibal on immatures and 0-group

Growth: See section 4.4

Spawning time: 31 March (end of quarter 1)

Spawning mortality: None

Spawning weight loss: Not modelled in this version since we do not directly model growth in weight, but read weight at length for each population group in each time step (Section 4.4)

Equation describing population dynamics processes

Symbols used:

t: time

y: year, = $[t/4]+1$, where $[\]$ denotes the integer part of the argument

q: quarter, = $\text{mod}(t,4)+1$

i, j: length groups

L_0 : Minimum length of length group 1 (smallest length group)

ΔL : width of length groups

L_{max} : number of length groups

l_i : mean length of fish in length group i , $l_i = L_0 + (i - \frac{1}{2})\Delta L$, $i=1, L_{max}$

a: age

u, v: population group

U: number of population groups

$\underline{N}_u(t)$: vector of length L_{max} , number of fish in population group u at time t

$N(u,i,t)$: number of fish in i -th length group of population group u at time t

$W(u,i,t)$: mean weight of fish in i -th length group of population group u at time t

f: fleet index

p: survey index

T: temperature ($^{\circ}\text{C}$)

For simplicity, the model description given here assumes that L_0 , ΔL and L_{max} are the same for all population groups, although this is not the case for the population groups described in Section 3, and

will usually not been the case. The Gadget software permits differing population groups to have different length groups, providing that the finer length groups are exact subdivisions of the larger ones.

We consider a model where survival, growth, maturation and recruitment only depend on the length and weight of the fish, but not on the age. Thus the index for age can be omitted in the description, and the state variables can be described by the vectors $\underline{N}_u(t)$. The model is structured by age and length groups, but the age of the fish is only taken into account when comparing the model to observations (Section 5). It is possible to extend this within the Gadget framework to model age-dependant processes if this is deemed necessary.

During a time step, mortality is applied before growth. Following Frøysa et al. (2002), the connection between stock abundance before and after mortality and growth takes place can be written as

$$\underline{N}_u^{(1)}(t) = S_u(t)\underline{N}_u(t) \quad (1)$$

and

$$\underline{N}_u^{(2)}(t) = G_u(t)\underline{N}_u^{(1)}(t) \quad (2)$$

where $S_u(t)$ and $G_u(t)$ are $L_{max} \times L_{max}$ matrices which describe survival and growth, respectively.

During a time step where only survival and growth takes place, we have:

$$\underline{N}_u(t+1) = \underline{N}_u^{(2)}(t) \quad (3)$$

For a more general matrix description of such models, including maturation and recruitment, see Frøysa et al. (2002).

Maturation

We use equation (4) to describe the probability of an immature fish becoming mature, assuming that this remains constant throughout the model period. Maturation is assumed to occur at the end of the year (quarter 4).

$$P_{mat}(a, i, t) = \frac{1}{1 + e^{-4\alpha(l_i - l_{50}) - 4\theta(a - a_{50}) - 4\lambda(\frac{W_{a,i,t}}{W_{ref}(l_i)} - K_{50})}} \quad (4)$$

The first term in the exponential function gives the length dependence of the maturation. If we assume the two other terms to be zero, l_{50} denotes the length at which 50% of the fish will become mature, while α denotes the rate of change of maturation when $l = l_{50}$. Similarly, a_{50} denotes the age at which 50% of the fish will become mature, while θ denotes the rate of change of maturation when $a = a_{50}$. Setting θ to zero removes the influence of age on maturation. The last term is more complicated. It describes how the maturation depends on the condition of the fish. The probability of maturing will be increased for a fish heavier than the average suggested by the length-weight relationship, and reduced for one with a weight below the length-weight relationship. K_{50} , the ratio between actual weight at length and reference weight at length for which this last term is equal to zero, is normally set to 1.0. λ describes how strongly maturation depends on the length-weight relationship. If the weight is equal to the reference weight for that length, this last term will be equal to zero.

The proportion maturing described by equation (4) is the same as the reaction norm (see e.g. Heino et al., 2002), defined as the maturation probability of immature fish given that they have reached a certain age and size. We assume that maturation does not depend on age, i.e. $\theta = 0$, a_{50} is then irrelevant.

The reference weight parameters are obtained externally to the model. The following length (cm)-weight (kg) relationship has been obtained by pooling all available data for 50-140 cm fish in the period 1946-2001 (ICES, 2003a).

$$W_{ref}(l) = 0.0000081l^{3.01} \quad (5)$$

If $\lambda = 1.2$, and $K_{50} = 1$, a change in condition factor of 20% from the reference value will give approximately an 8 cm change in length at 50% maturation, which fits with the data for proportion mature in Icelandic cod (ICES, 2003a). Very low values for the proportion mature at length have also been observed for Northeast Arctic cod in years with low weight-at-length (Marshall et al., 1998).

Fecundity

The main reason for modelling fecundity is that the correlation between total egg production, TEP, and recruitment at age 3 for Northeast Arctic cod is stronger than the correlation between spawning stock biomass and recruitment (Marshall et al. 2003). In addition, Marshall et al. (2000) found that for NEA cod, the correlation between total lipid energy in year y and recruitment to age 3 for spawning year $y+1$ is stronger than the corresponding relationship between spawning stock biomass and recruitment.

Bogstad (2003) suggested the following formulation of TEP for use in Gadget:

$$TEP(t) = \sum_{a,i} N(\nu, a, i, t) Fec_{\nu,a,i} = \chi \sum_{a,i} N(\nu, a, i, t) l_i^\alpha W(\nu, a, i, t)^\beta \quad (6)$$

where the subscript ν denotes mature female fish. TEP is thus dependent on numbers, length and weight of mature females.

ICES (2003b) give the following equation for fecundity (million eggs) for fish in length group i of Northeast Arctic cod:

$$Fec_{i,t} = 4.179 \cdot 10^{-7} l_i^{3.52} Kn_{i,t}^{2.16} \quad (7)$$

where $Kn_{i,t}$ is the relative condition factor, given by

$$Kn_{i,t} = \frac{W(i, t)}{W_{ref}(l_i)} \quad (8)$$

and the reference weight $W_{ref}(l_i)$ is given by

$$W_{ref}(l_i) = cl_i^b \quad (9)$$

For pre-spawning females, the following length (cm)-weight (kg) relationship has been established (ICES, 2003a):

$$W_{ref}(l) = 0.0000049l^{3.18} \quad (10)$$

The difference between the length-weight relationship for pre-spawning females (10) and the overall length-weight relationship (5) may be due to biological difference (the build-up of gonads may affect the length-weight relationship). However, (10) is based on a much smaller data set and a much shorter time series than (5), which also may be the reason for the difference. More work is required to identify the major reason for this difference.

Inserting (8) and (10) into (7), this gives

$$Fec_{i,t} = 4.179 \cdot 10^{-7} l_i^{3.52} \frac{W(i,t)^{2.16}}{0.0000049^{2.16} l_i^{2.16 \cdot 3.18}} \quad (11)$$

or

$$Fec_{i,t} = 123097 l_i^{-3.3488} W(i,t)^{2.16} \quad (12)$$

which can be used in equation (6), assuming the fecundity of female fish to be independent of age, i.e. $Fec_{a,i,v,t} = Fec_{i,t}$. For a 100cm, 10 kg cod this gives a fecundity of 3.57 million eggs.

Assuming a 1:1 sex ratio, equation (12) can be written

$$Fec_{i,t} = 61549 l_i^{-3.3488} W(i,t)^{2.16} \quad (13)$$

when the mature stock is not divided by sex.

Mortality

The number caught by fishing and eaten by cannibalism during each time step is calculated as described in sections 4.3.1 and 4.3.2, while spawning mortality and residual natural mortality are modelled as rates. The number of fish after mortality has taken place during a time step, $N^1(u,i,t)$, is then given by:

$$N^1(u,i,t) = (N(u,i,t) - C(u,i,t) - D(u,i,t)) e^{-M1(u,i,t) - M3(u,i,t)} \quad (14)$$

where C is the number caught by fishing, D is the number eaten due to cannibalism, $M1$ is residual natural mortality and $M3$ is spawning mortality.

Fishing mortality

The catch in biomass by each fleet f of fish length group i and population group u during a time step is assumed to be proportional to the biomass of available prey in that group, and the fishing effort. The biomass of available prey of length group i and population group u for fleet f at time t is given by

$$B_f(u,i,t) = N(u,i,t) W(u,i,t) \Xi_{f,u}(l_i) \quad (15)$$

where $\Xi_{f,u}(l)$ ($0 \leq \Xi \leq 1$) is the length-dependent suitability function (selection curve) for population group u and fleet f . A typical suitability function is

$$\Xi_{f,u}(l) = \frac{1}{1 + e^{-4\alpha_{f,u}(l - l_{f,u,50})}} \quad (16)$$

The biomass of fish in length group i of population group u caught by fleet f during time step t , $H(f,u,i,t)$, is then given by

$$H(f,u,i,t) = \zeta_f(t) B_f(u,i,t) = \zeta_f(t) N(u,i,t) W(u,i,t) \Xi_{f,u}(l_i) \quad (17)$$

and the number of fish caught is given by

$$C(f, u, i, t) = \frac{H(f, u, i, t)}{W(u, i, t)} \quad (18)$$

The total modelled catch in numbers by all fleets is then given by:

$$C(u, i, t) = \sum_{f=1}^{N_f} C(f, u, i, t) \quad (19)$$

where N_f is the number of fleets.

For Northeast Arctic cod, we estimate the yearly effort, and assume that the quarterly distribution of the effort within a year is the same as the quarterly distribution of the reported catch in tonnes, i.e.

$$\zeta_f(t) = \zeta_f(y)\theta_{f,q,y} \quad (20)$$

where

$$\theta_{f,q,y} = \frac{H_f(q, y)}{\sum_{q=1}^4 H_f(q, y)} \quad (21)$$

and $H_f(q, y)$ is the reported catch in tonnes by fleet f in quarter q and year y .

Cannibalism mortality

Cannibalism is an important source of mortality for young Northeast Arctic cod. The spatial and temporal variation in cod cannibalism, as well as the predator length- prey length distribution, is described by Bogstad et al. (1994). The consumption by cod is modelled using the same predation model as in MULTSPEC (Bogstad et al. 1997). 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. We consider two prey sources: cod and other food (largely capelin (*Mallotus villosus*)).

Let $D_{max}(L, T)$ be the maximum consumption rate (kg/time step) by a cod of length L when the temperature is T :

$$D_{max}(L, T) = \kappa\zeta(T)L^\delta \quad (22)$$

The temperature-dependence $\zeta(T)$ is assumed to be the same as in Bogstad et al. (1997), and the exponent δ is set to 2.4 (Bogstad et al. (1997) use $W^{0.8}$, which is equivalent to $L^{2.4}$ if $W = \text{constant} * L^3$). The consumption per predator in population group v and length group j per time step is given by the maximum consumption multiplied by a fraction $\psi(v, j, t)$ (equation 26). This fraction is called the feeding level and denotes the fraction of the maximum consumption that the predator is consuming.

$$D(v, j, t) = D_{max}(L_j, T(t))\psi(v, j, t) \quad (23)$$

The seasonal variation in overlap between large (predator) cod and small (prey) cod is strong and should be taken into account even in a model without explicit spatial structure. The mature cod migrates to the Lofoten area to spawn in March-April (Godø 1989), and does not prey on immature cod during this period. We assume that cannibalism by mature cod does not occur during the first quarter. Similarly, 0-group is not subject to major predation by older cod until it has settled to the bottom. This takes place

in autumn (Nakken 1994), and thus we assume 0-group to be subject to cannibalism only in the fourth quarter.

We thus assume that the preference of a prey for a predator can be split into a time(overlap)-dependent part and a size-dependent part. Define the biomass of prey group u , length group i suitable for predator group v , length group j as

$$\Phi(v, j, u, i, t) = \Xi(l_i, L_j)\Theta(u, v, t)N(u, i, t)W(u, i, t) \quad (24)$$

Here l denotes prey length and L predator length. We use the model for the size-dependent suitability $\Xi(l, L)$ ($0 \leq \Xi \leq 1$) given by Bogstad (2002):

$$\begin{aligned} \Xi(l, L) &= 0 && \text{if } \ln \frac{L}{l} \leq 0 \text{ and} \\ \Xi(l, L) &= p_0 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_2}} && \text{if } 0 < \ln \frac{L}{l} \leq p_1 \text{ and} \\ \Xi(l, L) &= p_0 e^{-\frac{(\ln \frac{L}{l} - p_1)^2}{p_3}} && \text{if } \ln \frac{L}{l} > p_1 \end{aligned} \quad (25)$$

with parameter values $p_0=0$, $p_1=1.12$, $p_2=0.015$, $p_3=0.228$.

The overlap factor $\Theta(u, v, t)$ is set equal to 1, except for the following cases: $\Theta(\text{immature, mature, } q)=0$ when $q=1$, and $\Theta(0\text{-group, immature, } q)=\Theta(0\text{-group, mature, } q)=0$ when $q=3$.

The feeding level $\psi(v, j, t)$ (equation 26) denotes the fraction of the maximum consumption that the predator is consuming:

$$\psi(v, j, t) = \frac{\sum_{i=1}^{j-1} \sum_{u=1}^U \Phi(v, j, u, i, t) + \text{other food}(t)}{H_{\frac{1}{2}} + \sum_{i=1}^{j-1} \sum_{u=1}^U \Phi(v, j, u, i, t) + \text{other food}(t)} \quad (26)$$

The 'half feeding value' $H_{\frac{1}{2}}$ is the prey density required to allow the predator to consume prey at half the maximum consumption level. We do not model food shortage here, so the 'half feeding value' $H_{\frac{1}{2}}$ is set to zero.

Capelin is the main prey item for cod (Bogstad and Mehl 1997). Here we model it as an externally defined other food. Because the variation in capelin abundance is very large (from 0.1 to 7.3 million tonnes in the period 1985-2003, ICES 2003b), we allow for less variation in the abundance of other food than the variation in capelin abundance by setting

$$\text{other food}(t) = \nu \text{Capelin}(t) + \gamma \quad (27)$$

where $\text{Capelin}(t)$ is the capelin biomass at time t . The constant ν describes the suitability of capelin for cod, while the constant γ is a measure of the other, non-capelin, food sources available to the cod, and may be estimated within the model. The calculation of capelin biomass at time t is described in Section 5.3. Note that predation by cod does not influence the capelin abundance in this model formulation.

The biomass of cod in population group u and length group i eaten by cod in population group v and length group j is then given by:

$$B(v, j, u, i, t) = \frac{N(v, j, t) D_{\max}(L_j, T(t)) \psi(v, j, t) \Phi(v, j, u, i, t)}{\sum_{i=1}^{j-1} \sum_{u=1}^U \Phi(v, j, u, i, t) + \text{other food}(t)} \quad (28)$$

The number of cod in population group u and length group i eaten by cod in population group v and length group j is then given by:

$$D(v, j, u, i, t) = \frac{B(v, j, u, i, t)}{W(u, i, t)} \quad (29)$$

and the total number of cod in population group u and length group i eaten by cod is given by

$$D(u, i, t) = \sum_{v=1}^U \sum_{j=i+1}^{L_{\max}} D(v, j, u, i, t) \quad (30)$$

The formulation given by equations (22-30) is a modification of the cannibalism equation given in Frøysa et al. (2002).

Spawning mortality

The spawning mortality M3 is at present set to zero.

Residual natural mortality

For each population group, the residual natural mortality is assumed to be variable only by year, i.e.

$$M1(u, i, t) = M1(u, y) \quad (31)$$

This yearly factor will be estimated for *Eggsandllarvae* and possibly for 0-group. For immature and mature fish, both female and male, we set $M1=0.2 \text{ year}^{-1}$, i.e. no year-dependant effect.

Growth

Mean growth in length

The mean length growth can be calculated by equation (32)

$$\frac{dl}{dt}(u, t) = k(u, t) l^q \quad (32)$$

where q is often set to 0, i.e. linear growth.

Within the Gadget framework it is possible to use other formulations, such as the von Bertalanffy equation, to describe the growth.

In this version of the model, we assume that the growth rate does not vary through the year, i.e. $k(u, t) = k(u, y)$. The year and stock factor $k(u, y)$ can thus be written in a separable way for immature and mature fish:

$$k(u, y) = k_1(y) k_2(u) \quad (33)$$

where $k_{\varnothing}(\text{immature})=1$, $k_{\varnothing}(\text{mature})<1$.

Implementing mean growth in length

After the mean growth for each length group is calculated, the length distributions are updated according to the calculated mean growth. This is done allowing a certain proportions of the fish to grow 0,1,2... length groups (no fish are allowed to shrink). Let

$$\mu_{u,i}(t) = \frac{1}{\Delta L} \frac{dl}{dt}(u, t, l_i) \quad (34)$$

be the mean growth of fishes in population group u and length group i measured in number of length groups and $g_{ij}(u, t)$ be the proportion of fishes in length group i growing to length group j . How $g_{ij}(u, t)$ are selected affects the spread of the length distributions but the following two equations must always be satisfied:

$$\sum_{j=i}^{L_{max}} g_{ij}(u, t) = 1 \quad (35)$$

and

$$\mu_{u,i}(t) = \sum_{j=i}^{L_{max}} (j - i) g_{ij}(u, t) \quad (36)$$

(35) ensures that the number of fish is conserved by the growth process, while (36) gives the correct mean growth. The number of fish in each length group after growth has taken place is given by

$$N^{(2)}(u, j, t) = \sum_{i=j-r}^j N^{(1)}(u, i, t) g_{ij}(u, t) \quad (37)$$

As in Björnsson and Sigurdsson (2003), the proportions are selected from a beta-binomial distribution, i.e. a binomial distribution $f(r; g)$ where r is the maximum number of length groups that a fish can grow in one time interval and the probability g comes from a beta distribution, described by parameters α and β (Stefánsson 2001; ICES 2003c). As in all discrete probability distributions equation (35) is automatically satisfied. The mean of this distribution is given by:

$$\mu_{u,i}(t) = \frac{r\alpha_{u,i}}{\alpha_{u,i} + \beta_u} = \sum_{j=i}^{i+r} (j - i) g_{ij}(u, t) \quad (38)$$

If $\mu_{u,i}$ and β_u is given, $\alpha_{u,i}$ can be calculated. β_u , which should be estimated, will affect the spread of the length distribution.

Modelling growth in weight

The variation in weight at length has been large for Northeast Arctic cod. The ratio between the minimum and maximum weight at length (yearly averages) is between 0.65 and 0.80 for pre-spawning females in the 50-90 cm range (Marshall et al. 1998), and variation in the length-weight relationship should thus be modelled. In this paper, we will, however, use the parameters in the maturation function based on this relationship. When this model is extended to multispecies, one may attempt to model growth in weight.

Data sources

The data sources available are survey data, commercial catch data and stomach content data. For a description of parameter estimation and objective functions used for fitting such a model to data, see e.g. Frøysa et al. (2002) or Björnsson and Sigurdsson (2003). The model is currently run from 1985 to 2004, with most attention being paid to the period after 1990.

Survey data

Joint Barents Sea winter survey (bottom trawl and acoustics)

A combined acoustic survey and bottom trawl survey for demersal fish in the Barents Sea has been carried out by Norway in January-March (mostly in February) since 1981. Since 2000, it has been a joint Norwegian-Russian survey. The survey methodology, which has changed somewhat over time, is described by Jakobsen et al. (1997). The time series has been corrected for some of those changes. It should be noted that the survey conducted in 1993 and later years covered a larger area compared to previous years. In 1991 and 1992, the number of young cod (particularly 1- and 2-year old fish) was probably underestimated, as cod of these ages were distributed at the edge of the old survey area. This change in survey coverage is not corrected for. Also note that the change from 35 to 22 mm mesh size in the cod-end in 1994 is not corrected for in the time series. This mainly affects fish < 20 cm. A trawl with 80mm mesh size is used. It is thus likely that the changes mostly affect the estimates of small, young cod. In order to deal with these difficulties data on one and two year old fish prior to 1994 have been excluded from the model.

From this survey, both acoustic and bottom trawl indices of abundance by age and length group are calculated. The survey mainly covers immature fish.

Lofoten acoustic survey on spawners

Since 1985, an acoustic survey has been carried out on the main spawning grounds in the Lofoten area in March/April. A description of the survey, sampling effort and details of the estimation procedure can be found in Korsbrekke (1997). Due to the introduction of new acoustic equipment in 1990, the time series should be split in two parts: 1985–1989 and 1990–present.

Russian autumn survey

The Russian autumn bottom trawl survey (November-December) is described by Lepesevich and Shevelev (1997). This survey covers the entire distribution of the cod stock, and has been carried out since 1982. A trawl with 125 mm mesh size and a 12 mm inner mesh size is used. The catchability of small fish (< 40cm) will thus be much lower than for the Norwegian surveys. This survey provides indices of abundance for all age groups from 0 upwards. (Age 0 indices are at present not available by length). Acoustic indices from this survey are also available, but were excluded from the assessment of cod several years ago because the indices were noisy and the methodology was changed.

Data from this survey in 1994 seem to be an outlier and have been excluded in Fleksibest runs. We exclude them also here. They show up as outliers in the diagnostics of the XSA model (ICES, 2004b).

International 0-group survey

An international 0-group survey has been carried out in the Barents Sea and adjacent waters annually since 1965. These joint Russian-Norwegian investigations (up to 1976 also British) investigations have taken place in late August and early September, with only a few days variation from year to year. The abundance of 0-group fish is found by fishing regularly with midwater trawl. From 1980, a standard trawling procedure recommended by ICES has been used (Anon. 1983). The data in the annual survey reports (e.g. Anon. 2003b) are reported as a logarithmic abundance index and a length distribution

(0.5cm wide length groups).

Age/length/time range of survey data used

Table 1 gives a suggestion for which age, length and time range to use for the surveys in the first version of the model. The population groups that each survey covers are also given.

Survey	Quarter	Year range	Age range	Length range	Length group width	Stock covered
Joint winter bottom trawl – 1	1	1981–1993	3–9	5–90 cm	5 cm	Immature
Joint winter bottom trawl – 2	1	1994–2004	1–9	5–90 cm	5 cm	Immature
Joint winter acoustic – 1	1	1981–1993	3–9	5–90 cm	5 cm	Immature
Joint winter acoustic – 2	1	1994–2004	1–9	5–90 cm	5 cm	Immature
Lofoten acoustic – 1	1	1985–1989	5–12+	55–110 cm	5 cm	Mature
Lofoten acoustic – 2	1	1990–2004	5–12+	55–110 cm	5 cm	Mature
Russian bottom trawl	4	1982–1993 & 1995–2003	1–8	6–106 cm	5 cm	Immature & Mature
International 0-group	3	1965–2003	0	1–15 cm	0.5 cm	0-group

Table 1. Year, age and length range covered by each survey, as well as population groups covered.

The maturity stage and sex is recorded for all fish which are age-determined (1 fish per 5 cm length group in the Joint winter survey, somewhat different routines in the Lofoten and Russian surveys). Thus it is possible to calculate length distributions on 1 cm resolution of immature and mature male and female fish separately for these surveys, while age-length keys should only be calculated by 5 cm length groups.

Commercial catch data

The catch in numbers at age and length (5 cm length groups) by quarter are available from the following six main fleets, which make up more than 95% of the total catch in all years:

Danish seine, handline, longline, gillnet (all these are Norwegian fleets), Norwegian trawl, Russian trawl. In our model runs, we have combined all the fleets except gillnet into one. Thus, we compare observations and model results for the two fleets *combinedfleet* and *gillnet*.

As with the survey data, maturity and sex is determined for all fish, which are aged, and thus the catch may be calculated divided on maturity stage and sex.

Capelin abundance data

The capelin stock is measured by an acoustic survey in September-October (Gjøsæter et al. 1998; Anon. 2003b). The abundance of capelin at other times of the year should also be calculated. The capelin stock fluctuates strongly from one year to the next (e. g. an increase from 0.8 to 5.8 million tonnes from 1989 to 1990). This rapid fluctuation means that, for example, using the survey estimate from autumn for the entire calendar year is not an appropriate approach.

At present we calculate the capelin abundance in each quarter based on the stock data in ICES (2003b) as follows:

- 1st quarter: biomass at 1 January biomass - winter fishing
 2nd quarter: biomass at 1 August x 0.75,
 3rd quarter: biomass at 1 August
 4th quarter: biomass at 1 January in year y+1.

Overview of model parameters

Parameters to be estimated by the model

Initial stock abundance: One parameter per age group, giving the number of fish by age group in the initial year. (May fix abundance of ages 7 and older in starting year). The abundance of cohorts spawned in the starting year or later is fit by the annual variation in natural mortality of *Eggsandlarvae*. For each age group, the proportion immature/mature fish and the sex ratio in the first year could either be estimated or taken from survey data.

Length distribution: mean length and standard deviation of mean length (immature and mature fish) for each age group in the starting year. Mean length and standard deviation of mean length of *Eggsandlarvae* and 0-group.

Fishing: For each fleet, a time-dependent fishing effort $\xi_f(y)$ (one parameter per year) and a length-dependent selection curve (two parameters).

Cannibalism mortality: Maximum consumption (cannibalism level) κ in equation (22) and the suitability of cod (p_0 in equation 25), and the suitability of capelin and the abundance of other food (equation 27).

Residual natural mortality: One parameter per year for *Eggsandlarvae* and possibly also for 0-group.

Growth: yearly factors $k_1(y)$, one set for 0-group and one for all immature/mature fish, the mature growth/immature growth ratio ($k_2(mature)$), one spread parameter (β_u) for 0-group and one for all immature/mature fish.

Maturation: assume no age dependence ($\theta = 0$), estimate l_{50} , α , γ , and kn_{50} .

Survey parameters: Parameters in the functions $q_1(p, u, l_i)$ and $q_2(p, u, t)$, 1-3 per survey, depending on whether length-dependence is allowed for or not.

Parameters fixed externally to the model

The following parameters are fixed externally to the model, using available biological knowledge.

Fishing: Quarterly distribution of fishing effort, based on quarterly distribution of catch in tonnes ($\theta_{q,y}$ in equations (20) and (21)).

Residual natural mortality: for immature and mature fish, AFWG has for many years used $MI=0.2\text{year}^{-1}$

Size dependence of cannibalism: (could also be estimated)

Fecundity parameters: (equation 13)

Parameter estimation

When comparing observations to model results, the Pearson objective function was used (Frøysa et al., 2002).

Relating survey data to stock abundance

The relationship between the modeled survey index I for survey p , $I(p, u, i, a, t)$, and the population number $N(u, a, i, t)$ can be described by:

$$I(p, u, a, i, t) = \Xi_{p,u}(l_i)q(p, u, t)N(u, a, i, t) \quad (39)$$

where $\Xi_{p,u}(l_i)$ ($0 \leq \Xi \leq 1$) describes the length selectivity for survey p , analogously to the length selectivity for commercial catch, see equations 15-17. $q(p, u, t)$ describes the time dependence, and is here set to constant.

Denote the observed survey index by $\hat{I}(p, u, i, a, t)$. The objective function for this survey is then given by

$$L_p = \sum_{i,a,t} \frac{\hat{I}(p, u, i, a, t) - I(p, u, i, a, t)}{I(p, u, i, a, t)^2 + \varepsilon} \quad (40)$$

For the catch data, the comparison was made on a yearly basis. Denote the observed catch by $C(f, u, i, a, y)$. The objective function is then given by:

$$L_f = \sum_{i,a,y} \frac{\hat{C}(f, u, i, a, y) - C(f, u, i, a, y)}{C(f, u, i, a, y)^2 + \varepsilon} \quad (41)$$

(Both (40) and (41) need to be adapted to the case where a survey or a fleet catch several population groups)

The total objective function is then given by:

$$L_{tot} = \sum_f w_f L_f + \sum_p w_p L_p \quad (42)$$

where the weighting factors w_p and w_f were set so that the total contribution to the objective function from survey data and from catch data was approximately equal, and each survey gives an approximately equal contribution.

Estimation procedure

Parameters are estimated using a two-stage optimisation process, combining Simulated Annealing and a Hooke & Jeeves stepwise estimation procedure. The optimisation begins with Simulated Annealing, which rapidly moves the parameter estimate to a region of possible solutions. Optimisation then switches to the "hill climbing" approach of Hooke & Jeeves, which provides a rapid method of converging to a nearby solution. The optimisation procedure was iterated until successive solutions are identical (ICES 2004c).

Model use

A detailed, biologically-based, population model as described here provides a framework for exploring the effect of including detailed process models in a population model. This can be useful both from the point of view of improving the population model, and to test and develop various process sub-models. Because the Fleksibest model has been run for Northeast Arctic Cod at an ICES assessment working

group (Arctic Fisheries Working Group), a considerable amount of effort has been put into ensuring that the modelled population has a realistic size and structure.

A biologically detailed cod model as described above may improve the assessment of present and past stock size and allow for better predictions. The inclusion of 0-group and extension of the immature stock down to age 1 should help the assessment by allowing the estimation of the abundance of all age groups in the stock, which can not be done by the present Fleksibest model.

Using an age-and-length based model instead of an age-structured model will in itself result in a revision of the reference points, as the effect of size-dependent mortality on size at age is modelled. Here the work of Kvamme and Frøysa (2004), who studied the influence of length-dependent selectivity curves on stock development using Fleksibest, could be utilised.

Results

The closed life cycle model described in this paper produces a stable, biologically realistic, simulation of the Northeast Arctic Cod. The numbers of the spawning stock and the 3+ cod (Figure 2) and the biomass of spawning and 3+ fish (Figure 3) are shown for the duration of the simulation. The equivalent biomass and number predictions from the Arctic Fisheries Working Group XSA assessment (ICES 2004b) are shown for comparison. Both models use essentially the same data sets.

Both models show the same population trends, and have similar sized stocks in both numbers and biomass. Total and spawning stock biomass and numbers are high for most of the 1990s under both models, declining to a low in 1999 and 2000, followed by a rise in the present decade. It can be seen that the two models are in good agreement for biomass (Figure 3), with the exception that the current model suggests that the high stock levels in the mid 1990s resulted in an even higher spawning stock biomass than that predicted by the XSA. The models are also in reasonably good agreement for stock numbers through time (Figure 2).

However the model presented here predicts fewer immature fish after around 1994 than is the case with the XSA. The recent rise in stock numbers is also markedly less pronounced than under the XSA, although the biomasses predicted by the two models is in close agreement in recent years. The total number of fish by age for both models is shown in Figure 4. The discrepancy post 1994 can be seen to be largely due to the current model predicting fewer younger fish, and slightly larger numbers of older fish than the XSA analysis. Thus, although the overall biomasses are similar in the two models, the underlying stock dynamics are slightly different.

The point at which stock numbers diverge in the two models is around 1994, which is the time of an improvement in the Barents Sea Winter Survey (section 5.1.1). After this date the data collected on the smallest fish are considerably improved. It might therefore be reasonable to suppose that the results in the present model, which explicitly considers these smaller fish, are more realistic during this latter part of the simulation period.

The numbers of age 1 and 2 fish are also shown. There is relatively little data available on small (less than 3 years old) fish prior to 1994 (Table 1), making it difficult for the model to assign mortalities from predation to these age groups. Post 1994 the absence of stomach content data in the estimation procedure makes modelling cannibalism length selectivity difficult. Cannibalism of small cod by larger cod is a major source of juvenile mortality. The results for 1 and 2 year old cod should therefore be considered preliminary until the stomach content data has been included.

The model presented here thus produces a realistic simulation of the Northeast Arctic Cod. The model results are broadly similar to those of the XSA model, though with differences in the simulated stock dynamics.

Further work

Including cannibalism data

The cod stomach content data were taken from the joint PINRO-IMR stomach content database. The procedure for sampling and analysis of the stomachs is described by Mehl and Yaragina (1992). The Gadget model calculates consumption, while the observations reflect stomach content at a particular point in time. In order to make a comparison between model results and observations, it is necessary to convert between these two entities (ICES, 2003c). At present, we do this by using the method described by Bogstad and Mehl (1997). This uses the evacuation rate model of dos Santos and Jobling (1995) to convert from stomach content to consumption. It should be noted that the evacuation rate is temperature-dependent.

Data on consumption of cod by cod (cannibalism) are at present available by predator age group and prey length group for each half-year for the period 1984–2003, but it is possible to prepare the data by predator length groups as well as prey length groups, and on a finer time scale. Including such data in the model would improve the ability to distinguish between mortality on one and two year old fish.

Including data on first time/repeat spawners

Data from the Lofoten survey split on first-time and repeat spawners could be utilised in the estimation of maturation parameters. The mature stock would then need to be split into two-stocks: First-time spawners and repeat spawners. Splitting the survey in this way gives better possibility for determining the proportion of *maturing* fish, and not only the proportion of *mature* fish.

Division by sex

Due to differences in growth and maturation, male and female fish could in the future be modelled separately. One would then have to split both immature and mature fish into males and females, and assume a 1:1 sex ratio of 0-group when they move into immature fish.

The difference in maturation between male and female Northeast Arctic cod is described by Ajiad et al. (1999). They found the length at 50% maturity to be about 65 cm for males and 75 cm for females, i.e. a difference of about 10 cm. The growth rate of immature fish is approximately the same for both sexes, but males mature at a smaller size. However, their analysis considered the proportion mature at age/length and not the proportion maturing, which is needed to determine the parameters in equation (4). l_{50} will be sex-dependent, while the other parameters in (4) could initially be assumed to be the same for both sexes.

In a model where fish are divided by sex, equation (12) could be used to model fecundity instead of equation (13).

The proportion of females by length group increases with increasing length (Marshall et al. 1998), and this could be interpreted as indirect evidence of sex differences in growth and/or mortality rates. The sex ratio seems to be close to 1:1 for fish < 90 cm. The results of Beverton et al. (1994) indicate that spawning mortality might be the main component of natural mortality among the mature cod. Jakobsen and Ajiad (1999) found that the data on sex ratio in survey and commercial catch data indicate a higher natural mortality in mature males than in mature females. The difference is close to 0.05 year^{-1} . A first approximation could be to set the spawning mortality M3 to be 0.05 year^{-1} for males and 0.0 for females, with the sex-independent component of spawning mortality continuing to be modelled as part of M1.

It is unclear whether the division into female and male fish will improve the assessment of the present stock size. However, this division should help the study of reference points by allowing for a more

realistic fecundity-recruitment relationship.

Relating growth in length to external factors

Individual growth of Northeast Arctic cod has been shown to be dependent both on capelin abundance (Mehl and Sunnanå 1991), and temperature (Michalsen et al. 1998).

Loeng et al. (1995) found that both mean length during the 0-group survey and growth rate in the period between the early juvenile survey and the 0-group survey are positively correlated with temperature. Several papers studying growth of juvenile (age 0-3) cod have recently been published (Ottersen et al. 2002; Helle et al. 2002; Dalpadado and Bogstad 2004). These papers have related length growth and length-at-age of NEA cod to various biotic and abiotic factors such as cod abundance, cod length at a younger age, food abundance (capelin, zooplankton), temperature and inflow.

Temperature data from several hydrographic sections in the Barents Sea are available. The most frequently used when correlating biological variables to oceanographic conditions is the Kola section (Tereshchenko 1996). A positive relationship has been found between mean individual growth and temperature, see e.g. Jørgensen (1992). The ambient temperature for each age group of cod has also been calculated and related to cod growth (Michalsen et al. 1998). It was found that the mean individual growth was highest for year classes experiencing high temperatures. It is possible to include the effects of temperature on growth within a Gadget model.

The diet of age 1 and younger cod (< 20 cm) mainly consists of invertebrates. The diet changes by cod size, so that cod of age 3 and older (> 30 cm) mainly prey on fish, with capelin as the most important prey species (Bogstad and Mehl 1997). The annual variation in growth rate may thus differ between age 0-2 cod and older cod.

Other surveys which could be used

The Norwegian bottom trawl survey in the Svalbard and Barents Sea area in August/September is described by Aglen (1999). The Svalbard area has been covered by a bottom trawl survey at this time of the year since 1981, while the Barents Sea has been covered each year since 1995. Since 1995, acoustic abundance indices are available both for the Svalbard area and the Barents Sea. The spatial coverage of the Barents Sea area has, however, been very variable. The methodology used in this survey is essentially the same as in the Joint Barents Sea winter survey.

Indices of abundance of early juvenile cod (age 0) from surveys in June-July are available for the period 1978-1991 (Helle et al., 2000; Helle and Pennington 1999). Mean length and length distributions from this survey are also available. This survey could be used in future studies of the dynamics in the first half-year of life, we do not plan to include it here.

Multi-species modelling

Cod are a major predator on small fish in the Barents Sea. The ability to model 1 and 2 year-old cod is important in constructing a multi-species model for the Barents Sea. Modelling cod predation on small fish (both cod and non-cod) using the relative proportions of prey species found in cod stomachs requires that all the major prey components be considered. The work presented here on modelling 1 and 2 year-old cod may thus provide an initial step towards extending the cod model to include other species.

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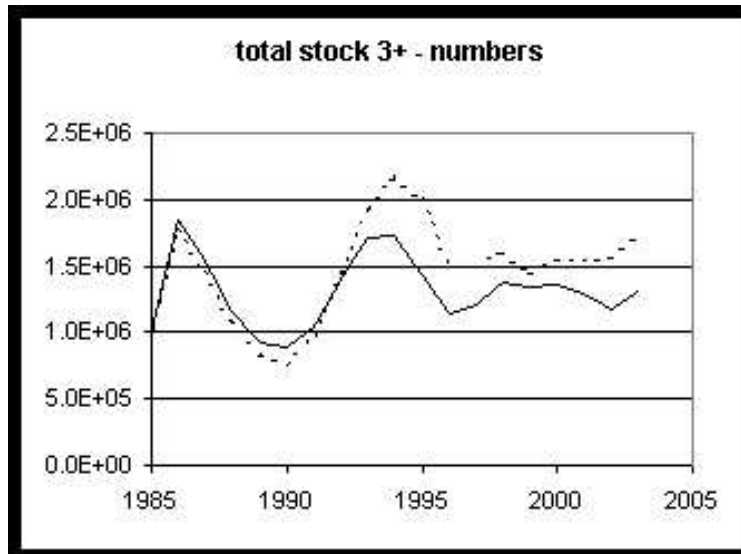
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Figures

a)



b)

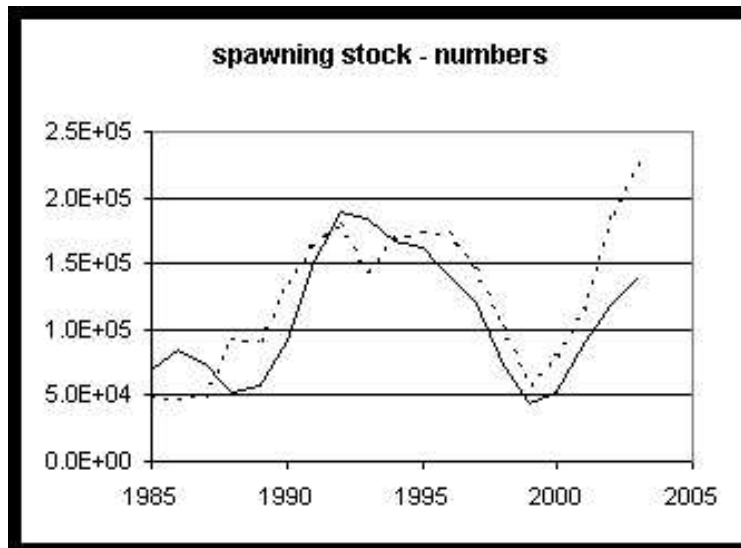
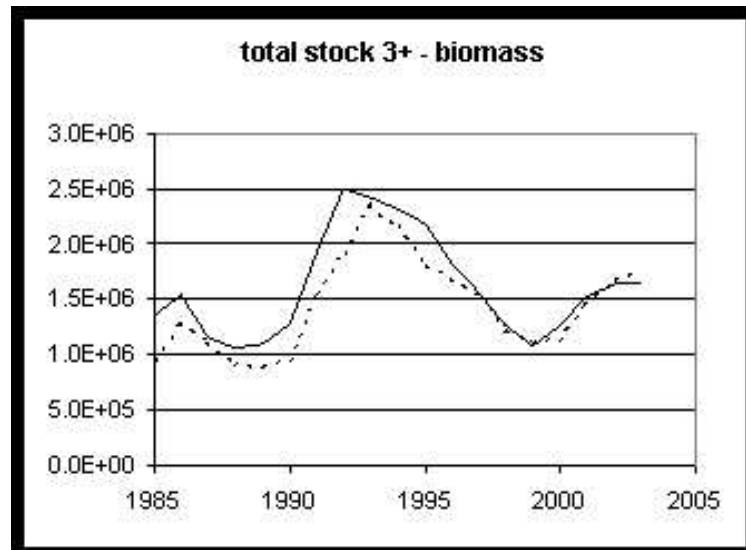


Figure 2. Number of fish of age 3+ (a) and in the spawning stock (b), in million fish. Solid line indicates the closed life cycle model described here, dotted line is the 2004 AFWG XSA assessment.

a)



b)

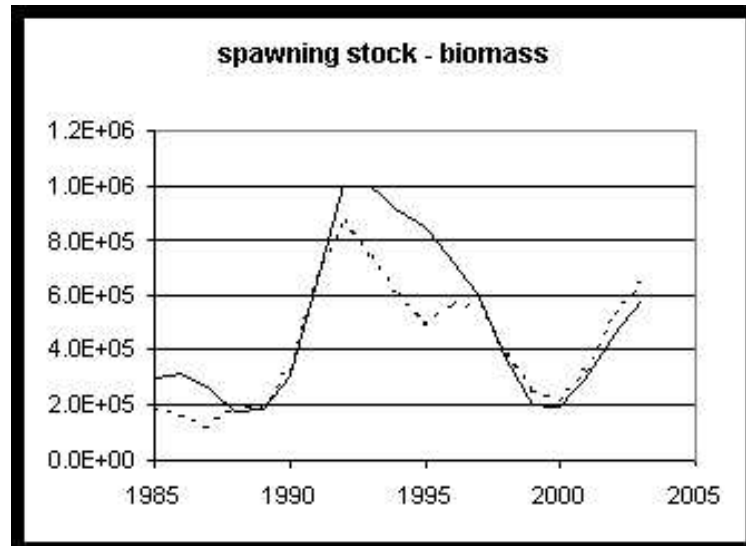


Figure 3. Total biomass fish of age 3+ (a) and in the spawning stock (b), in tonnes. Solid line indicates the closed life cycle model described here, dotted line is the 2004 AFWG XSA assessment.

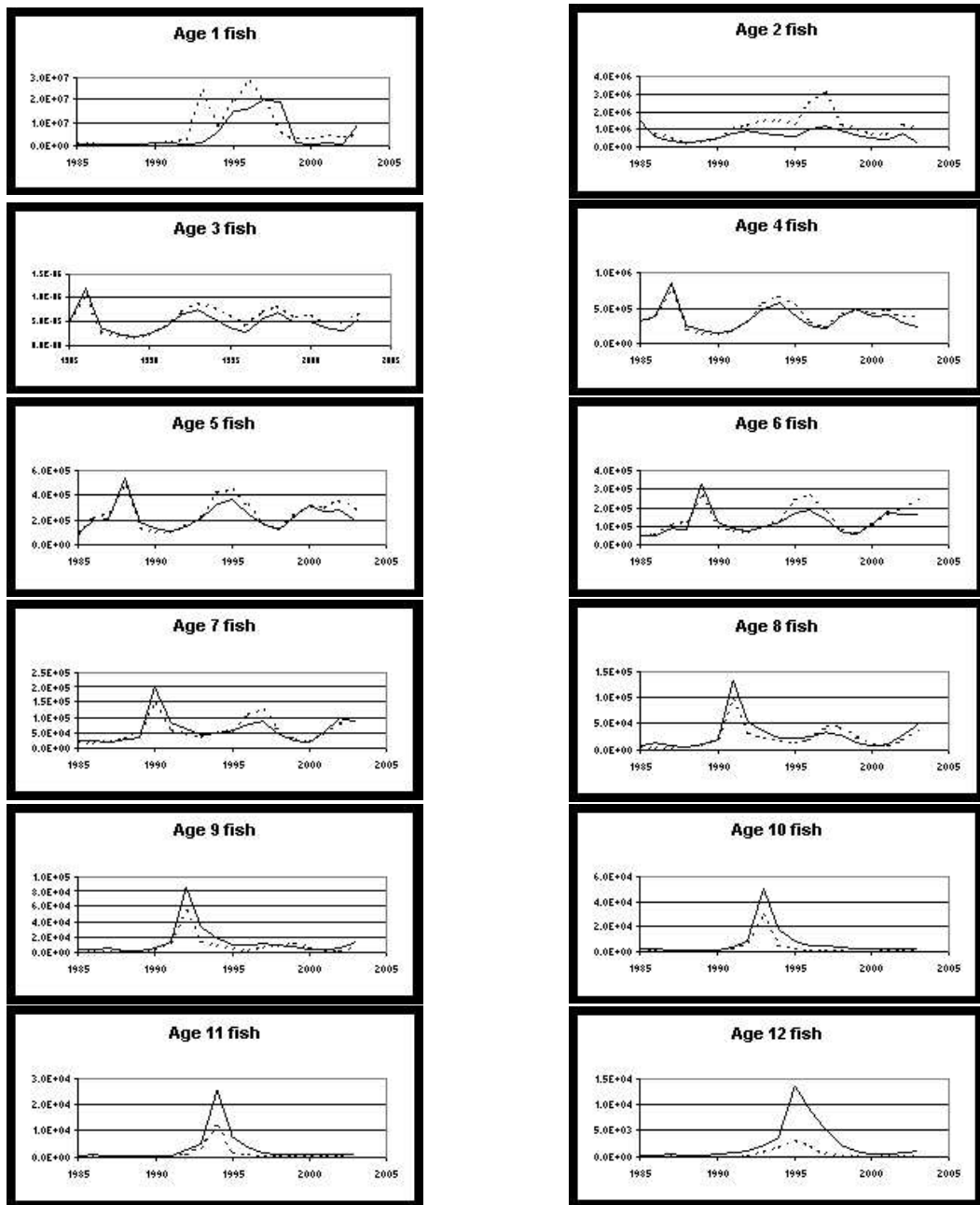


Figure 4. Total number of fish by age, in million fish. Solid line indicates the closed life cycle model described here, dotted line is the 2004 AFWG XSA assessment.

12.4 Further published/in press papers

Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth.

Dalpadado, P. and Bogstad, B.

Abstract: Diet investigations were carried out on 0-, 1- and 2-year-old Northeast Arctic cod (*Gadus morhua*) sampled in the Barents Sea during 1984–2002. Stomach content analyses showed that the 0 and 1 group cod fed mainly on crustaceans, with krill and amphipods composing up to 70% of their diet. Krill (*Thysanoessa* spp. and *Meganctiphanes norvegica*) and amphipods (*Themisto* spp.) were mainly found in cod stomachs sampled in the central and close to the Polar Front region in the Barents Sea where these prey organisms are reported to be abundant in summer. A shift in the main diet from crustaceans to fish was observed from age 1 to age 2. The diet of 2-year-old cod mainly comprised capelin (*Mallotus villosus*) and other fish, and to a lesser degree, krill and amphipods. Shrimp (mainly *Pandalus* spp.) was also an important prey in both age 1 and 2 cod. A statistically significant positive relationship was obtained between capelin stock size and the amount of capelin in the diet of 2-year-old cod. Results from this study also show that the larger age-2 cod preyed more on capelin in winter and that larger cod (>22 cm) prefer larger capelin (>12 cm). During periods of low capelin abundance, the 2-year-old cod shift their diet more to crustaceans, such as krill and amphipods. A positive significant relationship was also obtained between Total Fullness Index (TFI) and the amount of capelin in the diet and between TFI and the growth of 2-year-old cod, indicating that the growth of age-2 cod is to a large extent dependent on the amount of capelin consumed. Growth of age-1 cod was also positively correlated to TFI.

Dalpadado, P. and Bogstad, B. 2004. Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. *Polar biology* 27:140-154.

An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.).

Helle, K., Bogstad, B., Marshall, C. T., Michalsen, K., Ottersen, G., and Pennington, M.

Abstract: Abundance indices for Arcto-Norwegian cod (*Gadus morhua* L.) at various life stages were analysed to determine the index that provides the earliest reliable prediction of year class strength. The indices considered are an egg abundance index; an early juvenile (approximately 3-months old) abundance index; 0-group (age 4- to 5-months) abundance indices; bottom trawl and acoustic survey abundance indices for 1-, 2- and 3-year old cod and of spawning stock biomass. Based on a regression analysis, a cohort's relative abundance as early juveniles is the best early indication of its abundance as 2- and 3-year olds.

Helle, K., Bogstad, B., Marshall, C. T., Michalsen, K., Ottersen, G., and Pennington, M. 2000. An evaluation of recruitment indices for Arcto-Norwegian cod (*Gadus morhua* L.). *Fisheries Research* 48: 55-67.

Some environmental factors that influence the growth of Arcto-Norwegian cod from the early juvenile to the adult stage.

Helle, K., Pennington, M., Bogstad, B. and Ottersen, G.

Abstract: A high growth rate for Arcto-Norwegian cod, *Gadus morhua*, in the Barents Sea and adjacent areas from the larva period to the 0-group enhances survival and ultimately

recruitment to the fishery. However, it appeared that high growth rates for a cohort through the 0-group were not continued as the cohort ages. Based on survey data, there was a significant negative correlation between the average length at the 0-group and its average length at ages 2 through 8. We provided evidence suggesting that this phenomenon was caused by the inter-annual variability in inflow of warm, prey-rich Atlantic water into the Barents Sea from the Norwegian Sea. Enhanced inflow provided favorable conditions for cod growth during the larva and juvenile pelagic intervals. However, this same strong inflow carried a proportion of the cohort farther to the east in the Barents Sea, where the bottom water is colder than in the west. The colder conditions experienced by such cohorts, as compared to cohorts that have a more westerly settlement, led to slower growth prior to age 2. Slow growth during this interval appeared to be the reason for these cohorts' relatively smaller mean length at older ages.

Helle, K., Pennington, M., Bogstad, B. and Ottersen, G., 2002. Some environmental factors that influence the growth of Arcto-Norwegian cod from the early juvenile to the adult stage. *Environmental Biology of Fishes* 65:341-348.

Do abiotic mechanisms determine interannual variability in length-at-age of juvenile Arcto-Norwegian cod?

Ottersen, G., Helle, K. and Bogstad, B.

Abstract: For the large Arcto-Norwegian stock of cod (*Gadus morhua* L.) in the Barents Sea, year-to-year variability in growth is well documented. Here three hypotheses for the observed inverse relation between abundance and the mean length-at-age of juveniles (ages 1–4) are suggested and evaluated. Based on comprehensive data, we conclude that year-to-year differences in length-at-age are mainly determined by density-independent mechanisms during the pelagic first half year of the fishes' life. Enhanced inflow from the southwest leads to an abundant cohort at the 0-group stage being distributed farther east into colder water masses, causing lower postsettlement growth rates. We can not reject density-dependent growth effects related to variability in food rations, but our data do not suggest this to be the main mechanism. Another hypothesis suggests that lower growth rates during periods of high abundance are a result of density-dependent mechanisms causing the geographic range of juveniles to extend eastwards into colder water masses. This is rejected mainly because year-to-year differences in mean length are established by age 2, which is too early for movements over large distances.

Ottersen, G., Helle, K. and Bogstad, B. 2002. Do abiotic mechanisms determine interannual variability in length-at-age of juvenile Arcto-Norwegian cod? *Can. J. Fish. Aquat. Sci.* 59:57-65.

Part IV

Appendices

Appendix A

Publications and Dissemination

A.1 Project technical reports

Anon. 2001. Development of structurally detailed statistically testable models of marine populations (dst^2). QLK5-CT1999-01609. Progress report for 1. January 2000 to 31 December 2000. MRI Technical Report 78. 290 pp.

Anon. 2002. Development of structurally detailed statistically testable models of marine populations (dst^2). QLK5-CT1999-01609. Progress report for 1. January 2001 to 31 December 2001. MRI Technical Report 87. 292 pp.

Anon. 2003. Development of structurally detailed statistically testable models of marine populations (dst^2). QLK5-CT1999-01609. Progress report for 1. January 2002 to 31 December 2002. MRI Technical Report 98. 346 pp.

A.2 Peer reviewed papers

Babak, P., Magnússon, K. G. and Sigurðsson, S. Þ.. (2004) Dynamics of group formation in collective motion. *Mathematical Medicine and Biology*, 24(4): 269–292

Brynjarsdóttir, J. and Stefansson, G. 2004. Statistical Analysis of Cod Catch Data from Icelandic Groundfish Surveys. *Fisheries Research*. In press.

Dalpadado, P. and Bogstad, B. 2004. Diet of juvenile cod (age 0-2) in the Barents Sea in relation to food availability and cod growth. *Polar biology* 27:140-154.

Dalpadado, P., Borkner, N., Bogstad, B., and Mehl, S. 2001. Distribution of *Themisto* (Amphipoda) spp. in the Barents Sea and predator-prey interactions. *ICES J. Mar. Science* 58: 876-895.

Fiksen, Ø., and Slotte, A. 2002. Stock-environment recruitment models for Norwegian Spring-spawning herring. *Can. J. Fish. Aquat. Sci.* 59: 211-217.

Frøysa, K. G., Bogstad, B., and Skagen, D. W. 2002. Fleksibest - an age-length structured fish stock assessment tool with application to Northeast Arctic cod (*Gadus morhua* L.). *Fisheries Research* 55: 87-101.

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- Helle, K., Pennington, M., Bogstad, B. and Ottersen, G., 2002. Some environmental factors that influence the growth of Arcto-Norwegian cod from the early juvenile to the adult stage. *Environmental Biology of Fishes* 65:341-348.
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- Huse G, Railsback SF, Fernö A. 2002b. Modelling changes in migration pattern of herring: collective behaviour and numerical domination. *Journal of Fish Biology* 60:571-582.
- Johansen, G.O. 2002. Temporal and spatial variation in predation on juvenile herring (*Clupea harengus* L.) by Northeast Arctic cod (*Gadus morhua* L.) in the Barents Sea in 1984-1997. *ICES Journal of Marine Science* 59: 270-292.
- Johansen, G.O. 2003. Size-dependent predation on juvenile herring (*Clupea harengus* L.) by Northeast Arctic cod (*Gadus morhua* L.) in the Barents Sea. *Sarsia* 88: 136-153.
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A.3 Conference papers/In prep/Technical reports

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ICES C.M. 2004/K:26, 26 pp.

Dereksdóttir, E. H., Magnússon, K. G. and Sigurðsson, S. Þ. 2003. Simulations of spawning migrations of capelin in Icelandic waters based on temperature-, current- and potential fields. Report RH-16-2003. Science Institute, University of Iceland, Reykjavík.

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