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International Council for the
Exploration of the Sea

C.M.1992/Assess:16
Ref.: G

REPORT OF THE MULTISPECIES ASSESSMENT WORKING GROUP

Copenhagen, 16 - 25 June 1992

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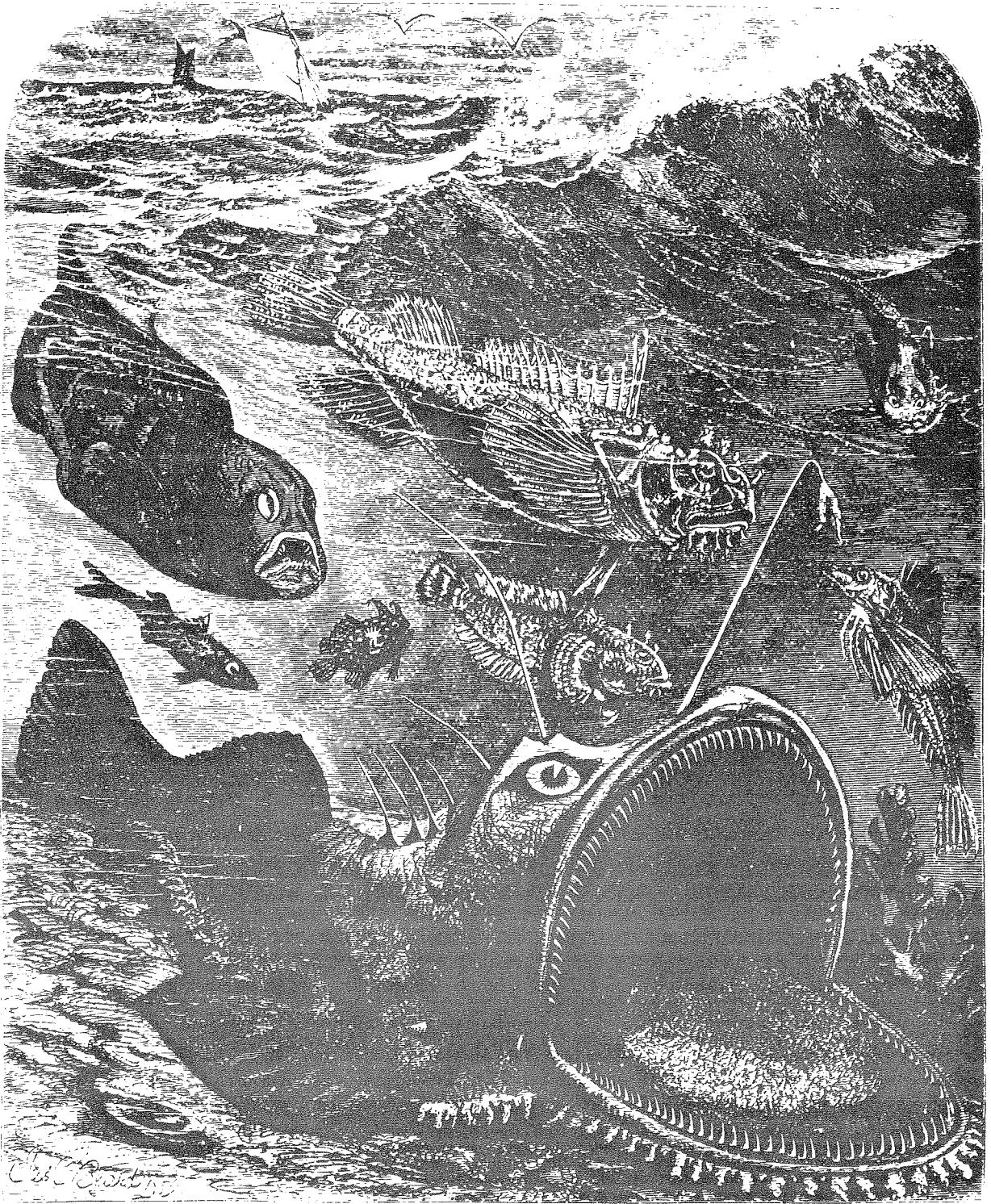


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1 INTRODUCTION

The meeting was held at the ICES Headquarters, from 16-25 June, 1992.

1.1 Participants

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1.2 Terms of Reference

The terms of reference (C.Res.1991/2:7:18) are:

- facilitate the transfer of the MSVPA and MSFOR models to area-oriented assessment working groups, particularly by providing documentation for these models and developing user-friendly interfaces for the maintenance of data files;
- for the diversity of ecosystems being studied by ICES member countries, evaluate the statistical properties of food and feeding data, with particular reference to variability in total food consumption and emphasizing the potential implications for such estimates of sampling design;
- evaluate the effect of alternative functional feeding relationships (including predator/prey switching) on retrospective multispecies analyses and predictive models;

- continue the development of multispecies models of assessment, especially in respect of the tuning of MSVPA to survey and CPUE data, and the incorporation of statistical model fitting to predation data.

1.3 Overview

The major focus of past meetings of the Multispecies Assessment Working Group has been on the development and testing of multispecies virtual population analysis, particularly with regards to the North Sea (see Anon. 1991a for a summary of previous Working Group activities). The North Sea work continues on two levels: data collection and methodological improvement. A second intensive 'year of the stomach' program was conducted in 1991 (Anon. 1992b) and data from this field study will be integrated into models of North Sea fisheries at the next meeting of the Multispecies Assessment Working Group (see RECOMMENDATIONS).

The current suite of computer programs for MSVPA and predictions do not meet ACFMs criteria of 'user-friendliness' necessary for transferral to the area-oriented working groups. These programs, although functional, also do not take advantage of advanced graphics and statistical analysis packages. Re-programming of these packages is a significant undertaking. The Working Group evaluated design features to be included in new packages, and proposed a strategy to accomplish the tasks of programming and documentation (Section 2; see RECOMMENDATIONS). The working group also developed a spreadsheet approximation to the long-term equilibrium prediction of the outcomes of various management scenarios. Although the spreadsheet does not produce the detailed output of the full prediction model, various salient features of the prediction are well behaved, and are presented in a format that is both easy to use (e.g. by ACFM and other semi-literates) and is especially easy to interpret. Copies of the EXCEL spreadsheet of this approximation will be made available to ACFM.

At this meeting two methodological improvements to the MSVPA approach were initiated. First, an objective basis for tuning of the MSVPA is a priority of ACFM. In the past, tuned single-species VPAs were the basis for starting Fs. This represents circular logic, particularly if one is comparing the results of single- and multi-species VPA (e.g. recruitment trends, etc.). An objective, internal tuning algorithm, based on CPUE and/or R/V surveys is a preferable alternative, but a substantial undertaking. The Working Group considered alternatives for internal tuning of MSVPA, and made substantial progress in the integration of the extended survivors algorithm (XSA) within the MSVPA code. Trial runs were completed and indicated this is a promising approach (Section 3). There remain some technical and logistical issues to be resolved before a tuning suite is

operational for the multispecies VPA [we suggest multispecies tuning be referred to as 'orchestration'].

The assumption of constant suitability remains the pivotal mechanism within MSVPA allowing the extrapolation of historical predation patterns from limited time-series of feeding data. Previous statistical analyses (Anon. 1991a) could not reject the assumption of constant suitability, and in fact showed substantial improvement in fitted suitability coefficients and M2s when additional feeding data sets were added to the analyses (to a point). While none of these analyses conclusively confirm the constant-suitability hypotheses, they do show that it is tenable in this case. An alternative approach to validating a suitability model, is to propose other (e.g., non-constant) suitability models, and to evaluate the relative differences in observed vs. predicted food composition and other variables that can be measured external to the models.

In this meeting the Working Group explored a flexible form of the suitability model allowing for both positive and negative 'switching' of predators to either abundant or rare prey items. These results were compared to a neutral switching model implied by the constant suitability assumption. In general, positive switching models performed much worse than neutral or negative switching models. In some cases, slight negative switching showed slightly better results than neutral models, although the improvements in model fits were marginal (Section 4). Data from the 1991 stomach program will be important in exploring this concept more fully.

Increasingly, and especially at the last meeting of the MSWG (Anon. 1991a), the Working Group has been examining species interactions in boreal systems. The approach taken at the last meeting was to evaluate variability of cod growth in boreal systems, and potential factors (both environmental and biological) that potentially influence cod growth. The major conclusion from intra-system work was that a variety of factors (temperature, prey population density) are significantly correlated with growth, and in most cases, there were still significant year effects remaining after correlation with these factors. Predator growth should be correlated with consumption of prey. Therefore, a natural extension of the growth comparisons is to examine variation in stomach content weight and prey composition, both over time within systems, and among systems.

A major focus of this meeting was the examination of cod feeding data for six widely divergent ecosystems (North Sea, Baltic Sea, Barents Sea, Iceland, Newfoundland, and Northeast USA). Available cod feeding data were assembled prior to the meeting (Anon. 1992a). Data from a total of 200,635 cod stomachs were examined in these analyses (Section 5). These results present the first integrated look at cod as an animal, inhabiting

widely differing physical and biological habitats (Sections 6 and 7). Results of these analyses are both complex and thought provoking. The 'natural' experiments imbedded within the ranges of environmental temperatures and predator and prey population size levels allow laboratory experimental data to be placed in context. For example, the finding a negative relationship between mean stomach content weight and average ambient temperature is consistent with stomach evacuation experiments.

An overall conclusion of empirical studies conducted during the last two meetings is that realistic models of interspecies dynamics in boreal systems must include features such as variable predator growth, and non-constant consumption levels, which are taken as simplifying assumptions in MSVPA. Since these factors are to an extent understood, there is no conceptual difficulty in making more complex models. It is recommended that the MSWG undertake model building and testing for boreal systems (particularly following the next meeting of MSWG, which will be particularly concerned with North Sea problems).

As usual, the Working Group considered 'food for thought' concerning new methods and approaches to multispecies problems (Section 8). Once again the issue of integration of marine mammal and fish predation studies (e.g., into an ecosystem approach) was examined. A significant problem facing the WG is dealing with years of missing catches in the historical time series. For the North Sea MSVPA this is particularly problematic in that important prey species were not adequately sampled in one year, which may be influential when considering the 1991 feeding results. The Working Group evaluated the performance of several alternative approaches for filling-in missing catches-at-age in the matrix of such data. Other issues considered in the 'food for thought' section include the development of length-based analogs to MSVPA, the smoothing of suitabilities, propagation of recruitment variability in multispecies predictions, and re-calculation of the North Sea food web, based on the ECOPATH II model (Christensen and Pauly 1992).

The final section of the report reviews approaches to the statistical treatment of stomach sampling data. These data are by their nature highly variable. This variability stems from the biological process in relation to the sampling designs chosen to monitor feeding habits. Understanding the underlying variability of average stomach content and species composition of prey is fundamental in documenting change -- and mechanisms responsible for variation in predation mortality rates. The Working Group considered both the statistical treatment of stomach sampling data, and the appropriate design of feeding studies to truly reflect the underlying variances of the quantities being measured. The WG

considers this to be a significant and ongoing activity, and proposes future work to examine statistical issues in more detail.

1.4 Acknowledgements

The Working Group acknowledges the considerable support provided by the ICES Secretariat, both in terms of assembling the report, and in providing considerable computing facilities necessary for the efficient conduct of the many analyses conducted at the meeting. The support of various national laboratories in assembling the predation data sets for comparative analysis is appreciated. The Danish Institute for Fisheries and Marine Research (DIFMAR) provided resources for MSVPA-related studies. Finally, the Working Group members express their thanks to the Chairman of the Study Group on the Analysis of Feeding Data (George Lilly) and Peter Shelton for their significant efforts in assembling predation data sets prior to the Working Group meeting.

2 UPDATE/DOCUMENTATION OF MSVPA AND MSFOR PROGRAMS

2.1 The Need for New MS-Software

The current MSVPA-program was developed some 10 years ago. It was written in FORTRAN for a mainframe computer, and a certain expertise is required to operate it. The MS-forecast program was developed a few years later, and has the same deficiencies as the MSVPA program. The programs are not user-friendly and they do not live up to modern software standards. It is difficult to modify and extend the current programs because of the program structure. The core of the current MS-programs has the same structure as the original program. The program has been extended with several new computational routines, but no facilities to improve the user-friendliness have been implemented. Therefore the current version is even less user-friendly than the original. It will become increasingly difficult to further extend the current program. The only (draft) user's manual for the MSVPA program was prepared in 1984 (Sparre 1984). The current programs do not meet ACFM's criterion for user-friendliness for export to the area working groups. Furthermore, these programs do not currently operate on computers available at the ICES Secretariat (e.g. HP-UNIX or PCs).

Therefore, the MSVPA computer program should be re-programmed and extended, so that it makes the full use of modern computer hardware and software. Until this goal has been achieved, the old programs may still have to be used, and for that purpose a user's manual will be prepared. This task will be undertaken by H. Gislason and P. Sparre, and will be in the form of an updated version of the user's manual from 1984 combined with

extracts from papers by the above mentioned authors. This 'emergency' manual will also review the theory behind the MSVPA and MSFOR models. There should be no further developments of the existing MSVPA/MSFOR FORTRAN programs.

The new MSVPA/MSFOR package, will, for the purposes of discussion, be referred to as 'MSFP'-- Multi-Species-multi-Fleet Package. However, the final name of the package still has to be decided.

The Working Group identified the need for two versions of 'MSFP' :

- a) A version for 'public' distribution: The primary customers are the ICES assessment working groups and the ACFM, and consequently it should address the problems as formulated by them. This version should be user-friendly and transferable. It should contain a limited number of options and be well documented. The public version should be so general that it can be applied to different ecosystems. The 'public' version will be programmed for the UNIX workstation at the Headquarters, but DOS versions may be produced, considering the limited number of options contained in the program.
- b) A 'developers version' for the multispecies and long-term management measures working groups: This version should be programmed specifically for operation on the UNIX workstation. The core of the developers version should be the public version. The developers version should, for example, contain options for sensitivity analysis and stochastic simulations. It should be documented as it develops on an ad hoc basis.

The public version is given the first priority and should preferably be developed during the next year. This package should contain all the features of the standard methodology applied by ICES WGs. It should strengthen the ability of the current MS-programs in dealing with technical interaction and it should initiate the application of models accounting for spatial distribution of resources and fishing fleets. That means that the public version of MSFP is not only intended for workers with interest in biological interaction. The public version of MSFP should have management as its primary objective, and therefore it should adhere to the developments in management oriented research, such as the Working Group on Long-Term Management Measures.

The forecast-part of MSFP should become a simulation model to predict based on scenarios for user-selected assumptions of the fishing patterns of the fleets considered.

The new programs should be structured into independent modules, and be based on object oriented programming.

2.2 Extension of the MS models (VPA and Forecast)

Below follows a list of possible extensions of the current MS-programs which could be implemented in MSFP. Some of the proposed extensions may or may not be included in the first version of the developers package, but the design of the first version should take into account that these extensions eventually will be implemented.

TECHNICAL IMPROVEMENTS:

- MSFP modules to interface with commercial analysis and presentation graphics software, (e.g., LOTUS 1-2-3 and SAS).
- Currently, options for running the MS-programs are written into an ASCII file. Entry of run-options in MSFP should be selected by a user-friendly and menu-driven program module.
- Internally, extensive facilities for graphical presentation of results.
- A module to interface with disaggregated data bases maintained in the ICES headquarters.
- Options to select sub-sets of species, predator-species and prey-species. Non-selected prey species should be transferred to other food in the stomach content data file.
- MSFP should contain options to select the range of years, for which the VPA is made.

SCIENTIFIC ELABORATIONS:

Biological processes:

- Options for growth rate and food consumption to be functions of available food.
- A suite of options for models of food suitability models. In the current version, suitabilities are assumed to remain constant, and are they the mean values for over the years with stomach content data. An extension of the suitability model is already in the current version, namely the option for "switching".
- Estimate parameters in user-selected stock/recruitment models, for subsequent use by MSFOR.
- Options for definition of minimum and maximum biological acceptable level of spawning stock biomass, to

classify long term predictions and to prevent unrealistic prediction results.

Spatial distribution of fish and fleets:

- Currently, the MS-models assume that the sea is one homogenous area in which the resources and the fishing fleets are evenly distributed. The model could account for temporal re-distribution of fish between areas and the allocation of effort among areas. The model could account for migration of fish between areas, but an appropriate migration model has yet to be formulated.

Spatial distribution of predation:

- The current version assumes that the spatial distribution of fish stocks remains constant, and that the degrees of overlap between prey and predator is reflected in the suitabilities. It is proposed that MSFP will allow for the use of spatially disaggregated feeding data, and will contain algorithms (yet to be developed) for computing predation on a finer scale of spatial resolution.

Other prey:

- Options for including 'other prey'. The current version allows for only 'other predators'. The 'other prey' input should be total stock number, body weights and stomach content in predators of the species in question, either by age group or by size group.

Tuning:

- VPA-tuning methods will be incorporated in MSFP. There should be options to tune for a variety of observations, such as effort from commercial fishery, abundance indices from trawl survey and total biomass from acoustic survey or egg survey.

Output options:

- MS-forecast should be able to produce result curves as a function of an effort-multiplier (or F-multiplier) for a selected fleet or a group of fleets. Result-curves include:
 - Yield curves
 - Value of yield curves
 - CPUE-curves
 - Biomass-curves (total and spawning stock)

Fleet definition:

- The fleet definitions used in MSFP should adhere to fleet definitions which are considered useful for management purposes. It should be able to use the ICES disaggregated data base for the allocation of effort on the North Sea sub-areas.

Quota-F-Biomass:

- MSFP should be able to predict biomass and fishing mortalities for given catch quotas, on a fleet basis.
- MSFP should assess the effects of effort limitations in the form of closed areas and closed seasons.

Stochastic simulation:

- The MSFP should include stochastic simulation of, for example, recruitment.

Sensitivity analysis:

- The MSFP should include options for sensitivity analysis. MSFP should have options to run multiple scenarios, and to compare results.

Use of environmental data:

- MSFP should contain options for using environmental data (for example, climatic data such as temperature) in the forecast part.

Maximum likelihood estimation:

- The current methodology is unable to provide confidence limits for the estimates of parameters and the forecast. A model formulation which allows for a statistical treatment of parameter estimates and forecast results should be pursued.

2.3 Production, Documentation and Testing

The production, documentation and testing of the new software will require an international effort in order to ensure an adequate input in the development. Therefore it is proposed that a coordinating group for the development of MSFP be established (see RECOMMENDATIONS). The composition of such a group will need to include members of the Multi-species Assessment Working Group and the Long-Term Management Measures Working Group, with representation from area working groups likely to be involved with running the public version of MSFP. This planning group will supervise the development, testing and documentation of the public version of MSFP.

The documentation of the public version should comprise:

1) User's manual including:

- a) Introduction to the theory behind the MSVPA/MSFOR models.

A presentation of the complete mathematical models with explanatory notes.

- b) Complete demonstration example, with representative examples of input and output.

- c) Parts of analyses of real data set.

- d) Examples of likely misuse of MSFP (don'ts).

2) Listing of source code of program, with comprehensive comments and a complete list of variables with explanations for each symbol.

The developers version should be documented on an *ad hoc* basis, on the highest possible level.

2.4 Simple Spreadsheet Approximation Models of Multispecies Forecasts.

A simple model which approximates the results of MSFOR would help assessment working groups and ACFM to quickly explore the likely response of the fleet/species yield and species SSB to modifications of the effort of different fleets included in multispecies predictions. Such models would help with the simple exploration of various scenarios which could then be verified by the use of MSFOR. A further advantage of such approximate models is that they typically have a simple mathematical structure which can be helpful for gaining insights in to the results of MSFOR and the likely position or direction of various biological reference points. Such a simplified model would also allow testing during the period in which full versions are being developed for new applications.

Such a approximate model approach was used by the Multispecies Assessment Working Group at its 1989 meeting (Anon. 1989a) to provide estimates of possible positions of multispecies MSY, MEY, and multispecies analogues to $F_{0.1}$. These were based upon a quadratic yield surface such as those adopted by Pope (1979) to describe the Gulf of Thailand fisheries. Such surfaces however imply linear surfaces for biomass changes with respect to effort change. This does not appear to accord very well with the biomass response to changes in fishing effort predicted by MSFOR. Since the management of SSB is an important current concern of fisheries management in the North Sea it seems appropriate to

chose a simple model with a more realistic response to effort change.

This year the model formulation:-

$$SSB(s) = \text{Exp}(A(s) - Sg B(s, g) * E(g) / E'(g))$$

$$CPUE(s, f) = \text{Exp}(A'(s, f) - Sg B'(s, f, g) * E(g) / E'(g))$$

was adopted where A, B and A', B' are constants; where E(g) is the proposed effort in fleet g and E'(g) is the status quo effort in fleet g; where SSB(s) is the spawning stock biomass of species s and where CPUE(s, f) is the catch per unit effort of species s for fleet f. The new yield of species s for fleet f then being given by CPUE(s, f) * E(f) / E'(f).

Such a model is simple to fit from the usual Jacobian matrix output results of MSFOR. The present model was fitted to the results of the 50% increase Jacobian analysis made in the 1990 working group (Anon 1991; Tables 4.11, 4.2.1a-4.2.7a). The s vectors of A(s), B(s, f) and the s'f vectors A'(s, f), B'(s, f, g) being calculated by multiplying the vectors of SSB(s) and of CPUE(s, f) at 8 combinations of effort levels (status quo and 50% increase in each of the 7 fleets in turn) through the inverse of the effort change matrix. A simple EXCEL spreadsheet model APPROX was then constructed using the estimated A, B and A', B' values. This calculates the SSB, CPUE and Yield values for each species and fleet and their percentage changes. The model provides 3D graphs of the yield and SSB % changes and tables of absolute and % change. Figure 2.4.1 shows the % yield changes by species and fleets when the various fleet efforts are manipulated by + 25% or - 25%. Figure 2.4.2 shows the equivalent SSB and overall yield and discard results for the same scenario. Both these figures show results only a few % different from the equivalent MSFOR results. The approximate nature of the model means that it gradually diverges from the MSFOR results particularly at low effort. Table 2.4.1 shows the comparison when effort is reduced to 50% in all fleets. While many of the results still indicate scales and directions of change approximately similar to MSFOR, some have diverged from the MSFOR predictions and are highlighted in the table. For this reason the model has been limited to changes of no more than plus or minus 50%. Inputs in the input sheet QUESTION.XLS thus generate error messages on the graphs and tables.

Figure 2.4.3 shows an example of the results of such abuse of the approximation. The formulation of the model means that the B(s, f)'s indicate the direction of change in the effort of each fleet f which would maximize the rate of change of SSB of species s (e.g. -grad (SSB(s)) with respect to each fleet. Table 2.4.2 shows appropriate directions of effort change to maximize the rate of increase of steady state SSB for each separate

species. Some of these directions will of course imply that the SSB of other species may decline. Compromise directions do however exist. These are where the SSB of all species would be 'expected' to increase under the effort modifications. Figure 2.4.4 shows one such modification. In this scenario all fleets are reduced to 70% of their current level except the saithe fleet which is increased by 20% and all SSB's increase although by very different proportions.

The simple model proposed above both aids our comprehension of the MSFOR programs likely behaviour under different scenarios and provides a simple communication tool for the use of other working groups and Committees of ICES. Using this simple model should enable them to propose scenarios for evaluation by MSFOR which approximate to the main changes they wish to achieve.

3 OBJECTIVE TUNING OF MSVPA

3.1 Extended Survivors Analysis (XSA)

Ad hoc methods for tuning single species virtual population analyses (VPA's) to fleet catch data can be applied to the VPA algorithm used within the multispecies assessment program. However, these techniques are sensitive to observation errors in the data for the final year (which is assumed to be exact), and fail to utilize the year-class strength information contained within the disaggregated catch data (Shepherd 1992). Extended Survivors analysis, XSA (Shepherd 1992), an extension of Survivors analysis (Doubleday 1981), provides an alternative method which overcomes these deficiencies.

Shepherd (1992) discusses the least squares derivation of XSA. CPUE indices from each fleet are assumed to be related to the population abundance by the constant catchability model:

$$(1) \quad U(yaf) = q(af) A(yaf) P(ya)$$

where y indexes year, a age and f fleet. A is an averaging factor relating the population during the time at which the catch was taken to the population at the beginning of the year P.

A is given by:

$$(2) \quad A(yaf) = \frac{\exp(-gZ) - \exp(-hZ)}{(h-g)Z}$$

where g is the start of the period of fishing and h the end (both expressed as fractions of a year). In practice XSA corrects the CPUE to the beginning of the year:

$$(3) \quad U'(yaf) = U(yaf) / A(yaf)$$

Population estimates at the beginning of a year are derived from each fleet:

$$(4) \quad \text{Pest}(yaf) = U' (yaf) / q (af)$$

The method assumes that the population values derived from the VPA (Pvpa) are exact and that the values of Pest are estimates of these values. Shepherd (1992) shows that by a rearrangement of Pope's cohort equation the VPA population for age a in year y is given by:

$$(5) \quad \text{Pvpa} (ya) = \text{ECM} (ya) \text{Pt}(k) + \text{Pc} (ya)$$

ECM is the exponential cumulative natural mortality summed from the greatest cohort age back through the cohort to (y,a). Pt(k) is the terminal population (survivors) at the end of the final year or oldest cohort true age and Pc is given by:

$$(6) \quad \text{Pc} (ya) = \text{sum}_i [\text{ECM}_i, C_i \exp (-0.5M_i)]$$

'sum_i' describes summation backwards up the cohort from the oldest cohort age to the (y,a) population. Pc therefore describes the contribution of the raised accumulated catches to the population in year (y,a). Within the traditional VPA and cohort analyses or one iteration of MSVPA, M, C_i and therefore Pc are constant. Shepherd (1992) derives the log of reciprocal catchability (1/q) used to calculate the Pest values using equation (4) by:

$$(7) \quad \text{Ln} [1/q(af)] = \text{sum}_y [\text{Ln}(\text{Pvpa}(ya)) / U'(yaf) / \sigma^2(af)] / \text{sum}_y [1/\sigma^2(af)]$$

where $\sigma^2(a,f)$ is the variance of the CPUE data. Finally the cohort terminal populations are estimated by:

$$(8) \quad \text{Ln Pt} = \text{sum}_r \text{sum}_i [w'(\text{Ln Pest-CUMZ})] / \text{sum}_r \text{sum}_i [w']$$

and

$$w' = w / \text{ECF}$$

This is a weighted geometric mean over all available data for the cohort estimated from the CPUE data reduced by total mortality to the end of the final year. The division by ECF progressively reduces the weight of the younger ages of the cohort. Within the XSA algorithm the w values are the variance of the log reciprocal catchability. Calculation of catchability and the terminal populations is an iterative process with new Pvpa values generated at each iteration. Various options for time series weighting, prior fleet weighting and exclusion of estimates with high standard errors are available. The RCT3/RCRTINX2 procedure (Shepherd 1990), which allows the CPUE of recruiting age classes to be non-linearly proportional to year-class strength, can be used to analyze the younger ages.

3.1.1 Incorporation of XSA in MSVPA

Prior to the meeting the code used for reading the fleet catch at age data files had been incorporated in the MSVPA. The files are in the format equivalent to that for the Lowestoft VPA, with the addition of the g and h parameters after the effort and sex codes. During the meeting there was only sufficient time for converting the algorithm for XSA for use within the MSVPA program and to carry out a few preliminary test runs. These established that the tuning of MSVPA using XSA is possible, but that minor problems in the interface between the two methods have still to be resolved and coded.

The XSA code was treated as a separate entity from the MSVPA code. An initial run of MSHIST the MSVPA VPA subroutine is used to initialize the population numbers and the natural mortalities induced by predators (M2). For each year and age, population numbers, the natural mortalities M1 and M2 and the total catch are extracted from the quarterly MSVPA arrays and restructured in the annual XSA format. XSA is then used to generate terminal populations for all of the species for which fleet catch at age tuning data is available. A one-step cohort analysis is used to generate the population values in the third quarter of the final true age or year and these values are then used with the terminal populations to calculate the terminal F values. The terminal F's are returned to the MSVPA fishing mortality array for use in further iterations. The 'pseudocode' algorithm for the main MSVPA procedure is given in Appendix A.

The XSA code was successfully interfaced with the MSVPA code and allowed some initial runs for testing output from the modified program. The MSVPA ran to completion with an increase in the required execution time resulting from the additional iterations. There still remain a few format problems concerning the XSA tuning output, but these are not considered to be significant.

MSVPA/XSA results were produced with the minimum of the available options available to the user in the full XSA tuning method. For each species with fleet catch data CPUE was assumed linearly related to population size for all ages up to the last true age -1, a necessary default option (Shepherd 1992). The various weighting options were set to 1, and perhaps of greater consequence, all g and h values were set to 0 and 1. This produces errors in the estimation of CPUE and catchabilities when using the research survey data in the tuning file which is collected during short time periods.

A preliminary survey of the terminal F values generated by XSA for the final quarter of the final year showed that after suitability convergence had been achieved, the final year terminal F values produced during the final

iteration showed some resemblance to those with which the program had been initialized. The initialization values were originally estimated by determining for each species, F values which result in population numbers equivalent to those recorded by the single species working groups. The methods are recorded in previous multispecies working group reports (Anon. 1984; Anon. 1986).

Given the deficiencies in the initial test run parameters selected for XSA, the results show that the method can be applied for tuning MSVPA. They indicate that where the cohorts are of short duration at the corners of the catch at age array (the younger ages in the final year), the technique may require a non-linear model or some additional tuning of the type used for single species VPA's (survey data, etc.). For cohorts with a longer time series in the catch at age array the results look promising.

After completion of the final implementation and testing of the XSA algorithm within the MSVPA program, a series of investigation runs are required to evaluate the potential of the various tuning options available when using XSA tuning. This will be required for each of the stocks for which fleet catch information is available. Tuning of the tuning procedure is also required to estimate the number of iterations of XSA for each MSVPA VPA. A 1:1 ratio seems appropriate, and may prevent possible clashes between the techniques.

3.1.2 Remaining discrepancies between XSA and MSVPA

During the transfer of the XSA code to the MSVPA program a problem arose which has still to be resolved to allow a full implementation of the technique. It was established that the MSVPA handles plusgroups in a different way to that in the Lowestoft VPA. In the former the VPA is started by entering a terminal fishing mortality for the plusgroup, while in the VPA the terminal fishing mortality is applied to the oldest age. The plusgroup mortality in the Lowestoft VPA is set to be equivalent to the mortality of the oldest true age group in the same year.

In the MSVPA the numbers in the plusgroup are estimated by the usual catch equation in each of the 4 quarters. At the beginning of the year a number of fish equal to the number of plusgroup fish which have died during the year is transferred to the oldest true age group. The underlying assumption being that the plusgroup represents a population in equilibrium. In a multispecies context this approach is convenient for two reasons:

- 1) Since the MSVPA is quarterly and natural mortality is allowed to vary, it is not straight forward to generate a level of yearly fishing mortality for the plus-

group corresponding to the level obtained for the oldest true age. This would require an additional iterative loop, including estimation of predation mortalities.

- 2) The approach corresponds to that followed in the forecast model where fish are transferred from the oldest true age group to the plusgroup. The plusgroup is therefore dealt with in a consistent way throughout the multispecies program.

At the end of the time available for the work this problem had still to be resolved. In the current development stage of the program, terminal F values for the last quarter of the final year are used to tune the MSVPA above the leading diagonal of the population at age array. The terminal F values for the plusgroup remain the input values from the data file.

Given that the MSVPA will always require an input of the terminal F values to the plusgroup and XSA generated terminal population values are to be used to estimate the terminal F for the plusgroup. The inverse process to that used within the MSVPA to estimate the last true age population from the plusgroup population, should be applied to the XSA terminal populations to derive the plusgroup population estimates and subsequently terminal F's. This will result in the MSVPA VPA reproducing the XSA terminal populations in the next iteration.

Alternatively, a solution to the problem is to use an iterative solution for the estimation of the plusgroup populations that would be required to produce the terminal population estimated by the XSA method.

The plusgroup catch in the first quarter is derived from the terminal population of the last true age by the equation:

$$Cq1_{est} = \frac{Pt * Fq1_{est}}{Fq1_{est} + M1q1 + M2q1}$$

Where $Cq1_{est}$ is the estimated catch in the first quarter $Cq1$ is the actual catch, Pt the XSA generated terminal population, $Fq1$ the fishing mortality, $M2$ the predator induced mortality and $M1$ the remaining natural mortality. If an initial estimate of $Fq1$ is made then an estimated $Cq1$ can be calculated. A new $Fq1$ estimate is then derived by:

$$Fq1_{est+1} = \frac{Cq1_{est} Fq1_{est}}{Cq1_{est}}$$

The process is iterated until $Cq1_{est}$ approximates to $Cq1$. The procedure is then applied to all subsequent quarters

for the plusgroup. This algorithm will only hold if the catch from the plusgroup being handled is less than the terminal population for the oldest true age or the population in the previous plusgroup quarter.

The MSVPA handle plusgroups in a different way than in the Lowestoft VPA. In the former the VPA is started by entering a terminal fishing mortality for the plusgroup, while in the Lowestoft VPA the terminal fishing mortality is applied to the next oldest age group.

In the MSVPA the numbers in the plusgroup are estimated by the usual catch equation in each of the 4 quarters. At the beginning of the year a number of fish equal to the number plusgroup fish which have died during the year is transferred to the next oldest age group, the underlying assumption being that the plusgroup represents a population in equilibrium. In a multispecies context this approach is convenient for two reasons. Since the MSVPA is quarterly and since natural mortality is allowed to vary it is not straight forward to generate a level of yearly fishing mortality for the plusgroup corresponding to the level obtained for the next oldest age group. This would in fact require an additional iterative loop, including estimation of predation mortalities. Secondly the approach corresponds to the approach followed in the forecast where fish are transferred from the next oldest age group to the plusgroup. The plusgroup is thus dealt with in a consistent way throughout the multispecies program.

3.2 Possible Analysis of Suitability and M2 Outside of MSVPA Models

Singh and Pope (1992) suggest that to some extent M2 levels generated by particular predator sizes on particular prey size classes can be investigated outside of MSVPA. They suggest that this could be done by comparing stomach contents of different predator species and sizes taken at the same station and assuming that the local abundance of prey of species s and size l have an abundance of:

$$\bar{N}(s, l, r) \text{ at rectangle (or station) } r.$$

The amount of the prey in stomachs, if the Shepherd model of predation is adopted (constant predation mortality per predator), or the relative amount of prey in stomachs, if the MSVPA predation model is used can, therefore, be viewed as a multiplicative model of the local unit predator $\Delta M2$ (or local suitability) and a local abundance factor such that

$$\begin{aligned} \text{Numbers in stomachs } \{S, L, s, l, r\} &= \\ D(S, L, s, l, r) &= \bar{N}(s, l, r) \times \Delta M2(S, L, s, l) \end{aligned}$$

or relative numbers in stomachs:

$$\{S, L, s, l, r\} = N(s, l, r) \times \text{Suit}(S, L, s, l).$$

$\Delta M2(S, L, s, l)$ can thus be estimated using an ANOVA of Prey-size * and Predator-size interactions and Prey/size * position interaction terms. That is:

$$\begin{aligned} \ln D(S, L, s, l, r) &= \\ \text{Prey-size} * \text{Pred-size} &+ \text{Prey-size} * \text{Station} + \text{error} \end{aligned}$$

With this formulation it will be impossible to scale both terms absolutely within the model since multiplying $\Delta M2$ by 2 and dividing \bar{N} by 2 would give the same results. The model could, however, be scaled using global estimates of the values of $\bar{N}(s, a, \cdot)$ where \cdot indicates summation over all rectangles.

Practically, the approach involves some problems since the data set including zero observations is large. The most appropriate statistical model would be Poisson error distribution model and a log-link function, i.e.:

$$\begin{aligned} D(S, L, s, a, r) &= \\ \exp\{(\text{Pred-size}) * (\text{Prey-size}) &+ (\text{Prey-size}) * \text{station}\} \\ + \text{Poisson error} \end{aligned}$$

This may, however, be difficult to fit to the large data sets required and some consideration of simpler alternative models may be worthwhile. It may, therefore, be worth considering the analysis of one prey species at a time in order to reduce the size of the model to more tractable dimensions. The (Pred-size) * (Prey-size) interaction term could of course be simplified to a Pred * Prey effect and a relative size function as has been used in past fittings of suitability.

4 PREY SWITCHING IN MSVPA

4.1 Introduction

In the MSVPA the food composition of a particular predator age group is predicted from the relative abundance of the various prey age groups weighted by their relative suitability as prey. One of the basic assumptions of the MSVPA is the assumption of constant suitability for each predator age prey age combination over time.

Suitabilities [or preferences, as they are called in the ecological literature (e.g. Manly 1974; Chesson 1978; 1983)] may be interpreted as being proportional to probability of encounter between the prey and the predator multiplied by the probability of the predator eating the prey once encountered. If suitability is to remain constant the product of these two probabilities should be constant.

The probability of encounter will only be constant if the relative spatial overlap between predators and prey does

not change over time. In the North Sea changes in distribution have taken place for several species. Herring, which in 1981 was distributed mainly in the northern part of the North Sea became abundant throughout the area in 1985, 86 and 87. Sandeel has also changed its relative distribution (Anon. 1990a). In 1981 28% of the total North Sea biomass of sandeel was found in the northern area, while the corresponding percentages for 1985, 1986 and 1987 are 15, 20 and 35, respectively. It is probable that similar changes have occurred for other species as well. Thus, if changes in suitabilities are seen they may result from changes in spatial overlap of predators and prey.

The probability of eating the prey once encountered may also change, e.g. as a function of prey biomass. Thus an abundant prey item (or year class of prey) may attract more predators than a less abundant. Murdoch (1969) introduced the term "switching" to refer to the situation where the ratio of the abundances of two prey species, in the diet of a predator, increases faster than proportionally with their ratio in the environment. As shown by e.g. Oaten and Murdoch (1975) such a change in preference (in this context called 'positive switching'), is likely to stabilize prey species densities in models of interacting populations of predators and prey, and have therefore attracted considerable interest. We do not know if and to what extent such changes in the behaviour of the North Sea predators occur.

However, the distinction between spatial effects and behavioral changes is not perfect. Changes in spatial distribution of predators may result from changes in spatial distribution of prey, and the two cannot be distinguished from stomach content data only. Studies of how prey density affect the distribution of predators are needed.

A third possibility for introducing changes in suitability over time results from the way in which suitability is estimated within the model. Since suitability is a non-linear function of food composition, the average suitability in a given year cannot be determined directly from the average stomach content of a given predator population, except if all the individuals share exactly the same array of suitabilities. To estimate the population suitability it is necessary to sum the individual responses to the various prey items. This is a simple matter if individuals are identical in all respects. However, if individuals differ summing the effects of the individuals can be quite complicated and the response of the entire predator population may not be directly predictable from the qualitative behaviour of each of the individuals making up the population. If suitability thus differs among predator individuals, but does not change with the relative density of the prey, i.e. no switching on the level of the individual, theoretical considerations show that the overall suitability of the population does change with the

relative density of the prey (Chesson 1984). This phenomenon, which may be regarded a mathematical artefact due to the way in which the average population suitability is calculated, may result in switching on the population level. The switching may be positive or negative depending on the circumstances, with negative switching being the more likely.

Differences between individuals may also arise because of differences in spatial distribution between prey and predators, and such situations are common in the North Sea. Consider for example the situation where one prey item can be found only in the northern North Sea, while the predator is distributed throughout the North Sea (e.g. whiting and Norway pout). Table 4.1 shows a theoretical example where the distribution area of the predator is divided into two parts, in the southern other food is the only food item available, in the northern both other food and another prey item is available. Let us estimate the overall population suitability of the prey in two situations; one with a prey biomass of 1.0; the other with a prey biomass of 2. Assume that the biomass of other food is the same in both situations and that the suitability of the prey is 0.5 within each area in both situations. The food composition within each area may now be estimated by the usual formula:

$$\text{Rel. stom. cont.} = \frac{\text{Suit} \cdot \text{Biom}}{\sum_{\text{over prey}} (\text{Suit} \cdot \text{Biom})}$$

Since half the predator population is found in the northern area and the other half in the southern, the overall av. prop. of the prey in the stomachs can be estimated as the average of the food composition in the two areas. The average food composition may then be entered into the formula for estimating overall suitability:

$$\text{suit} = \frac{\text{Rel. st. cont.} / \text{Biom}}{\sum_{\text{over prey}} (\text{Rel. st. cont.} / \text{Biom})}$$

In situation 1 the overall suitability of prey 1 has thus been estimated to 0.4, which is less than the within area suitability of 0.5. Not taking differences in spatial distribution into account may thus introduce a bias in the estimate of overall suitability.

The same procedure was applied to situation 2. The result was an overall suitability of 0.33. Suitability is thus a declining function of prey biomass, a situation which will appear as 'negative switching', i.e. the prey becomes more attractive (suitable) as its abundance decreases.

In summary, switching may result from changes in relative spatial overlap, from behavioral changes and from the use of average stomach content to estimate overall population suitabilities in the situation where prey preference differs between individual predators.

4.2 Incorporating Switching in the MSVPA and MSFOR

In the MSVPA switching was modelled by making suitability a function of prey abundance:

$$\text{Suit} = a * N^b$$

where a and b are constants and N is the average population numbers of a particular prey age group within a given quarter. If b is zero Suit is constant (no switching), if b is either positive or negative suitability will either increase (positive switching) or decrease (negative switching) as a function of prey abundance.

In the MSVPA, the expression for calculating the proportion of the food of a particular predator age group which constitutes of a particular prey age group becomes:

$$\begin{aligned} \text{Food comp.} \\ &= aN^b * N^*w / \text{SUM}_{\text{over prey}}(aN^b * N^*w \\ &+ a*(\text{Oth. food})^{b+1}) \end{aligned}$$

where w is the average body weight at ingestion of the prey age group within the quarter and Oth.food is the biomass of other food. The equation may be solved with respect to the constant a :

$$\begin{aligned} a &= (\text{Food comp.}/w * N^{b+1}) / \\ &(\text{Sum}_{\text{over prey}}(\text{Food comp.}/w * N^{b+1}) + \\ &\text{Food comp.}(\text{Oth. food})/\text{Oth. food}^{b+1}) \end{aligned}$$

Given b it is thus possible to estimate the constant a within the MSVPA for each predator species age group prey species age group combination.

However, some care is needed when interpreting the results. Introducing switching in the MSVPA may introduce a situation where the MSVPA equations for estimating $M2$ do not have a just one solution, but three, two stable and one unstable (Hildén 1988). Whether or not a unique solution is present will depend on the value of b . Extreme values are most likely to result in non-unique solutions.

4.3 Results from the Introduction of Switching in the MSVPA: The North Sea

In order to evaluate the data from the North Sea and the Baltic for the existence of switching phenomena, the MSVPA was run with various values of b . The objective was to test values in the range -1.0 to 1.0, but that was not possible. For high and low values of b the $M2$ iteration failed to converge, probably caused by the existence of several solutions. For the North Sea it was possible to run the model with values between -0.6 and

0.4 and for the Baltic the values tested were between -1.0 and 0.4

The test for switching was a study of the concordance between estimated and observed stomach content. For cod, whiting and saithe stomach content data are available for several years. This allows the computation of a mean suitability and a prediction of stomach content. The sum of squared deviations between observed and estimated stomach content was the goal function in the test.

The optimal test would be to run the model when each predator prey interaction was assigned a series of values of switching, all other interactions being fixed. This would produce a landscape of sum of squared deviation values in a n -dimensional space, the task being to find ridges in this landscape. For practical reasons, however, it was not possible to test that number of runs so for all runs the same value of switching was assigned to all predator prey interactions.

The stomach content of a given prey species prey age is given as a weight proportion of the average stomach content of a given predator species predator age. By multiplying with the average stomach content, the weight of the prey in the stomach is obtained. If this number is divided by the weight of the individual prey at ingestion, the number of prey items in the stomach is obtained. Both values for stomach content was used in the computation of the sum of squared deviations. In both cases the number was weighted with the number of stomachs sampled.

During the test it became obvious, that the use of the number of prey items was less desirable since division with some 0-group weights gave extremely high values and deviations. So only the squared deviation on weight basis was tested.

Figure 4.1 shows the results for the North Sea for the predators cod, whiting and saithe with all prey items pooled. For cod and whiting it is seen, that a value for the degree of switching around -0.5 produces a minimum in the sum of squared deviation. This is not the case for saithe. In Figure 4.2 (a) all predator species are pooled, but the contribution to the sum of squared deviations are split on prey species. Herring and *N. pout* gives high contributions, especially at high degrees of switching. The presentation has the weakness that important prey species gives high loadings, thus covering the contribution of less important species. This is taken into account in Figure 4.2 (b) where the contribution of each prey species is normalized by division with the sum of the contribution over all values of switching. It is seen that some prey species reach a minimum value for the sum of squared deviation for switching degree -0.5, while others do not.

In order to further investigate the deviations between the estimated and observed stomach content the distribution of the differences were computed. The difference on weight basis makes comparison between predators difficult due to differences in rations. Instead the relative difference were computed as the difference between the estimated fraction and the observed fraction that a prey item would constitute of the stomach content. The results are shown in Figure 4.3 a-c. The distribution is expected to be symmetrical around 0.0, but for increasing degree of switching, the distribution is more skewed with a clear left hand tail.

To check the models concordance with IYFS index a series of correlation analysis were done on the model $\ln(MSVPA) = a \cdot \ln(IYFS) + b$ for various degrees of switching. For the 1 year old year class the results are shown in Table 4.3. The R^2 value is in general unchanged and independent of the degree of switching.

4.4 Results from the Introduction of Switching in the MSVPA: The Baltic Sea

Parts of the exercise was repeated on data from the Baltic. Plot of the sum of squared deviation are shown in Figure 4.4 (a) and (b) [comparable to Figure 4.2 (a) and (b)]. For the Baltic the introduction of switching in the MSVPA is of no significance. The sum of squared deviations has a minimum in 0.0, indicating no switching. The introduction of switching makes no difference in the prediction of the stomach content, except for sprat at high values.

The distributions of deviations are shown in Figure 4.5 (a) to (c). It is seen that switching introduces skewness in the distribution.

4.5 Conclusions

It can be concluded that the introduction of a moderate degree of negative switching in the MSVPA for the North Sea can improve the model in terms of increasing the concordance between observed and estimated stomach content.

It is, however, not possible to make any behavioral interpretation of this, since we have no way of distinguishing 'behavioral switching' from the other causes to apparent switching. However, if the observed switching was of behavioral nature, it would probably be positive.

Among the alternative explanations mentioned in the introduction, the apparent switching might first of all be the result of changes in spatial coincidence between the predator and the prey or be a mathematical artefact. Further development in area based models might elucidate that.

In terms of prediction of recruitment in the historical analysis, the introduction of switching gave no improvement.

For the Baltic the MSVPA will not improve by the introduction of switching. One explanation could be that local variations in abundance at least partly is taken into account by the division of herring into two separate stocks.

5 DESCRIPTION OF DATA SETS FOR COMPARATIVE FEEDING STUDIES

5.1 Introduction

Apart from modelling approaches used to test hypotheses of feeding interactions, there is much potential insight to be gained from empirical analyses of stomach content data. Several properties of the feeding data are critical to the MSVPA modelling project: is the total feeding level constant? Are the variance properties stable, and of such a magnitude that tests of changing feeding levels are estimable? Do results from empirical analyses shed any light on tests of the assumptions of constant suitability?

For all systems, the intercomparison of feeding data may be important in revealing underlying processes that may be generalizable and thus form the basis of models that may be used widely. In boreal systems, the scope for compensatory feeding on other prey types when capelin biomass is low is of primary concern. Likewise, the effects of year, temperature and quarter (as aliasing spatial overlap among predators and prey) on total stomach constant are important, but have not been quantitatively evaluated, in most cases. Additionally, there are technical questions on the effects of bulking of stomach samples on the estimation of statistical properties of feeding data.

The Study Group on the Analysis of Feeding Data (Anon. 1992a) proposed a wide range of testable hypotheses to be considered with intra- and inter-system data sets. Because of its ubiquitous distribution and economic importance, cod, *Gadus morhua*, was considered the primary species for comparison. That group also identified data sets on North Sea Whiting and two hake stocks as being useful for comparison. Because of the diversity and intensity of analyses undertaken for cod, it was not possible to extend these analyses to the other stocks. These data are described however, in Section 5.8.

Feeding data sets constructed for these analyses are reviewed in detail in Sections 5.2-5.8. For cod, six data sets were available (Figure 5.1; Table 5.1). These data sets include three that are collected in a bulking scheme (North Sea, Baltic Sea, Iceland) are three collected as individual predator stomachs (Barents Sea, Newfound-

land, Northeast USA). Data were made available in a common aggregated format as provided by the Study Group on Analysis of Feeding Data (Anon. 1992a). A total of 96,728 feeding records, representing 200,635 cod predator stomachs were included in the common data set.

5.2 North Sea

The North Sea is relatively shallow. The southeastern part is generally less than 50 m, whereas the northern North Sea is between 60 and 200 m up to the shelf edge. The mean quarterly temperatures range between 6-10° in the northern and 3 - 16° in the southern North Sea.

Cod is widely distributed over the entire North Sea. However, distribution patterns vary with age and between years. Spawning takes place in January through March over wide areas including the southern Bight. However, the large cod seem to avoid high temperatures and leave this area in summer. Tagging experiments have shown that migrations within the North Sea are limited in extent and that there is little exchange between the southern and northern North Sea. Some mixing occurs in the Channel, Skagerrak and around the coast of Scotland. Although pelagic 0-group cod are widely dispersed, the highest concentrations of 1-group cod are generally found along the continental coast.

Stomachs have been collected during all quarters of 1980, 1981 and 1982 and in the 1st and 3rd quarters of 1985-1987 (Table 5.2.1-3). Most of these samples have been collected during research vessel cruises aimed at estimating the spatial distribution and abundance of demersal fish. However, these collections have been supplemented by samples taken on board of commercial vessels. In 1980 and 1982, sampling was only carried out by the Netherlands and the surveys were restricted to the southern North Sea, whereas in 1981 and 1985 - 1987 the sampling was internationally coordinated over the entire North Sea. In addition data are available from a diel sampling program within a restricted area in the 2nd quarter of 1984. These data are not representative for the North Sea cod population.

The surveys followed a stratified random sampling scheme, where the strata were defined as ICES rectangles of 30*30 miles. The catches were sampled for length and age distributions and sorted by predefined size categories. In 1985, the size classification was changed. Full details of the sampling procedures have been described by Daan (ed. 1989) and Anon. (1992b).

Everted stomachs were dismissed straight away. If there were more than 10 fish in a size category, a maximum of 10 fish were selected at random. Otherwise all fish were included in the sample. All fish were opened and the stomach contents were preserved as a bulked sample

in a jar with formalin. Although the number of animals in the sample showing evidence of regurgitation were recorded, these contents were not included in the sample. The number of regurgitated fish (which had obviously been feeding) were used as a correction factor for estimating the average amount of fish actually feeding and the average stomach content weights. Also the numbers of entirely empty stomachs were recorded. In 1984, all fish caught were sampled and the stomach contents stored in individual jars with records of the cm class. The size frequency distribution of all the specimens included in the data base is given in Figure 5.2.

The contents of the jars were washed and screened before they were sorted by prey category and size category in the laboratory. All fish were identified to the species level if possible and for other prey also as far as practical. Weights (in 0.1 g) and numbers were recorded by prey size category.

Most countries collect hydrographical data during their surveys, but these data were not made available for incorporation in the stomach content data base. However, they have been stored in the ICES hydrographical data base and it should be possible to extract these data in due course and combine them in the data base.

From the internationally coordinated surveys, the average catches of the numbers by size class by statistical rectangle have been calculated and incorporated in the stomach content data base in order to weight the samples collected according to the catch rates.

5.3 Baltic Sea

An international cod stomach data base has been established at the Danish Institute for Fisheries and Marine Research (DIFMAR) on the initiative of the Working Group on Multispecies assessment of Baltic Fish.

The purpose of the data base is to facilitate the compilation of cod stomach data for use in the MSVPA model for the Baltic Sea (Anon. 1989b; 1990b). However, the data base contains more information than needed by the MSVPA model and can be of value in other connections too.

The data base contains stomach data sampled by Denmark, Finland, Germany, Poland, Sweden, and USSR from Sub-divisions 22, 24-30, and 32 for the period 1977-1990. In total, about 50,000 stomachs have been analyzed and are reported to the data base. Around 40,000 of these have been reported from Sub-divisions 25, 26, and 28 (Central Baltic Sea; Tables 5.3.1 to 5.3.3). The data in the data base are aggregated by country, year, quarter, sub-division, and cod length group (Anon. 1992c; Degnbol 1992).

Digestion stage A items are reported in 1-cm units and digestion stage B in the length groups <11 cm, 11-19 cm, and >19 cm.

Unfortunately, the data are not totally standardized and compilation of data is therefore difficult. Differences between countries exists as regards the length grouping of cod, the length unit used for preys, and the identification level used for the digested preys. Today the standardization has improved so that the data from later years and, hopefully, also the data, which in the future will be reported to the data base, will be much easier to compile. The size distribution of cod sampled for stomach contents is given in Figure 5.3.

Often more than one gear type have been used for collection of the material. Bottom trawls are the most commonly used sampling gear, followed by pelagic trawl. Gill nets have only been used for sampling of a minor proportion of the stomachs.

Some preliminary analyses have been made (Sparholt et al. 1991) with the primary aim of showing the possibilities in the data, of giving a broad description of the food habits of cod in the Baltic Sea, and of detecting problems in the data such as systematic differences between countries due to, for instance, differences in the working up procedure used when analyzing the stomach contents.

Details about formatting of the data base for the present purpose are given in Anon. (1992a).

5.4 Barents Sea

Description of system

The Barents Sea is a high latitude ecosystem, extending from the coast of Northern Norway (70°N 20°E) north to the western coast of Svalbard (80°N 10°E) and east to Novaya Zemlya (55°E). It covers about 1.5 million km². The system is characterized by relatively warm currents with Atlantic water from southwest and cold currents with temperatures below 0 from northeast. The main depth-range is 100-400 m. There are relatively few species in the system, cod being one of the major predators and capelin the most important fish prey, both for cod and some other predators, e.g. harp seal. Cod and capelin are also the two most important commercially species in the system.

Years and quarters of sampling

A multispecies model for the Barents Sea (MULTSPEC) is being constructed with basis in the cod-capelin system. An essential requirement for the model is quantitative data on the cod stock's food selection, and a stomach sampling program has been running since 1984. The aim

has been to sample most size or age groups of cod over the main area of distribution throughout the year. Norway and Russia have cooperated in sampling and exchanging stomach data since 1987 (Mehl and Yaragina 1991). Quarter 1 and 3 are best covered with samples (Table 5.4). [Most of the stomachs sampled in quarter 4 were inadvertently placed in quarter 3 when transferred from the Norwegian data base. It was not possible to correct this during the meeting, and therefore analyses of quarterly effects using these data should not be considered definitive.] The last part of quarter 1 and the first part of quarter 2 is the spawning season for both cod and capelin. Mature cod will be outside the system for a part of this period, and mature capelin will migrate through the area where immature cod is distributed, and is therefor eaten in large amounts by medium sized (30-60 cm) cod. In the second half of the year the capelin stock is feeding in the northern part of the Barents Sea, and mature cod to some extent migrates northwards to feed on capelin. Immature cod have east-west migrations, being further to the east during summer-autumn.

Source of stomachs

All the samples have been collected on board Norwegian and Russian research vessels during routine surveys in the Barents Sea and the Svalbard area. The gears used are both pelagic and bottom trawl, but the bulk (>95%) of the samples are taken by the latter. The stations might be fixed, stratified random or made on basis of acoustic information (Bogstad and Mehl 1992).

Stomach sampling protocol

The stomach sampling strategy has been adjusted to the two countries' survey programs. On Norwegian surveys, the aim has been to collect up to 5 individual stomachs of cod for each 5-cm length group on stations with other biological sampling (otoliths etc.). At least 1 station within each stratum is sampled, but normally 2-3 stations are sampled. Figure 5.4 shows the length frequency by predator length group midpoint. Fish which shows signs of regurgitation is replaced by non-regurgitating feeding fish. Based on the work by Bogstad et al. (1991) now (from winter 1992) only 2 stomachs are sampled within each 5-cm length group, but more stations (4-5) are sampled within each stratum.

Stomach examination protocol

The methods used for stomach analysis and data recording are mainly the same as for the ICES 'Stomach Sampling Project 1981' in the North Sea (Anon. 1980; 1981). Norwegian and Russian modifications are described in Anon. (1974), Westgard (1982), Mehl (1986) and Tretyak et al. (1990). All stomachs are analyzed individually, and for most Norwegian data the predator's length, age, weight, sex and maturity stage is

recorded. Fish prey and crustaceans are identified to species level when possible. Each prey category is split into size classes and then for each size class the weight (to the nearest milligram for small prey), numbers and digestion degree is recorded.

Temperature

On Norwegian surveys temperatures are normally taken at individual trawl stations, but being stored in a different data base than the stomach contents data, it has up to now been difficult to merge the two data sets. The temperatures in the present data set is therefor calculated in the same way as in the MULTSPEC model, based on data from standard hydrographical sections (Alvarez and Tjelmeland 1989; Bogstad and Mehl 1992). The temperature range is 1.5-3.4° C.

CPUE

The CPUE for the Norwegian data is calculated as the number of fish caught per hour of the actual 1-cm group. The CPUE for the Russian data is unknown.

5.5 Iceland

Description of system

The Icelandic cod stock is distributed more or less over the entire continental shelf around Iceland to depths of approximately 500 meters. The main part of the stock spawns at the SW-coast during March-May and migrates from other areas around Iceland and Greenland to this area. These migrations coincide roughly in time and space with migrations of spawning capelin. The main nursery grounds are off the northern and the eastern coasts. The growth of cod varies considerably with respect to the hydrographic regime, showing lower growth rates in the nursery areas compared to the southern areas.

Years and quarters of sampling

The bulk of the material was sampled on research vessels and some additional material on commercial trawlers. Sampling was most extensive in area and most continuous in time in the 1st quarter of the year. A total of 38210 stomachs were sampled in 9364 samples in 1979-91 (Tables 5.5.1 and 5.5.2; Pálsson 1992).

Source of stomachs

The stomach material was obtained by bottom-trawl from a predefined ground fish survey scheme. Prior to 1985 this was a fixed station scheme (Pálsson 1984), whereas since 1985 a semi-stratified random approach was used (Pálsson et al. 1989).

Stomach sampling protocol

Stomach sampling was stratified with respect to sub-areas. During 1980-84 9 sub-areas were defined in the sampling area north and east of Iceland. During 1985-91 18 sub-areas were defined for the continental shelf waters around Iceland.

The decision to sample on a specific station has not been a random one, but rather related to where an entry into a new sampling area occurred, the amount of fish in a haul as well as the number of stomachs to be sampled. Other work to be carried out on a specific station has also influenced the stomach sampling protocol.

The prescribed number of stomachs per sub-area has been 10 stomachs per cod length group. Prior to 1989 this number was sampled on one station if the amount of fish was sufficient. Otherwise the lacking numbers were sampled on following stations. Since 1989 a maximum of 5 stomachs has been sampled on any one station in order to increase the spatial coverage of the sampling. Additional samples have been taken from hauls larger than approximately 250 kg of cod per nautical mile towed.

The length groups sampled are as follows in centimetres: 5-6, 7-9, 10-14, 15-19, 20-24, 25-29, 30-39, 40-49, 50-59, 60-69, 70-79, 80-89, 90-99, 100+. The stomachs in each predator length group have been bulked on each station. Fig. 5.5 shows the sampling intensity by length groups.

Stomach examinations protocol

Fish prey and commercial species are identified to species level when possible. Number of each prey is counted and the total weight of each prey type in a sample is recorded to the nearest decigram. The length of fish prey and commercial species is recorded and stored in a separate file. Stage of digestion has not been recorded.

Temperature

Prior to 1985 near-bottom temperature was measured on most stations sampled by means of reversing thermometers. The temperature was calculated by standardized hydrographical methods. Since 1985, however, temperature has been obtained by means of Scanmar sonde mounted on the headline of the trawl. The Scanmar sondes were calibrated with respect to reversing thermometers.

Calculation of CPUE

The CPUE for a given length group (l) was calculated for a standard haul of 4 nautical miles as follows:

$$CPUE(l) = Nm(l) + ((Nm(l)/Nm) \times Nc) \times 4/n.m.$$

Nm = Number of fish measured in a haul

Nc = Number of fish counted in a haul

n.m. = nautical miles towed

5.6 Newfoundland

General comments

The cod stock occupying the southern Labrador Shelf and the Northeast Newfoundland Shelf (Northwest Atlantic Fisheries Organization Div. 2J+3KL) tends to be aggregated on the outer part of the shelf and the upper continental slope in winter and early spring, and moves over the shelf in late spring and summer. A portion of the stock migrates into shallow coastal waters to feed intensively on capelin for 6-8 weeks in summer. The stock is usually spread over the shelf in autumn. Feeding intensity at this time is thought to be intermediate between the intensive feeding experienced by a portion of the stock in summer and a very low level of feeding experienced by most of the fish in winter and early spring (Lilly 1987). Spawning occurs primarily near the shelf break in March-April. Many young spend the first 2-3 years of life in shallow coastal waters before moving onto the banks. Growth rate is a little higher in Div. 3K than in Div. 2J. The continental shelf in this area is broad and deep. The Labrador Current, which flows southeastward along the shelf, is coldest toward the coast. Temperatures below 0° C are found to depths of about 200 m in most years. Maximum bottom temperatures in the survey area are about 4°.

Years and quarters of sampling

Stomachs were collected in the northern divisions (2J,3K) during research bottom-trawl surveys in the fourth quarter (generally early November to mid-December) in 1978 and 1980-1991 (Table 5.6; Lilly and Shelton 1992).

Stomach sampling scheme

Fishing stations were allocated randomly within depth strata with a new station selection being conducted each year. Doubleday (ed. 1981) provides illustrations of the strata and information on their sizes and depth ranges. Prior to 1991, the number of stations allocated to each stratum was roughly proportional to the size of the stratum, but in 1991 the number of stations assigned to each stratum was selected so as to minimize variance as observed during surveys in earlier years. Thus, the

number of stations per unit area varied considerably among strata. Additional detail on the survey pattern is provided in Lilly (1991). In all years, fishing was conducted on a 24-h basis. The stomach sampling request in 1978 called for a stratified-random sample of up to 5 cod per 10-cm length group to be taken from the catch at every station. The sample size was reduced to 3 per 10-cm length group for 1980-1982, and changed to 3 per 9-cm length group in 1983-1991 so that the size categories would be multiples of the 3-cm size categories used to describe the length frequency of the catch. The length frequency distribution of the specimens included in the present data base is provided in Fig. 5.6. Stomachs were not collected from fish which showed signs of regurgitation. Stomachs were individually tagged and excised, and fixed and preserved in 4% formaldehyde solution in seawater.

Stomach analysis

Stomachs were opened in the laboratory. Fish and decapod crustaceans were identified to species, but most other groups were combined into higher order taxa. Items in each taxon were placed briefly on absorbent paper to remove excess liquid, and then counted and weighed to the nearest 0.1 g.

Temperature

The temperature provided is the near-bottom temperature measured at the station at which the specific fish was caught. There are some missing values.

CPUE

There were two levels of sampling. Fishing stations were selected on a stratified-random basis, and fish were selected for stomach collection and analysis on a stratified-random basis within stations. The CPUE provided with the stomach content data was the catch (number) per standard 30 min tow in the station and 9-cm length group from which the specified fish was taken. This index lacks information on nil catches and size of stratum. An alternate CPUE, available in a separate data set, is an index of population size by year, stratum, and predator 9-cm length group, where the population index was estimated by areal expansion of the mean catch (number) per tow. Two such indices were provided: one derived from the arithmetic mean catch per tow and the other from the mean of $\log_{10}(\text{catch} + 0.5)$.

5.7 Northeast USA

Description of system

The Northeast USA is a low latitude system, extending along the continental shelf from 35°-45° longitude, and 65°-76°W latitude. Two main Atlantic cod stocks are

recognized in this system: Georges Bank and Gulf of Maine. Some samples from the Scotian Shelf stock have also been included. The system undergoes wide seasonal temperature fluctuations (Murawski and Mountain, 1990), resulting in changing distribution patterns of various prey species in relation to cod distribution. Prior studies of feeding of Atlantic cod in the region are summarized in Langton and Bowman (1980).

Year and quarters of sampling

Feeding data have been collected off the northeast USA in a variety of formats since the 1960s (Anon. 1992a). For the purposes of comparative analysis, the most consistent sub-set are those data available from 1981 to present. However, since data from 1989-1992 have not been completely audited, the set includes the years 1981-1988. Numbers of fish sampled by year and quarter are given in Table 5.7 (Overholtz and Murawski 1992).

All data were collected aboard research vessels. In the spring (generally March-May) and autumn (September-November), routine bottom trawl surveys are conducted, and food habits collections are a part of the standard protocol. Additionally, in four years (1984-1987), special food habits collections were made in the summer months (July-August) on Georges Bank, as part of a juvenile fish ecology program.

Stomach sampling protocol

During standardized spring and autumn surveys, fish were collected within the stratified random sampling plan. Sampling quotas were established for each 6-hour watch, by fish size. More recently these quotas have been changed to a station-by-station, rather than watch-by-watch basis. Following are the sampling quotas in force for spring and autumn trawl surveys during 1981-1988:

Atlantic cod

Length categories	Minimum number per watch
1-30 cm	5
31-50 cm	10
51-70 cm	15
71-90 cm	15
> 90 cm	All

The size composition of cod sampled for stomach content is given in Figure 5.7. Sampling during summer surveys was done on a station-by-station basis, since

these cruises were directed at feeding ecology studies. For some early years, a number of cod stomachs from Georges Bank was preserved for later analysis ashore, and are not included in the data sets.

In all cases, data were recorded at sea, using a series of volumetric measurements of stomach contents. Where feasible, individual prey items were enumerated, and the volume (in cc³) determined with the aid of graduated dowels. In all cases data were obtained on an individual predator basis: no bulking of samples was employed. In order to convert stomach content volumes to weights, we used the following empirical conversion: weight (grams) = 1.1 * volume (cc³). This conversion is based on data for silver hake (Bowman 1982), and is supported by recent information provided by G. Lilly (pers. comm.). Mean weight:volume ratios for various prey consumed by cod were: capelin = 1.07, crab = 1.08, shrimp = 1.07.

Temperature data were collected from most trawl tows using a bucket thermometer for surface, and an XBT for bottom temperatures. In principal, CPUE from the research vessel catches associated with the stomach sampling could be used to weight the sampled to the proper sampling intensities. However, since some quarters were not sampled with standard survey protocols (e.g., during summer sampling), CPUE data were not included in the current data set.

5.8 Other Feeding Data Sets

Apart from the six cod feeding data sets described above, two feeding databases were available at the meeting: North Sea whiting and silver hake from the N.E. USA shelf. A data set on hake sampled from ICES Area VIII was partially analyzed outside the meeting.

Although not feasible at the meeting, analysis of the North Sea whiting data set is considered important in the development of MSVPA. Disparities in the mean total stomach content weight between the 1981 and 1987 feeding data sets were down to have potentially large effects on annual estimated consumption by the whiting stock (Anon. 1991a). However, data for years other than 1981 covered only a few year/quarter cells. The 1991 stomach data, when available, will allow more complete investigation of this problem. The feeding data set available for North Sea whiting consists of 2,755 bulked records, representing 21,342 individual predator stomachs. The average total stomach content was 3.14 grams (CV = 1.78). Average fish length (weighted) is 23 cm. The average prey composition of whiting stomachs consists of 88% fish, 7% crustaceans, and 5% of assorted other prey types. The average percent empty stomachs was 28%; substantially higher than for North Sea Cod (14%).

Hake data sets requested by Study Group on Analysis of feeding data are those for silver hake from the northeast USA, and hake from ICES Area VIII (Figure 5.8). The silver hake data set is included in the aggregated data set and some analyses of the hake data set were provided by I. Olaso (pers.comn.).

The size composition of animals sampled in Area VIII is showed to significantly smaller animals than off the northeast USA. In both cases fish was the predominant prey item, with crustaceans and molluscs accounting for most of the remainder. No firm conclusions can be drawn concerning the average stomach content weights among the systems, due to the lack of standardization to predator size. A common feature of hake stomach sampling is the large proportion of empty stomachs (presumably due to regurgitation): 55% for silver hake and 52% for Area VIII. Resultingly, the CVs of total stomach content weight are higher than observed for cod and whiting. In the case of silver hake the CV of non-transformed total stomach content was 3.55. These data clearly indicate the need for more appropriate statistical estimators for dealing with the problem of structural zeros in the analysis of feeding data (Section 9).

6 HYPOTHESIS TESTING WITH FEEDING DATA SETS

6.1 Statistical Analyses of Feeding Data Within Ecosystems

6.1.1 Treatment of data

Data sets analyzed were all drawn from the alldata.ssd data sets, as described in Section 5. Whiting data from the North Sea were deleted, as were North Sea data from 1984. Otherwise no cases were excluded a priori from all analyses. However, many of the multivariate statistical analyses deleted cases if data were missing for even one variable. Hence different analyses often used different numbers of cases from the full data sets. If a large fraction of cases were deleted in a multivariate run, due to missing values for one variable, the analyses were repeated excluding the problematic variable, so the pattern of variance in the larger number of cases could be examined.

For all MANOVA analyses, and all GLM analyses except the ones reported in 6.1.2.3, data were used at the finest level of disaggregation available: individual stomachs for Barents Sea, Newfoundland, and eastern US; bulked by haul for Iceland, Baltic Sea, and North Sea beginning in 1985; and by statistical rectangle for North Sea before 1984. Except in the exploratory GLM runs reported in 6.1.2, all cases were transformed prior to analysis, to approach assumptions of the statistical analyses more closely, and to have consistent biological

meanings. The first transformation was an allometric scaling - dividing the value of each type of food by $1/\text{length}^{**3}$. This should remove the basic size effect of larger fish having larger stomach volumes, and by expectation, greater weights of stomach contents. The allometric scaling created very small values (the denominator, length^{**3} is very large), so allometric scaled values were multiplied by 100,000 to return them to the general range of the original variables. Following the scaling, consumption variables were \ln transformed to reflect the lognormal distribution generally expected in diet data. Zero values had 1 mg of food added, so the \ln value was 0.0.

For all the principal component analyses, data were "bulkied". That is, for ecosystems where stomach contents were quantified individually, the mean of each variable by haul and 10 cm size category was computed (Appendix program 6.1.1). Where data were collected bulkied, the transformation could not be made on values of individual stomachs. Therefore for the other ecosystems bulkied variables were transformed AFTER bulkied, rather than transforming individual stomachs before bulkied.

To facilitate comparisons among results, stomachs from cod less than 20 cm and greater than 80 cm were deleted. For analyses when size was treated as a categorical variable the remaining cases were binned in 10 cm categories. When time of day was used in an analysis, it was also categorical (00:00-05:59, 06:00-11:59, 12:00-17:59 and 18:00-23:59).

6.1.2 Selecting core GLM model - exploring alternative formulations

6.1.2.1 Alternative models

Discussions identified several questions relating to the best models to use to test the hypotheses identified at the Study Group Meeting in Newfoundland. These included:

Should the consumption variables be scaled by allometric size?

Should the consumption variables be \ln transformed?

Should predator length be treated as a continuous or discrete variable?

If length is treated as a categorical variable, how many categories?

The 6 10 cm intervals between 20 and 80 cm give more opportunity to detect effects, but sample sizes in each interval will be smaller, particularly when further disaggregated by year, quarter etc.

The 3 categories 20-30, 30-50 and 50-80 would provide larger cell sizes, and might reflect comparable levels of change in diet across intervals.

If length is continuous, should models contain one overall term for size, as well as additional slopes for size effects nested under years, or only slopes nested under years with no overall slope? In the first case year effects would be measured by the significance of the nested slopes, given the common size effect had been removed. In the latter case, the overall presence of size dependent diets would be measured by the significances of the individual slopes, whereas differences among years in the size dependency of feeding would be tested by comparisons of differences among slopes.

The Newfoundland and North Sea data sets were chosen for tests of the alternative models. The Newfoundland data come from a boreal ecosystem, cover only a single quarter but for 13 years, and each record is from an individual stomach. The North Sea data are from a more temperate ecosystem, cover all quarters in at least some years, and each record is bulked over all samples within a length category, statistical rectangle, quarter and year. If models fit to both data sets showed consistent patterns, it was thought that valid general conclusions could be made about their relative properties.

Within each system, both Totalfish and Totalfood were fit with each model.

A total of 16 models were fit to each dependent variable:

- dep. var. unlogged, dep. var. unscaled, length continuous, nested slopes only -
- dep. var. unlogged, dep. var. unscaled, length continuous, common & nested slopes -
- dep. var. unlogged, dep. var. scaled, length continuous, nested slopes only -
- dep. var. unlogged, dep. var. scaled, length continuous, common & nested slopes -
- dep. var. logged, dep. var. unscaled, length continuous, nested slopes only -
- dep. var. logged, dep. var. unscaled, length continuous, common & nested slopes -
- dep. var. logged, dep. var. scaled, length continuous, nested slopes only -
- dep. var. logged, dep. var. scaled, length continuous, common & nested slopes -
- dep. var. unlogged, dep. var. unscaled, length discrete, 6 categories -
- dep. var. unlogged, dep. var. unscaled, length discrete, 3 categories -
- dep. var. unlogged, dep. var. scaled, length discrete, 6 categories -
- dep. var. unlogged, dep. var. scaled, length discrete, 3 categories -
- dep. var. logged, dep. var. unscaled, length discrete, 6 categories -
- dep. var. logged, dep. var. unscaled, length discrete, 3 categories -
- dep. var. logged, dep. var. scaled, length discrete, 6 categories -
- dep. var. logged, dep. var. scaled, length discrete, 3 categories -

6.1.2.2 Results

Results are tabulated in Tables 6.1.1a and 6.1.1b. In all cases more of the variance was captured in models which used ln transformed dependent variables than models fitted to unlogged values. Models with 6 categories performed better than models with 3, and variances of parameter estimates for categories did not indicate instabilities due to small sample sizes (Table 6.1.2). The allometric scaling of the dependent variable eliminated a very large amount of the variance explained by size, suggesting most of the size effect was simply allometric, and could obscure the search for other types of changes in diet due to size. Particularly for fits to scaled dependent variables, although year, quarter, and length effects were often significant, little of the variance in stomach contents was captured by any of the models. In the scaled categorical models, it was usually the diets of small sizes (20-30 and occasionally 30-40cm) which differed from diets of larger sizes; the larger sizes differed more rarely. The common and nested slopes models captured the same amounts of variance when matched on other features, but in the allometrically scaled fits, any small differences in size dependent diets among years were more apparent in the nested slopes model.

Based on those results, the following options were selected for model fits and hypothesis testing in all of the ecosystems:

- Include allometric scaling of dependent variables.
- Log dependent variables.

Fit a model with predator size as a continuous variable, with slopes nested under years.

Fit a model with predator size as a categorical variable with 6 levels.

6.1.2.3 Effect of scaling and transforming during bulking

If scaling or log transformation of the dependent variables was done, there are statistical reasons to transform before bulking. However, that was not possible for the North Sea, Baltic Sea or Iceland ecosystems, where stomachs were bulked as they were collected. Therefore the effects of scaling and transforming before and after binning were investigated with fits to the Newfoundland data. A number of differences between the runs were noted (Table 6.1.3). The differences are expected; logs of means differ from means of logs.

Scaling the means produces data which are fit slightly better by the same models, however, and the residual size effects are stronger in both Total Food and Total Fish. Had one been foolish enough to conduct all possible pair-wise tests of equality of the 13 least-squares estimates of means by year, only 1 of 169 decisions would have been different had scaling and transformation of Total Fish been done on the means rather than the individual observations. For Total Food, 6 of 169 decisions would have been different, with 5 fewer "significant" differences ($p < 0.001$) detected. Based on these contrasts, there seems to be no serious cost to scaling and transforming the means of the bulked data rather than the individual observations, whereas there is the noteworthy gain that "apples" can be compared to "apples" across ecosystems (or crustacea to crustacea), even if the apples are a bit bruised compared to statistically perfect fruit.

6.1.3 GLM Models

For each system two GLM models were tested, one where predator length was treated as a continuous variable and one as a class variable by 10 cm class intervals. SAS code for core GLM models is given in Appendix B. Completely empty samples (stomachs) were deleted. Samples with no fish but with other food were included as zero's after the log transformation. In the case where data were routinely collected on the time of day when the sample was collected, records without this information were deleted. Time of day was treated as a class variable of 6 hour intervals. The GLM models included, where possible, year, quarter, and time of day as independent variables and in addition year was nested under length. Where length was treated as a class variable, it was treated as an independent variable but the interaction term for year and length class was included in the model. There has been no discrimination between bulked

samples and individual stomachs, but a general weighting by sample size (1 in case of individual stomachs) was applied.

The basic GLM models tested were thus:

$$\begin{aligned} \text{StomachWeight} &= \text{Year Quarter TimeOfDay} \\ \text{PredatorLength(Year)} & \\ \text{StomachWeight} &= \text{Year Quarter TimeOfDay} \\ \text{LengthClass*Year} & \end{aligned}$$

For the North Sea no data were available on time of day for most of the years except for 1984, when samples were collected for a special study of diel variation in a restricted area. Therefore, the data set was split into two sets, one to investigate year and quarter effects and one to study the effect of time of day. In the latter case, time of day was nested under length class.

For the Baltic, no information on time of day was available for any of the samples and therefore this factor had to be deleted from the models.

All data from Newfoundland were collected in the 4th quarter and in this case the quarter was dropped from the models.

Table 6.1.4 summarizes the results of the models tested in terms of r-squared, F-ratio's and degrees of freedom for each of the 6 areas and for total food and fish food separately.

Year, quarter, length class as well as length nested under year and the year*length interaction term proved significant in all cases investigated. However, with the exception of the Baltic and Iceland only small proportions of the variance (below 10%) could be explained by the models. The values of r-squared for the two models within each area are generally very similar, although in general the length class models performed slightly better than the continuous length models. Particularly in the Baltic, the class model explained a good deal more of the variance. Also the time of day effect was significant was always significant except for the North Sea data set, where only the length class model for the amount of fish was significant. This appears also the only case where there is a large difference between the variance explained for total food (4-6%) and the amount of fish in the stomachs (13-17%). In all other cases, the differences between total food and fish food were only minor.

The fact that the models for the Baltic and Iceland explain considerably more of the variance might suggest that combining stomachs in bulked samples could influence the results. Although considerably lower, the results from the bulked samples from the North Sea are also higher than for any of the other systems where stomachs have been collected individually.

The models tested are still unsatisfactory to the extent that empty samples had to be deleted from the analysis and therefore the mean stomach weights do not accurately reflect feeding levels. Appropriate methods to take the empty stomachs into account should be further investigated. Although scaling stomach content weights by predator length cubed has reduced the explanatory power of the models (see section 6.1.2), there is still a significant length effect left. Therefore, possibilities for more appropriate scaling should be investigated.

6.1.4 MANOVA's

In order to investigate the effect of temperature on total stomach content weight and fraction empty combined, a multivariate analysis of variance was carried out for each system for which temperature data were included in the database. Records with no information on temperature were deleted. Stomach content weights were scaled to predator size according to the method described in section 6.1.2. Empty stomachs (samples) were included and treated as zero's after log transformation. Because it can be expected that the quarter effect is confounded with the temperature effect, quarter was excluded from the model. Three different temperature models were used. Firstly, the actual temperatures were used. Secondly, a standardized temperature by year and quarter was used by calculating the difference between observed temperature and the average temperature in that particular year and quarter divided by the standard deviation. Third, the standardized temperatures were classified according to 4 categories (< -0.67 ; $-0.67 - 0$; $0 - 0.67$; > 0.67).

The basic MANOVA models tested were thus:

StomachWeight FractionEmpty =
Year Temperature PredatorLength

StomachWeight FractionEmpty =
Year StandardizedTemp Predatorlength

StomachWeight FractionEmpty =
Year CategorizedTemp Predatorlength

These models were tested for no overall year effect, no overall Temperature effect and no overall predator length effect. A summary of the results is presented in Table 6.1.5.

Data on average quarterly temperatures by year and quarter were not available in time to include these systems in the comparative analysis, but will be extracted from the ICES data base. The year and temperature effect on fraction empty and total food was significant in all models tested. The length effect on total food was also always significant but the length effect on fraction empty was not significant for Iceland and the USA east coast. In general, however, the variance explained by

these models for the fraction empty is extremely low (less than 7% in all cases). The variance in total food are also low for the Barents Sea and USA east coast, but rather higher for Newfoundland and particularly Iceland. The fact that including the temperature in the model gives much more explanatory power (c.f. r-squared values in the order of 0.03 in Table 6.1.4) and the very high F-ratio for temperature appears to indicate that the temperature effect is particularly strong for the Newfoundland cod.

The overall effect of year and predator length on fraction empty and total food combined is significant in all models, whereas the overall temperature effect is significant for all models in all systems but the USA east coast, where only the actual temperature model is significant. Again the values of r-squared are low in most cases, but the values for the overall year effect at Iceland and for the temperature effect at Newfoundland stand out.

The results for the three temperature models applied vary between ecosystems. In the Barents Sea and the USA east coast, the actual temperature model explains generally more of the variance than the standardized and categorized temperature models. However, opposite and variable trends are present in other systems and it is not obvious which of these formulations is in general the more appropriate one.

6.1.5 Principal component analyses

6.1.5.1 Introduction

The GLM models asked the statistical question, how much variance in a dependent variable (amount of fish or total food consumed) can be explained by independent variables such as year, time, and predator size. Principal components analysis does not discriminate among dependent and independent variables. It asks the different statistical question, is the pattern of variation in variable x (say, a diet variable) similar to the pattern of variation in variable y (say, temperature) - for all of the input variables. With the low r^2 values of the GLM models variation in the dependent variables is not associated closely with the independent variables in the models. PCA should be informative in identifying what correlated patterns of variation do occur in the data.

The analysis comes with a USER WARNING, however. Principal components analysis is a powerful but coarse method for summarizing patterns in multivariate data. Results can be distorted by nonlinearities in associations, outliers in data sets, and other attributes of input data sets which aren't multivariate normal. Results can be informative, but should be used with discretion.

6.1.5.2 Data treatment

For each ecosystem, all individual diet variables were included. Total Fish and Total Food were not used, because they are linear combinations of other variables and would cause singularities in the data matrix. When available, depth, temperature, CPUE and mean length of the bulk unit were all included as well. The environmental variables were not transformed. Depth and temperature were not available for the North Sea. Depth, temperature, and CPUE were not available for the Baltic Sea. Temperature was not usable for eastern USA cod. For the other systems all environmental variables were available. Weight of Capelin was only available for the boreal ecosystems.

6.1.5.3 Results

A summary of the PCA results for all system is presented in Table 6.1.6, with more information on the component structure of each system in Tables 6.1.7a-f. Although each system had 3 or 4 eigenvalues > 1.0 , the largest eigenvalues were not particularly large, and together the eigenvalues > 1.0 rarely captured even half the variance in the system. Communalities of the diet variables are generally modest (< 0.5), particularly for ecosystems where all the variables were available. A great deal of the variability in the diet variables is apparently noise, consistent with the GLM results, and results of fitting suitabilities to diet data at previous meetings of the Working Group.

Of the patterns which were present in the higher components, there were marked similarities among ecosystems. When depth and temperature were both available, they generally weighted together, and usually on PC 1. However, diet variables were quite weakly associated with the temp-depth axis and the patterns differed among Barents Sea (weak positive association with capelin), Iceland (even weaker negative association with capelin, and Newfoundland (modest negative association with crustaceans).

In every ecosystem except Newfoundland and the Baltic, there was a strong inverse association between predator length and feeding on crustaceans. In Newfoundland the crustacean diet was more strongly associated with temperature, but the other diet variables reflecting feeding on invertebrates were all inversely associated with length. In the Baltic it was Other Food that was associated with predator size, and crustaceans in the diet varied inversely with fish in the diet. Only on the North Sea was predator size associated with feeding on fish, as well as (inversely) on crustaceans. In the other ecosystems, the variables reflecting fish in diets generally covaried among themselves, but generally lacked strong associations (positive or negative) with other aspects of diet or environmental variables.

Each case (haul or statistical unit by quarter and year) can be positioned on each component, and the scores analyzed further. Figures 6.1.1 show mean (a,c) and standard deviations (b,d) of cases averaged over 10 cm intervals. For a & b the factor in each system relating size to invertebrate feeding is graphed; for c & d the factor best reflecting feeding on fish. Several noteworthy patterns are apparent. In each ecosystem scores were multiplied by the sign of the component weight of predator length, so any influence of size should increase along the y axis. This means feeding on crustaceans (or other invertebrates for Newfoundland and Baltic) is highest when scores are low.

The strong effect of size on feeding on invertebrates is apparent in 6.1.1a. The size effect is much stronger in the relatively temperate ecosystems (North Sea, Baltic Sea, eastern US), than for boreal systems (Barents Sea, Iceland, Newfoundland). Although the mean scores change less for the boreal systems, the variance in scores goes up markedly with size, particularly for Newfoundland and the Barents Sea. The scores of the largest size group in the Baltic are much more variable than all the other sizes groups of that system.

Mean scores of the component best reflecting fish in stomachs increase with predator size for most of the systems, but generally at a much slower rate (Fig. 6.1.1c). The exception is the North Sea, where it is the same component on both 6.1.1a and c. The tendency for variance to increase with size is also present in the component reflecting feeding on fish, but again, generally more weakly than in the component reflecting feeding on invertebrates.

Figures 6.1.2a-f display the scatter plot of cases on the fish (X) and invertebrate (Y) feeding axes, stratified by size category for Newfoundland. Viewed in sequence, the series of figures display clearly how the average diets (whatever "average diet" is) of cod in Newfoundland changes with size, and overall feeding domain expands.

Mean scores can also be graphed by year (Figs 6.1.3a-b - note the signs are arranged so high scores reflect strong feeding on fish [a] or invertebrates [b]). Some noteworthy patterns are apparent. For early years of the time series in Newfoundland cod appear to have had poor feeding overall, with relatively low scores on both axes, compared to more recent years. A similar period of poor feeding is apparent in Iceland in the mid-1980's, with improvements, particularly in fish late in the decade. A change away from fish and toward invertebrates early in the decade is suggested for cod diets in the Baltic Sea with the change tending back towards fish in recent years. From component scores in Barents Sea, it appears that in the mid 1980's feeding was largely on invertebrates.

6.1.5.4 Summary

The PCA appears to be quite successful in partitioning independent trends in diet from the feeding data sets. Many similarities in these patterns appear across the 6 ecosystems. It is noteworthy that, except for the Baltic and North Seas, it seems that feeding on invertebrates, particularly crustaceans, and feeding on fish are not inversely associated, but are independent trends. The former is more strongly size dependent than the latter. The principal component analyses are a broad exploratory tool, and results could not receive detailed examination at the working group. The results do indicate further, more detailed analyses of these data are justified, and are likely to provide useful tests of many of the hypotheses formulated at the meeting of the Study Group.

6.2 Statistical Analyses of Feeding Data Among Ecosystems

6.2.1 Growth data

Survey data were available giving length at age for each of the areas discussed in Section 5. Table 6.2.1 describes the year and age range of each length data set used and their sources. For the Baltic Sea, Gulf of Maine and Georges Bank, only mean lengths at age across several years were available. For the other areas, lengths at age were available by year. All age data were corrected for the time of year when the respective surveys took place.

Where necessary, lengths at age across all years were calculated by area and plotted against age for all areas (Figure 6.3.1). This was done to contract gross, average growth across systems and is not intended as a dynamic model of cod growth for any of the areas. No effort was made to fit smoothed or parametrically estimated curves to the data. Instead, systems were contrasted by dividing the data into 10 cm length classes, corresponding to those defined in Sections 6.1 and 6.2. The mean age of fish within each length class was calculated and used as a measure of the average length of time taken by cod within each area to reach the mid-length of each length class. Results are given in Table 6.2.2. On a few occasions it was necessary to interpolate between mid-length values in order to fill in for missing values. In these cases the relationship between mid-length and age was taken to be linear for adjacent length classes. The mean age per length class was then used as a categorical variable in subsequent analyses.

6.2.2 Comparative prey weights

The six cod stomach data sets provided an opportunity to look at effects among ecosystems, for example using GLM. Analyses were carried out primarily on the natu-

ral logarithm of the mean bulked total stomach weight after scaling by length^3 over a cod length range of 20-80cm. Samples were bulked according to 10cm cod length classes within hauls or strata and the natural logarithm of the mean total stomach weight scaled by length^3 was calculated (see Section 5 for details) in order to obtain an independent variable for analysis using general linear models. This process resulted in an independent variable that was reasonably symmetrically distributed for the Barents Sea, Newfoundland and NE USA (initially unbulkied data sets), whereas the distribution of values for the North Sea, Baltic Sea and Iceland (initially partially bulkied data sets), remained positively skewed (Figure 6.2.2-7). The effect of the bulking carried out on initially partially bulkied data to combine samples into 10cm length classes in cases where the initial bulking was on a finer scale, to group samples not already grouped into strata for the North Sea and Baltic Sea, and to group hauls not already bulkied for a trawl for Iceland (this is non-trivial and should be checked).

Several main effects models were examined to explain variability in mean total stomach weight. Two models of the logits of the proportion of empty stomachs were also considered. An ecosystem effect (Model 1) was significant and accounted for 18% of the variability in the data (Table 6.2.2). The predicted values are shown in Figure 6.2.8. The mean total stomach weight is lowest for the Baltic Sea and highest for Newfoundland. An ecosystem effect on the logits of the proportion of empty stomachs was also significant (Model 2, Figure 6.2.9). The expected values mirror those obtained for Model 1, with the exception of values for The Barents Sea and Iceland. The expected stomach weight was higher for the Barents Sea than for Iceland, whereas the expected proportion of empty stomachs was also higher.

Although the measure of stomach weight used in the analyses is scaled by length^3 , it is possible that a residual length effect remains. This was examined in Model 3. Length explains less than 1% of the variability in mean scaled stomach weight, but because of the large sample number, is a significant effect. Length had the biggest effect on scaled mean total weight for the 40-60cm cod length range (Figure 6.2.10).

Using mean age at 45cm for each ecosystem (Model 4), i.e. an ecosystem effect, obviously explained the same amount of variability as Model 1. What is of interest is the relationship between the expected value and mean age at 45cm (Figure 6.2.11). There is a tendency for the mean weight to be higher in systems in which cod grow slower (Newfoundland, Barents Sea) and lower in systems in which cod growth faster (North Sea, Iceland). The value for the Baltic Sea is not in keeping with this pattern - here slow growing fish have a low stomach weight. It is possible that this discrepancy could be accounted for by including temperature at the trawl or

stratum, however temperature data were not available for either the Baltic Sea or the North Sea at the meeting.

Temperature effects were examined for those ecosystems for which values were available at the meeting. With respect to mean stomach weight (Model 5) there was a significant negative slope with temperature (Figure 6.2.12), whereas with logits of the proportion empty (Model 6) the slope was significant and positive (Figure 6.2.13).

If the temperature effect is first removed from the mean total stomach weight, then a large proportion of the residual variability can be explained by a growth effect (mean age at 45cm) for those systems for which temperature was available (Model 7). Further, the pattern of increasing stomach weight with decreasing growth rate is clarified (Figure 6.2.14). It will be of considerable interest to be able to account for the temperature effect in the North Sea and the Baltic Sea and to add these data points to the plot. Removing the length effect from the mean total stomach weight (Model 8) results in only a weak ecosystem effect in the residuals, rather than a stronger effect as that which occurred in the case of temperature (see text table below). The pattern of ecosystem effects is similar to that which was obtained in Model 1, with the exception that the expected mean total stomach weight for the North Sea is now lower relative to before, and the value for the Baltic Sea is somewhat higher (Figure 6.2.15).

GLM model fits are summarized below. Note, 'Tot wt' refers to the logarithm of the mean bulked stomach weight scaled by length³ in 10cm cod length classes; 'Logit' is the logit of the proportion of empty stomachs in the bulked sample within 10cm cod length classes.

#	Variable	Model	n	r ²	F
1.	Tot wt	Ecosystem	27138	0.18	14908
2.	Logit	Ecosystem	27138	0.15	10980
3.	Tot wt	Length	27132	<0.01	11411
4.	Tot wt	Growth rate	27132	0.18	14908
5.	Tot wt	Temperature	17557	0.05	904
6.	Logit	Temperature	17557	0.04	718
7.	Tot wt	Temperature, Growth rate	17557	0.42	Large
8.	Tot wt	Length, Ecosystem	27132	0.01	Large

In addition to the GLM models analyzed above, the relative effect of change in size of cod on the composition by mean weight of the diet across ecosystems was examined graphically. First ecosystem differences in mean total stomach content of samples (unbulked for Barents Sea, Newfoundland and USA East Coast, empty

stomachs retained) were plotted by 10cm length class of cod between 30 and 70m (Figure 6.2.16). The ecosystem effect becomes more apparent with increasing size class of cod. Above 40cm the mean weight of the total stomach content is lowest in the Baltic Sea. Above 50cm it is clear that the mean total stomach content weight is highest in the North Sea, followed by Newfoundland. Above 60cm mean stomach weight for the remaining ecosystems is ordered (descending) Barents Sea, USA East Coast, Iceland, Baltic Sea. The ecosystem effects described above differ from those shown in logarithm of the mean of the bulked total stomach weights scaled by length³ (note:- need to come up with a name for this thing to use in the report) (Figure 6.2.8) in several ways. In the log mean total stomach weight data, the expected value for Newfoundland is higher than that for the North Sea, the later value being lower than that for both the Barents Sea and USA East Coast. The expected value for the Baltic Sea is the lowest in both analysis. The above comparison emphasizes the significance of the initial treatment of the samples on the outcome of the subsequent analyses.

The mean weight of fish in the samples from the USA East Coast is the lowest. In the 20-29cm length class (Figure 6.2.17) the amount of fish in the diet increases in all ecosystems with the exception of the Baltic Sea, although the mean weight of fish from the USA East Coast remains low - the major portion of the diet being composed of crustaceans. In the 30-39cm length class. In the 30-39cm length class it is apparent that the change over to a predominantly fish diet is underway although in the Baltic Sea and the USA East Coast diet data the weight of crustaceans in the diet remains relatively high, in keeping with the pattern in the 20-29cm length class (Figure 6.2.18). Comparing the mean weight by prey category in the 40-49cm, 50-59cm and 60-69cm length classes among ecosystems shows that the ontogenetic change over from an invertebrate diet to a fish diet occurs later of the USA East Coast than in the other ecosystems (Figures 6.2.19-21). Mollusks appear to form an important component of the diet of cod mainly in the intermediate size classes (30-60cm), and then only in the North Sea and USA East Coast ecosystems. Above 70cm fish is clearly the predominant component of the diet, although in all ecosystems crustaceans remain an important component (Figure 6.2.22).

The comparison of growth rate, total stomach weight, proportion empty and the weight of individual prey components described using the GLM models and graphical analyses suggests considerable difference among ecosystems, and in relation to variables such as temperature and growth rate. In general the patterns are coherent - ecosystems with a high mean stomach weight tend to have a low proportion of empty stomachs. In ecosystems with slow growing cod, the mean stomach weight tends to be higher and the proportion empty

lower. Although temperature data were not available for all ecosystems, taking temperature into account appeared to clarify the effect of growth rate - there being a negative relationship between temperature and mean stomach weight and a positive relationship between proportion empty and temperature. Relationships with temperature need to be clarified after incorporation of data for the North Sea and the Baltic Sea into the data base. In particular the Baltic Sea cod have a slow growth rate (comparable to Boreal ecosystems) but has a low mean stomach weight - this may be explained by higher ambient temperatures. Conversely, the high expected stomach weight at slow growth rates in the USA East Coast is accounted for by relatively high temperatures (am I getting confused here?). Mean total stomach weight based on the analyses here indicates a relationship of $e^{-0.0129T}$. This means that digestion rates are related to temperature as $e^{-0.0119T} = 1.01^T$. The value 1.01 is lower than what is obtained from experimental work on digestion rates and metabolic rates, which is typically 1.10 (+ 0.05).

7 HYPOTHESIS TESTING: COD/CAPELIN INTERACTIONS

7.1 Surface Plots

Figures 7.1.1 - 7.1.3 present 3-D plots of scaled and logged stomach content weights vs. year and predator length group for cod from the Barents Sea, Iceland and Newfoundland. The stomach contents plotted are total content and the content of capelin (without redistribution of unidentified fish) for predator length groups from 20-29cm to 70-79cm.

For the Barents Sea and Iceland data from quarter 1 are used since the major part of the cod's predation on capelin takes place during the first part of the year. For Newfoundland only data from quarter 4 is available.

The total content plot for the Barents Sea (Figure 7.1.1a) looks very smooth between length groups, but there are strong year effects. In 1986 the content started to decrease and was very low in 1987-1988 and then started to increase again. The capelin content plot (Figure 7.1.2b) looks very much the same, except for the smallest length groups where the year effect is less pronounced. For cod > 40cm most of the year-to-year variations in total stomach content is explained by the variations in the content of capelin. Smaller cod is less dependent on capelin during the first part of the year and preys more upon crustaceans. The two plots also indicate that the cod's ability to fill up the stomach increases with increasing length up to about 50-60cm.

The plots for Icelandic cod (Figure 7.1.2a and b) look a little bit more rough and spiky, both between length

groups and between years. As for the Barents Sea the two plots have a quite similar surface. There seems to be a year effect caused by variations in the content of capelin. This content decreased after 1979, stayed low in 1981, increased again up to 1988, then decreased and was low in 1990 and finally started to increase again. The effects are not as strong as in the Barents Sea because capelin makes up a smaller part of the total stomach content in years when both contents are low.

For Newfoundland the total content plot (Figure 7.1.3a) is quite smooth and flat, except for the largest length group where few fish are sampled. This indicates that the feeding level of the cod stock here is relatively constant, at least in quarter 4. The capelin content plot (Figure 7.1.3b) however shows some year-to-year variations, but capelin contributes much less to the total stomach content than in the two other systems

7.2 Capelin Biomass vs. Cod Stomach Content of Capelin

The feeding relationships between cod and capelin were investigated by plotting the biomass of capelin versus average, scaled and logged values (indices) of capelin weight in cod stomachs of length groups 30-69 cm. For the Barents Sea and Newfoundland biomass estimates of total (catchable) capelin stocks were used, whereas spawning stock biomass was used for Iceland waters. These were plotted against capelin stomach indices in the 1. quarter for the Barents Sea and Iceland and in the 4. quarter for Newfoundland. The data are summarized in Table 7.2.

For the Barents Sea there is a rapid increase in the capelin stomach index for capelin biomass values up to 1 million tonnes. Only three observations are available for higher capelin biomass values yielding highly variable capelin stomach indices (Figure 7.2). For Iceland there is also a clear increase in capelin stomach index with increasing capelin biomass (Figure 7.2). A linear regression is plotted on each Figure for reference, but a nonlinear regression would be more appropriate. Both plots are suggestive of a type 2 (3) functional response.

For Newfoundland waters biomass indices for the Div. 2+3K capelin stock are available from two series of hydroacoustic surveys (Table 7.2.). The two series are not well correlated (Lilly 1991). The Canadian series is recognized to have yielded anonymously low results in some years. The unreliable estimates of capelin biomass make description of the cod feeding response very difficult (Figure 7.2). Additional complexity is added by changes in biomass and distribution of both cod and capelin in recent years.

These plots are not directly comparable to the ones in Magnusson and Palsson (1991) where capelin consump-

tion per unit weight of cod was plotted against biomass of mature capelin. Here, on the other hand, the average of the logarithm of the scaled weight of capelin in the stomach is used. Furthermore, the capelin catches in the interval between the acoustic measurement of the capelin stock and the collection of the feeding data have not been taken into account. The consumption of capelin in the Magnusson and Palsson paper included only 3+ capelin, as opposed to total capelin in the present analysis. In the years 1982-84 when the capelin stock was at its lowest level the cod switched to some extent to immature capelin (Magnusson and Palsson 1989).

7.3 Can Cod Find Alternate Prey When Capelin Availability is Low?

The quantity of capelin in the stomachs of cod varied considerably among years, particularly in the Barents Sea and off Newfoundland (Section 7.1). To test for compensation during periods of low availability of capelin, the mean quantity of food other than capelin was compared with the mean quantity of capelin alone (Figure 7.3). There was no compensation ($b=-0.05$; $p=0.67$) in the Barents Sea, a suggestion of compensation at Iceland ($b=-0.22$; $p=0.08$), and partial compensation at Newfoundland ($b=-0.54$; $p<0.001$).

The evidence for partial compensation at Newfoundland is in disagreement with an earlier study (Lilly 1991), which concluded that cod in that area in the autumn did not compensate at times of low capelin availability by feeding more intensively on other prey. The disagreement may be related in part to changes in feeding behavior since 1986, the most recent year included in the former analysis. However, the former analysis was conducted on scaled stomach content weights which were not logged. The effect and appropriateness of the log transform deserves additional study.

7.4 Predation on Fish and Alternate Prey in Non-Boreal Systems

An analysis similar to that described above for the boreal systems was conducted for the other three systems, with the weight of prey other than fish being compared to the weight of fish alone (Figure 7.4.1). A negative relationship was evident in all three systems: North Sea ($b=-0.78$; $p<0.001$), Baltic Sea ($b=-0.44$; $p<0.001$), USA ($b=-0.49$; $p<0.001$).

8 FOOD FOR THOUGHT

8.1 Some (more) Thoughts on the Inclusion of Marine Mammal Feeding

The Working Group considered again the issue of the incorporation of predation by predators biomasses not

specifically estimated within multispecies models. This issue had been broached several times in the context of accounting for predation by various predators including rays, seabirds, horse mackerel, and marine mammals in the North Sea MSVPA. The context focused on the review provided by selected members of the MSWG of a national program to investigate aspects of marine mammal feeding ecology in the context of multispecies fishery models.

Four significant issues arise when attempting to incorporate marine mammal predation:

- 1) first-order calculations of likely impacts,
- 2) the spatial scale of marine mammal foraging behaviour in relation to prey field densities,
- 3) the conduct of process-oriented *versus* surveys of feeding volumes and species compositions, and
- 4) the general predictability of the outcomes of multi-species interactions in relation to the complexity of trophic interactions within ecosystems.

First-order calculations of marine mammal feeding serve to define the scope for resolving the predatory impact of marine mammals, relative to other sources of mortality on prey consumption (feeding level * frequency * population size) can be illustrative in determining the feasibility of resolving components of the total mortality rates of prey. That the variances on the estimates of the above three components are generally high would indicate that only high levels of predation by marine mammals will be detectable. The spatial scale of marine mammal feeding interactions is likely to be key in determining the functional response of these predators to prey abundance. Thus, studies at spatial scales appropriate to investigate non-neutral switching among prey are necessary to resolve these processes. In this context, the MSWG views process-oriented studies rather than general surveys of food composition as having more immediate importance to marine mammal predation studies. Finally, the Working Group briefly considered the general topic of the predictability of outcomes of individual species interaction *versus* the complexity of food web structure (e.g., highly networked temperate water systems *versus* systems wherein predation is focused on by a few key prey. A more complete evaluation of this issue is to be found in the report of the Study Group on the Ecosystem Effects of Fishing (Anon. 1992d). In general, the issue of predictability of ecosystems is unresolved, and clearly a topic worth considering in more detail not only in this context, but for providing long-term advice for fisheries management in general.

8.2 On the Assessment of Norway Pout and Sandeel

8.2.1 Missing catches at age

For 1990, it was not possible for the Industrial Fisheries Working Group (IWG) to obtain the age distribution of the catches for Norway pout in the North Sea and for the northern and southern sandeel stocks in the North Sea (Anon. 1992e). The reason was a breakdown in the sampling system. Since then, sampling has improved, and is now at a fairly satisfactory level.

The lack of catch-at-age data causes problems both for the assessments in the IWG and for future running of the MSVPA. The approach taken by the IWG to overcome this problem, was to attempt to construct age distributions in the catches, which would convey as far as possible the information available about the 1990 fisheries, and take into account all other information about the cohorts involved.

The IWG attempted two approaches. One was a newly developed seasonal separable VPA (SSV) (Cook 1992a), the other an extended survivors analysis (XSA) supplied with a routine to find an optimal age distribution of the catches. These methods are further described below. For both approaches, the IWG experienced problems that could not be solved at its meeting. The XSA approach turned out to give different results for different choices of initial numbers used to start the search for optimal catches at age, while the SSV on some occasions gave unrealistically large population numbers. Therefore, no catch-at-age results could be provided by the IWG.

Since then, further work has been done on the SSV, which was presented as a working document to the MSWG (Cook 1992b). It appears that many of the problems can be remedied by careful weighting of tuning data.

8.2.2 Quality of the input data for the industrial species

The work with the missing catches at age illustrate many of the problems encountered when the assumptions underlying an assessment method are violated. These problems may be amplified when short lived species are considered. The IWG has described in some depth problems influencing its assessments of Norway pout and sandeel. (Anon. 1992e) These include variations in age compositions and growth rates between different fishing grounds, a harvesting strategy which may violate the proportionality between CPUE and stock size, and a relatively low exploitation rate. Due to the high natural mortality, the assessments also tend to be very sensitive to errors in the age readings, and to the representative-

ness of the samples. Both these problems are relevant to the industrial species.

8.2.3 The XSA approach to missing catches-at-age

As it was used by the IWG, the XSA was a slightly simplified variant of the Lowestoft version. During the present meeting, the Lowestoft version was implemented as a tuning procedure for the MSVPA, as is described in more detail under that heading. Essentially, the parameters (survivor numbers and catchabilities) are selected to minimize the weighted squared log ratio between population numbers estimated from the tuning data and those generated by the VPA, summed over all observations. This was also used as criterium for the missing catches at age. This was done using a simple routine searching for changes in the age composition which would reduce the total sum of squares, with the constraint that the SOP for each season should equal the actually known seasonal total catch. The method was tested quite extensively by the IWG, and, as noted above, it turned out that in some instances the final result was very sensitive to the choice of initial data, indicating local minima for the sum of squares. The reason for this seems to be that various sources of information about the cohorts point in different directions.

An alternative to the optimization procedure, which was tried during this meeting, is to use the catchabilities at age in the commercial fleet as a selection pattern, and tune the exploitation level in the seasons with missing catches to the right SOP. Apparently, this eliminated the problem with sensitivity to the initial data.

This approach was tested in a similar way as done by the IWG, taking the data for Norway pout from 1982 to 1989 and assume that one years catches were missing for each of these years except 1989. The data used were the catches, efforts and weights as used by the IWG (Anon. 1992e). As research vessel data, only the IYFS series for ages 1 and 2 in the first quarter was used. The estimates of the missing catches and the actual catches for each year are shown in Table 8.2.

8.2.4 Seasonal separable VPA (SSV)

As noted above, this approach which is a CAGEAN-type model (Deriso et al. 1985), was suggested by Cook (1992 a; b). The primary intention was to provide an assessment for the Shetland and Division VIa sandeel stocks, where the fisheries have been greatly reduced or totally stopped due to management actions and market conditions respectively, but where survey data are available in the absence of a fishery in the former case. The method was used by the IWG for its assessment of these stocks.

The method assumes that the fishing mortality is separable, i.e.

$$F(\text{age,season,year}) = s(\text{age,season}) * f(\text{season,year})$$

where s is the selection pattern and f the exploitation level. Using the catch equation, a fitted catch in each [age,season,year] - cell can be written as a function of catches and natural mortalities, with the s - and f -vectors and the terminal population numbers as parameters. Furthermore, effort data are taken as measures of the f 's, and the survey indices as measures of the population numbers, with catchabilities as parameters. Assuming lognormally distributed errors, this can be treated as a parameter estimation problem, which leads to the minimization of the total weighted sum of squares of the logarithmic residuals of the fitted catches, efforts and survey indices. This minimisation can be solved using standard numerical tools, if specified constraints are imposed, eg. selectivity at age is constant above a given reference age.

Accordingly, this method combines the separability assumption with the utilization of traditional tuning data, without treating any of them as exact. Being a statistical parameter estimation approach, this method also has the advantage that variance estimates for the fitted values can be provided.

As far as there are sufficient data to estimate all parameters, the method provides fitted catches for all years, seasons and ages, which can be used as estimates for the missing catches. The SOP (sum of mean weight*catch at age) of these catches is not constrained by the actual total catches. If the SOP are far away from the actual catch, the actual catch levels represent additional information about the involved cohorts, which at present is not taken into account in the SSV model.

Test runs were provided with this model in the same way as for the XSA, using the same set of data. The results are shown in table 8.2.1. It should be noted, that the present tuning data are not the best ones available for this method (Cook 1992b)

8.2.5 General considerations about missing catches

The problem of filling in missing catch data is in many ways connected to the problems with assessment of short-lived species. In both cases, the result will be more sensitive to inaccuracies in the input data and to the validity of the assumptions underlying the model than usual. In this respect, the SSV approach should be advantageous, since it does not assume that any of the data are exact, and because it offers the opportunity to consider the statistical properties of the estimates. The experience with the industrial species is, however, that it may give very misleading results if the input data are

sufficiently poor. The occurrence of large residuals may give a warning. Apart from that, there is at present few clues to the validity of the data. Further studies of the dynamics behind the pathological results and of the robustness of the method would be useful. The XSA, on the other hand, takes the catch data as exact. The main difference between this and conventional tuning is that last years tuning data are treated as no better than previous years'. In common with other ad hoc tuning procedures, it has the drawback that it gives no estimates of the variances of the parameters.

A third approach, which was tried during this meeting, was fit the catches to a general linear model. Various model formulations were studied, again using the 1982-89 Norway pout data set. The most promising seemed to be to model the catches with a Poisson distributed error function and a logarithmic link function. The explanatory variables entered were age, fleet, quarter and year-class, and in addition either log effort or year were entered. No attempt was made to constraint the catches to give an SOP equal to the actual total catch. This approach seemed to predict the missing catches with the same level of accuracy as the two other approaches.

One may address the question whether the catch estimates should be constrained by the known total catch or not. Suppose that the fitted catches give an SOP above the actual catch. This may be because that year, the catchability was below normal, because the stock in fact was smaller than indicated by the available information, or because the catch data are inaccurate. In the latter case, one should probably accept the fitted catches as a better estimate of what happened than the reported data. If one rather would accept year-to-year variations in the catchabilities, it may be appropriate to scale the fitted catches down to the exploitation level indicated by the total catch. If one would rather stick to the hypothesis underlying the model, estimating the missing catches as additional model parameters, with the constraint given by the SOP equalling the catch would be the most appropriate approach.

Finally it should be noted that, even if catch-at-age numbers can be provided that are optimal in a single-species framework, they may not be so in a multispecies model because of the variable natural mortalities involved. It may be possible, however, at least with the XSA approach, to adjust the natural mortalities according to the MSVPA results iteratively, or perhaps to incorporate the catch estimation part into the newly developed tuning module for the MSVPA.

8.3 A Simple Length-Based Multispecies Model

A conceptual simple length based multispecies (LBMS) model for the central Baltic was presented to the Working Group (Bundgaard and Sparholt 1992). The model

was based on estimates of the length distributions of the prey consumed by cod and on estimates of the length distributions of the prey in the sea (Figure 8.4.1-2). Cod is the only predator in the system and herring and sprat are prey. The cod cannibalism is small. The estimates were made on a quarterly basis. The predation mortalities, M_2 , by length values are simply obtained by dividing the number predated with the number in the sea for each prey species length group.

The length distribution of the prey stocks in the sea are obtained by combining stock numbers at age from an MSVPA (Anon. 1992f) and ALKs. The length distribution of the prey consumed by cod are obtained by combining data on cod stomach content with data on cod stock numbers from VPA and cod consumption rations.

The M_2 s can in principle be obtained independently of the MSVPA by using other information of stock numbers at age or length, for instance from hydroacoustic surveys. For the Baltic acoustic data might be considered, although it has been shown that the acoustic survey for this area underestimates the abundance of young herring (Sparholt 1990a).

The M_s estimates from the LBMS are similar to those from the MSVPA for sprat in Sub-divisions 25-28 and for herring in Sub-divisions 28-29S for equal size of fish. However, for herring in Sub-divisions 25-27 the LBMS values are somewhat higher. The reason for this is unknown. Eight GLM analysis have been used for these comparisons, one for each species/quarter combination and the results can be seen in Table 8.4.1. The difference is most significant (about a factor of two) in the first and fourth quarter.

The LBMS model can be regarded as a simple alternative to the MSVPA, especially if commercial catch data are lacking and acoustic estimates of stock numbers at length are available.

The LBMS model can also be used for checking the internal consistency of the MSVPA if the MSVPA stock number estimates are used as input to the LBMS.

Finally, the LBMS might be a useful tool for examining the predator/prey size preference, because there is no transformation back and forth between length and age as needed in the MSVPA if the MSVPA is used for these kinds of analysis.

8.4 Smoothing of MSVPA Suitabilities

The LBMS was used to examine the prey size preference by cod for the central Baltic. By applying the above procedure for each cod length group the partial M_2 s for each prey length group are obtained. Parabolas were fitted to plots of log (partial M_2) vs log (predator

weight/prey weight) for each cod length group (Figure 8.5).

It can be seen that the optimal predator prey size ratio is not independent of the predator size. There is a clear indication that larger cod prefer relatively smaller prey. When the present Working Group in previous reports has attempted to smooth the suitabilities from the MSVPA, it has always been assumed that the optimal size ratio is independent of predator size. This might be the reason for the high variability obtained previously of the smoothing.

A possible biological explanation of the phenomena might be that large cod do not waste time searching for large prey as they are very scarce, but rather stay in areas with plenty of small prey. From an energetics point of view this might be a more favorable strategy. Energy budget calculations might be pursued in order to check whether this fits with the above observations.

8.5 Effects of Alternating Recruitment Levels on Long-Term Predictions

MSFOR predictions are highly sensitive to the level of future recruitment (Finn et al. 1991). In last years report it was thus concluded that any long-term advice should be regarded as contingent upon the validity of the underlying stock-recruitment relationship assumed (Anon. 1991a). Since recruitment is extremely difficult to predict and since few, if any, of the attempts to do so have been successful, this is a major obstacle to the application of MSFOR in fisheries management (Gislason 1992).

Recruitment changes take place over various temporal scales, from year to year variations to changes which span several decades.

Gislason (1991) showed that year to year changes in recruitment, modelled by drawing recruitment at random from lognormal distributions, produced predictions of average long term biomass and yield identical to those predicted with constant recruitment. The conclusion was that even though the species interactions in the MSFOR are modelled by non-linear equations this non-linearity does not appear to be strong enough to generate a difference between the results of stochastic and constant recruitment runs, provided the average recruitment is the same in both cases. This is comforting as it signifies that it is possible to neglect year to year variations in the predictions and concentrate on the effect of changes in the average level of recruitment. As an example of how such changes may affect the results we have estimated the percentage difference between a *status quo* prediction and a prediction in which the fishing mortality generated by the roundfish fleet was reduced by 30%.

The results of a run in which recruitment was assumed to remain at a level identical to the average recruitment in the period from 1974 to 1988 are shown in Tables 8.6.1 and 8.6.2.

Table 8.6.1 shows the percentage difference in the predicted catch from the roundfish fleet. All landings are predicted to decrease. The largest percentage change is seen to take place in the discards of whiting and haddock which decrease by 25 and 37 percent, respectively.

Table 8.6.2 shows the percentage changes in total biomass, spawning stock biomass (SSB), total catch (including discards) and value of landings. The SSBs of cod, whiting, haddock and saithe are predicted to increase, while the SSBs of herring and Norway pout decrease. For cod, the SSB will increase by 61%, for the other species the changes are smaller. With the exception of saithe, the value of the landings will decrease. In total, a 4 percent reduction in the value of the landings is predicted.

In order to investigate the sensitivity to recruitment changes, the difference between the status quo and the 30% reduction in roundfish effort was estimated in a series of additional runs in which recruitment to each species was set to either +50 or -50% of the average historic recruitment estimated by the MSVPA for the period 1974 to 1988.

A factorial design in which all combinations of high and low recruitment levels to each of the 11 stocks are covered requires a total of 2^{11} comparisons between the status quo and the 30% reduction in fishing mortality. However, since sole and plaice do not interact with other species and are caught only by the flatfish fleet, the results for these two species will not be affected by changes in roundfish effort. The recruitment to sole and plaice was, therefore, kept unchanged. With two levels for each of the remaining 9 interacting species included in the model, a total of 2^9 (512) combinations of levels are possible. For each of these combinations, the percentage difference between the status quo situation and a 30% reduction in roundfish effort was estimated.

Table 8.6.3 shows the distribution of the percentage change in landings and discards by species in the roundfish fleet. Out of the 512 recruitment scenarios, 27.3% resulted in a 10 to 20% reduction in the long term landings of cod, 66.2% in a .01 to 10% reduction and 6.4% in a .01 to 10% increase. It must therefore be concluded that the 8% decrease in cod landings predicted assuming average recruitment (table 8.6.1), is sensitive to changes in recruitment level. In 6.4 percent of the investigated scenarios, the predicted long term loss is even converted into a long term gain. In the case of whiting, the landings from the roundfish fleet are predicted to decrease between .01 and 20% and the discards

between 20 and 30%. Saithe, which is not predated upon in the model and for which the traditional single species Y/R model may be applied, is, as expected, insensitive to changes in recruitment level. All runs result in a 9% decrease in saithe landings. Haddock, on the other hand, is extremely sensitive to changes in recruitment level. Within the levels of recruitment defined above, the results range from a 40 to 50% reduction to a .01 to 10% increase in landings and to a 20 to 60% decrease in discards.

The distribution of the percentage change in spawning stock biomass is shown in Table 8.6.4. For cod, whiting and saithe, a relative increase in SSB is expected in all cases. The SSBs of herring and Norway pout show a relative decrease for all combinations of recruitment levels, while the reduction in the fishing effort of the roundfish fleet may result either in a relative decrease or in a relative increase in SSBs of haddock, sandeel and sprat. Sole and plaice are not caught by the roundfish fleet and do not serve as prey for any of the 5 predators. They are, therefore, unaffected by the effort reduction.

The results for cod, whiting, herring and Norway pout are promising as they show that definite statements about the sign of a long term percentage change in SSB, landings and discards can be made even though the future level of recruitment is uncertain. However, in other cases such statements cannot be made and for haddock, in particular, distribution of the percentage change is surprisingly wide.

In order to investigate whether this is caused by changes in the recruitment level to haddock itself or by changes in recruitment level to the other stocks, an ANOVA was made in which the percentage changes in landings, discards and SSBs were considered as the response variables and the recruitment levels as classification variables. The ANOVA explains the variation in percentage change as due to differences in recruitment level with random error to account for all remaining variation.

The parameter estimates are shown in Table 8.6.5. The intercept, i.e. -9.7% for cod, may be interpreted as the expected percentage change in landings resulting from the reduction in effort in the roundfish fleet if recruitment is at a high level for all species. The other parameters show the effect of a change in recruitment level from a high to a low level. They may be added to the intercept in order to estimate the expected response. Consider, for example, the situation where cod recruitment is at a low level and recruitment to all other stocks at a high level. The expected percentage change in landings of cod can then be estimated as $-9.7 + 6.8 = -2.9$ percent. The parameters thus summarize both the expected direction and the magnitude of the percentage change in landings upon changes in the level of recruitment.

The only situation in which a decrease in roundfish effort may result in an increase in cod landings is when the recruitments to both saithe and cod are at a low level. In all other cases, the percentage change will be negative. The change in whiting landings and discards is negative irrespective of recruitment level. However, the change in haddock landings may be positive if saithe recruitment is at a low level. The percentage changes in haddock landings and discards are very sensitive to changes in the level of recruitment to saithe and Norway pout. When recruitment to saithe is at a low level, the natural mortality of haddock is reduced. In this situation, growth overfishing is possible, in which case the landings will increase when fishing mortality is reduced.

The results of an ANOVA of the percentage SSB changes are shown in Table 8.6.6. Saithe, mackerel, plaice and sole which are not predated upon and for which a change in recruitment level does not change the percentage increase/decrease in SSB have not been included in the Table.

The predicted changes in SSB for cod and whiting are most sensitive to changes in the level of recruitment to the species themselves. For haddock, the results show that the very wide range of predicted SSB change, i.e. the large spread of the values in Table 8.6.5, is due mainly to changes in the recruitment level of saithe and Norway pout. Changing the recruitment level of whiting from a high to a low level would add 3.6% to the predicted SSB change, while a similar decrease in saithe recruitment would add 30.1%. These results point to the importance of saithe as a predator and stress the significance of improving the estimates of food composition and stock size for saithe in particular.

The correlation, R^2 , expresses the proportion of the total variance which is explained by the analysis. Since we have one observation per cell and only include main effects in the ANOVA, R^2 may also be interpreted as a measure of the importance of second and higher order interactions. With the exception of sprat and sandeel SSB the effects of changes in recruitment level on the percentage change in catch and SSB seem to be well explained by the main effects (R^2 around .90). In the case of sprat and sandeel SSBs, R^2 is lower and, for these species, second-order interactions seem necessary to explain the changes.

Even though the approach appears promising there are limitations to its applicability.

First of all the results should not be interpreted as reflecting the probability distribution of the percentage long term changes. For most fish stocks, only a very short time series of recruitment data is available. With only a short time series at hand, it is very difficult to use historic data to determine the probability of a change in

recruitment level. Furthermore, even if a longer time series had been available, it would still be unlikely that an analysis of historic data would help us in determining the probability distribution of future recruitment levels. We do not know enough about the factors determining the level of recruitment, and even if we did these factors would most likely depend on future environmental and ecological conditions which would be difficult, if not impossible, to predict.

Secondly, although the results suggest that some of the predictions are independent of changes in recruitment level, it is important to remember that the MSFOR can only be used to make predictions within certain limits. The main reason being that it assumes constant growth, constant other mortality and recruitment to be independent of adult stock sizes. All of these assumptions seem to require that the predicted stock sizes (and spawning stock sizes) are kept within certain limits. If not the outcome from the model cannot be trusted.

The lower of these limits should probably correspond to the stock size above which it is likely that recruitment is unaffected by changes in adult stock size. Below this stock size, recruitment may depend on adult stock size, and one of the assumptions behind the model breaks down. In the same way, the upper limits may be defined as the stock sizes above which it is likely that recruitment, growth and mortality are influenced by changes in competition and predation not accounted for by the model.

At present, the SSB is below the "minimum biologically acceptable level" defined by ACFM in a number of cases. The spawning stock biomass of mackerel seems to have been below the "minimum biologically acceptable level" since the beginning of the 1970s when the last large year classes were produced. The spawning stock sizes of cod and haddock are presently the lowest on record and below the minimum levels indicated by ACFM (Anon. 1992g). In these cases, the possibility that future recruitment depends upon changes in SSB cannot be excluded and if this is the case one of the assumptions of the model breaks down. The predictions for cod and haddock should, therefore, be treated with caution. At present recruitment may depend upon spawning stock biomass for these species in which case results, such as those which predict an increase in yield from the roundfish fleet upon an increase in effort (and a further reduction in SSB's) cannot be trusted. Likewise a 30% reduction in roundfish effort may result in more than a 60% increase in spawning stock biomass of cod (if this increase results in an increase in the level of recruitment compared to the status quo prediction).

8.6 The North Sea Food Web - Revisited

The Working Group at its meeting in 1989 discussed two possible pathways for flow of energy in the North Sea. These descriptions were based on Jones (1984) and an update, which included data from the MSVPA. The two descriptions were compared, and the trophic structures of the major groupings in the North Sea in the late 1960s and early 1970s were discussed.

In addition the Working Group elaborated on the biomasses of and interactions between the MS fish species in the mid 1970s, the mid 1980s, and the far future. This was done in form of graphical representations summarizing some of the main data of the MSVPA and MSFOR programs.

The present Working Group reexamined the North Sea food web in a more detailed form. Adopting the ECOPATH II methodology and software described by Christensen and Pauly (1992) the North Sea ecosystem was described as consisting of 22 groups of living organisms plus detritus.

For each of the living groups it was attempted to describe as many as possible of the following parameters: biomass, production/biomass ratio, consumption/biomass ratio, and average diet compositions.

The description focused on 1981, the first "year of the stomach." Based on a run of the MSVPA data on production (estimated as biomass at the end of the year minus biomass at the start of the year plus catch plus amount lost due to predation and other mortality), consumption and average biomasses were obtained for the MS fish species. Diet compositions for the MS species were mainly based on information in Daan (ed. 1989), Daan et al. (1990), while diets for other fish species were based on an array of sources (e.g., DeSilva 1973, Baden 1986, Dahl and Kirkegaard 1987).

The parameters for 'other predatory fish' were mainly based on *Trachurus trachurus*, while 'other prey fish' mainly were focused on *Limanda limanda*. 0-groups of the MS fish species were not included in this preliminary analysis. Biomasses for the "other" fish species were based on average data for 1983-1985 estimated by Sparholt (1990b).

Only very limited information on the invertebrate groups was available to the Working Group. The production, biomass and consumption of these groups were therefore estimated using a top-down modelling approach based on the consumption by the predators, and an assumed gross food conversion efficiency of the invertebrates (of 15%). The diet compositions of the invertebrates were mainly guesswork based on qualitative information from various sources.

For total primary production an estimate of 1514 t wet weight km⁻² year⁻¹ was used based on Jones (1984).

All rates and biomasses were expressed on an areal basis to facilitate comparisons with other systems. The total area of the North Sea was assumed to be 570,000 km² (Jones 1982). Some of the major results from this preliminary estimation of the 1981 North Sea food web structure are presented in Table 8.7.1. The total primary production, and the total flow to and from the detritus box served as check in the model.

A noteworthy result is that the primary production as modelled here is able to sustain the consumption in the system. It is estimated that 82% of the primary production is used in the system. It is clear though that inclusion of 0-group fish would shift this balance, and lead to an increased estimate for zooplankton production, and hence also of utilization of phytoplankton production. Because of this it may be appropriate to reexamine the primary production estimate. Fransz and Gieskes (1984) found Jones estimate to be too low, as they estimated the production to around 200 t C km⁻² year⁻¹, or some 2300 t wet weight km⁻² year⁻¹ (Conversion: 1 g C = 15 kcal; 1 g wet weight = 1.3 kcal).

Table 8.7.1 also points to very high (32-45%) food conversion efficiencies ("Gross eff.") for the four gadoid MS species. An efficiency in the range of 10-20% seems more realistic which means that the feeding rates of the gadoids in the MS programs are very conservative estimates. The result of this is that the effect of predation is more likely to be underestimated than overestimated.

A graphical representation of the quantified food web for the North Sea in 1981 is shown in Figure 8.7.1. All groups are balanced so that input equals output, and the graphs shows one possible representation of the food web. Other assumptions would lead to somewhat, but probably not grossly, different representations. One may notice though that better parameter estimates for the invertebrates would help to restrain the range of possible descriptions of the system.

A major property of the representation in Figure 8.7.1 is that it makes trophic interactions in the food web very visible. The representation also opens possibilities for using a wide array of network analysis methods. Noteworthy here is the mixed trophic impact routine illustrated in Figure 8.7.2.

The mixed trophic impact is a data exploratory method derived from economical input-output analysis (Ulanowicz and Puccia 1990), here used in the form it is implemented in the ECOPATH II software. The analysis reveals all direct and indirect trophic impacts of all groups in the system. The impact routine is not a predictive tool, one cannot say what will happen if the conditions in the system change, only describe how the groups

in the given situation impact each other through trophic interactions.

The mixed trophic impact routine can also be seen as a simple sensitivity analysis. It gives an idea of how important the different groups in the system are for the trophic dynamics, and therefore of where gains from improved parameter estimation can be expected.

The Working Group found that the described network analysis provided an easily accessible and useful tool for exploratory data analysis, and recommended that future attempts to use the methodology for more refined descriptions should be encouraged. It was noticed that the methodology could be useful for comparative descriptions of the results from the 1981 and 1991 North Sea 'years of the stomachs'.

9 STATISTICAL ESTIMATION OF FEEDING PARAMETERS

9.1 Treating Zeros

As with trawl survey data, a recurring problem with stomach content data is the proper interpretation of empty stomachs ('zeros'). In this section, statistical approaches to developing models of factors contributing to empty stomachs are considered, as a basis for developing better methods to handle such data.

Basic data used for the analysis:

In this part of the analysis only data from the North Sea have been investigated. All analysis was performed with SPSS-PC/V4.0. From these data all records were excluded, which referred to an individual stomach. All data for 1984 were excluded, which were - except from being unbulked samples - not comparable at all with the other subsets due to very restricted spatial coverage. Subsets for the years 1981 and 1985-87 cover the total North Sea, whereas subsets for 1980 and 1982 refer only to the southern North Sea (area 6).

Calculation of the proportion of empty stomachs per bulked sample:

The number of empty stomachs was divided by the total number of fish in the sample including regurgitated stomachs. Mean values of the percentage of empty stomachs are weighted by the sample size of the original bulked sample in the data set.

The mean stomach content of those stomachs in a bulked sample, which contained food, was divided by the length cubed of the predator (lower length class) and then multiplied by 100,000 (=SMSCFOOD). For some graphs natural log was taken from these 'scaled' values

(=LSMSCFOD). All mean values were again weighted by sample size.

The logit model was fitted to the data pairs: number of empty, number of total stomachs in the sample. The mean stomach content of the non-empty stomachs (SMSCFOOD) or the predator length were used as continuous variables in this model.

There is no general agreement on the treatment of regurgitated stomachs in the analysis, since this term can refer to different things. Either it stands for a 'real' regurgitated stomach, where food pieces have been detected in the gill rakers or the mouth of the fish, or it stands for everted stomachs with no food rests at all. In the first case the stomach would have been not empty and therefore had to be included in the calculation. In the second case it could have been either empty or not and should therefore not be included in any analysis. This classification (regurgitated = with food / everted = with or without food) was not always followed strictly on board of the research vessels (Anon. 1992b).

To estimate the effect of including or not including the regurgitated stomachs in logit analysis, the analysis was for one example done with both approaches.

Results from descriptive statistics:

Total North Sea:

The weighted means for the total North Sea (Figure 9.1.1) vary between 0.17 (Quarter III in 1981) and 0.10 (Quarter II and IV in 1981). The third quarter has the highest proportion of empty stomachs on average, followed by the first quarter, the lowest proportions occur in the second and fourth quarter. The largest difference between years shows up in the third quarter, with 0.17 in 1981 and 0.13 in 1985.

The southern North Sea:

The proportion of empty stomachs in the total North Sea was relatively high in 1980 (0.2 in Quarters I-III). This result, could however not be compared with other years (except from 1982), because sampling was restricted to the southern North Sea in 1980. In order to see, whether this major discrepancy was an area rather than a year effect, subsets for the southern North Sea were generated from the data sets of the other years for comparison. The results (Figure 9.1.2) show, that in fact 1980 was an anomalous year, the differences among the other years are within the range of those in the data of the total North Sea.

The majority of the data indicate no substantial differences in the feeding level (reflected by the proportion of empty stomachs) between years. This is in line with the

data on mean stomach content, which do neither show a comparable deviation between 1980 and other years nor among other years (Figure 9.1.3). It can therefore well be, that the difference in the proportion of empty stomachs did not correspond with any depression in consumption rate in 1980.

Statistical treatment of the proportion of empty stomachs:

The statistical analysis of the demonstrated year and quarter effects on the proportion of empty stomachs is not straight forward. On the one hand the significance of a certain effect does not tell much, since with the given amount of data even very minor differences will turn out to be statistically significant. On the other hand tools like ANOVA, which could quantify the proportion of the explained variance, can only be used with great caution, since the distribution of the data is far away from being normal (Figure 9.1.4).

The extreme peak at the left end of the distribution consists of bulked samples which contained no empty stomachs. This maximum is not unlikely to occur, with an overall proportion empty of 0.14 and a relatively small sample size. Since an arcsine-square root transformation failed to produce a more symmetrical distribution, samples were aggregated, from which then the proportion of empty stomachs was derived per grouped (bulked) sample. As a first step all size groups within a stratum were aggregated. The distribution pattern of the proportion empty, however, was not affected at all by this procedure.

A possible interpretation for this is, that the occurrence of samples without of any empty fish is a spatial effect. On grounds with sufficient food the probability for the occurrence of empty stomachs is very low.

The peak at the left tail was, however, significantly reduced, if all samples with less than 20 stomachs were excluded from the database. This indicates that the distribution pattern is also influenced by the sampling strategy. On the other hand those excluded small samples could refer to situations with low predator density (at a particular size class), where all fish find sufficient food. In this case the exclusion of these samples introduces a systematical bias.

Logit analysis:

The problems of the distribution can be circumvented by the use of logit analysis. Some preliminary analysis were conducted with the following logit model:

$$P = \frac{\exp(2 * (\text{int} + \text{regc} * X - 5))}{1 + \exp(2 * (\text{int} + \text{regc} * X - 5))}$$

with regc = regression coefficient
int = intercept

P gives the Probability for the occurrence of an empty stomach as a function of the continuous variable X. The predator length and the mean stomach content of stomachs with food (SMSCFOOD) were used as continuous variables. The underlying hypotheses are: (1) for larger fish there is less food of the appropriate size available, so the proportion of empty should increase with size and (2) if within a bulked sample from the same station (or stratum) the mean stomach content of fish with food is high, it is likely, that proportion of empty fish is low, so a negative correlation is to be expected.

The effect of the mean stomach content (of fish with food) is tested by year, quarter and 10 cm length class separately. The results (Table 9.1.1 and Table 9.1.2) show on average a negative regression coefficient which supports the hypothesis. The scatter of the regression coefficients however, is large, ranging from -3.0 (Q1, 1981, 60-70cm) and -1.9 (Q4, 1981, 50-60cm) up to +0.5 (Q3, 1981, 40-50cm) and +0.7 (Q3, 1981, 30-40cm). In general the negative correlation is reversed in the third quarter, when the proportion of empty stomachs is at maximum. Thus, although the mean stomach content of fish with food is high, there is a high proportion of empty stomachs in the sample.

For one example (Q1, 1981, 30-40cm) with a clear negative regression coefficient (-0.7), a scatter plot of the proportion of empty stomachs is given (Figure 9.1.5), with the logit model superimposed on the data. This example shows that the fraction of the total variance in the data which can be explained by the model, is low, even though the fit of the model is statistically significant. For this example also the effect of including or not including the regurgitated stomachs has been tested, which turned out to be non-significant.

The effect of predator length on the proportion of empty stomachs is in general negative (mean regression coefficient: -0.2), in spite of the simple hypothesis stated above. However, the scatter is again large. Regression coefficients vary from -0.9 (Q3, 1985) to +0.5 (Q1 and Q3 1981). It can be assumed, that the spatial effects will govern the situation, since there may be locations with plenty suitable food for small fish and less suitable food for large food and vice versa.

Future analysis:

Would the proportion of empty stomachs have an effect on consumption estimates in 1980?

Is the year-to-year variation larger in other species (e.g. whiting)?

What is the effect of the distribution of sample sizes on the distribution of proportion empty?

Are effects clearer if only small subareas are investigated?

Which methods could better quantify the fraction of the explained variance by all continuous and categorical variables?

9.2 Aspects of Estimating Variance

Sampling from fish populations often gives rise to rather skewed p.d.f.'s. Two important variables contributing to the skew in stomach content weight are the sampling density of fish and stomach content weight. Both these distributions usually also includes a proportion of zeros (e.g. no fish or empty stomach). This is due to the patchy distributions of fish populations and their prey. Both estimated mean and variance can be driven by large observations (sometimes very few). Estimating mean and variance within a station is straightforward, but although one get unbiased estimates (conditional on the trawl station) increasing sample sizes also increases the probability of hitting extremely high values. Plotting estimated mean vs. number of samples will show a discontinuity whenever an extreme sample occurs. The following mainly lists considerations to be made when estimating the variance of stomach content data.

The mean and variance of stomach content data are usually considered to be dependent (close to proportional) on the predator weight. The mean weight of the predator changes significantly through 'large' length intervals. Either the length intervals has to be small enough to give a 'reasonably' small range of predator weights, or the stomach content weights has to be scaled to give comparable means within the length interval. This is equally important when estimating the variance. (The CV seems to be quite stable between length classes, Figure 9.2)

The degree of patchiness (both of predator and prey) may vary from season to season, area to area and year to year. Similar abundance of predator (and prey) can give large differences in the variance if the degree of patchiness varies.

Intuitively, samples taken at one station are more correlated than samples from different stations (Bogstad et al. 1991). This means that to gain precision in both mean and variance estimate, there is less to gain by increasing the number of samples within a station, than to increase the number of stations where stomachs are sampled.

To decide on an optimum sample strategy (within an total survey effort) one also has to take into consider-

ation the cost of extra stations compared to extra stomach samples.

9.3 Weighting in Analyzing Stomach Data

9.3.1 Introduction

If estimates/information should be considered representative for a population/population within an area, incorrect weighting will lead to biased results. Weights used in calculations/estimations will depend on the sampling strategy applied. Anything else than pure random sampling leads to more complex procedures including the use of different weighting factors and combination of these at different levels. The weighting factor agreed on for this meeting was a CPUE factor (CPUE or a related measure). The Russian-Norwegian stomach data supplies a weighting factor equal to the total catch (per 1 hour trawling) in the same 1 cm length group as the individual observation. The data from Newfoundland has normalized catch per length-stratum as the CPUE variable. The Icelandic stomach data uses the numbers sampled in the length-stratum + a normalized catch in the same stratum as the CPUE variable. No CPUE variable for stomach data from the Baltic or for USA cod was available at the meeting.

9.3.2 Possible weighting factors within a trawl-station

The set of weighting factors depends on the sampling strategy. Usually one samples stomachs either by representative (purely random) sampling from a catch, or the samples are taken from the different length-strata (5 or 10 cm length intervals). In addition stomachs are either analyzed individual by individual or they are bulked.

List of weighting factors

Individual random sampling :

- total catch in numbers (normalized to per. nm, per. 10nm, per. 1 hour towing or a similar normalization) divided by sample size.
- A length based measure of ship/trawl efficiency (as compared to a 'standard vessel').

Individual and bulked stratified random sampling :

- total catch within length-strata (normalized) divided by within length-strata sample size.
- ship/trawl efficiency (by length-strata).

Rule of thumb: Weights should sum up to total (normalized) catch. If needed the weights can be normalized so that their sum equals 1.

9.3.3 Weighting between stations

Fairly straightforward estimates of means (within an area-stratum) can be obtained directly from using each observation within the stratum with the weights mentioned in Section 9.3.2. Both overall estimates and separate estimates for the different length-strata are obtained in the same manner. Population parameters should be estimated by using the abundance estimates for each area-stratum and length-stratum divided by total number of observations in the same area-stratum and length-stratum as weights. Note that if one chooses to use the abundance estimates (indices) from the same survey that sampled the stomachs, the data can possibly be correlated in peculiar ways.

9.4 The Use of Covariates

Stomach data are quite expensive to collect, and one is usually restricted to quite low number of samples. The use of covariates could be a way of increasing precision in the estimates. The most efficient covariates will be those that are sampled with a higher density (denser grid) than the stomach-sampling trawl stations. Such covariates could include environmental data having effect on the predators feeding. This includes also environmental data affecting different prey species. It is also reasonable to believe that additional sampled data could help. Examples are prey densities measured either with traditional sampling gear or by acoustics.

10 CONCLUSIONS AND RECOMMENDATIONS

Conclusions

- 1) Development of the next generation of software tools for Multi-species, Multi-fleet analyses is a complex undertaking. This complexity results from, on one hand, the requirement of ACFM to make these tools 'user friendly', while at the same time accommodating the needs for increasing complexity in the analysis (e.g., spatial dynamics in predation and fleets). The requirements and features for such new software are reviewed. It is envisaged that a 'core' model be made available to area-based working groups, while a more speculative 'research version' be developed to test various hypotheses regarding Multispecies, Multi-fleet interactions.
- 2) Given the complexity of the tasks of developing new software, an international cooperative approach to the development, coding, testing and documentation of the tools is deemed critical. These tasks are best shared among various interested parties, with a coordinating group created to guide the software development program.
- 3) Results of long-term predictions of the impacts of effort reductions applied to the various North Sea fleets was used to fit a statistical model to the response surface of yields and SSBs, contingent on fleet effort change. This simplified version of the prediction model can be used to investigate, to a first approximation, the influences of manipulating effort within the context of interacting fish stocks and fleets. The model exists on a microcomputer spreadsheet, thus allowing its distribution to ACFM and various other technological neanderthals for exploring the consequences of management scenarios. Users are, however, cautioned that results are only an approximation to the exact results from MSFOR predictions, and that running scenarios with effort changes $\geq 50\%$ in any fleets or drive stocks to extreme abundance levels (e.g. below MBAL).
- 4) The incorporation of objective tuning methods within the MSVPA model was initiated, with trial runs indicating that the extended survivors (XSA) algorithm was generally feasible for this purpose. Further development and testing of this method is desirable and necessary before the next meeting of the MSWG.
- 5) The potential for 'switching' among alternative prey by predators, as a function of prey abundance, was investigated with a flexible form of the MSVPA suitability equation. Trial analyses indicated that invocation of moderate 'negative switching' (i.e., prey under-representation in predator diets at high prey stock sizes, and vice-versa) generated marginally better fits to predicted stomach contents and fitted suitabilities, than neutral or positive switching. This result, although tenuous, was evident in trial runs undertaken both for the North Sea but was less evident in the Baltic. The 1991 stomach data for the North Sea will be important in fully evaluating this result. Likewise, comparisons among all predator/prey combinations are necessary to evaluate the generality of the result.
- 6) Analyses of cod growth in boreal systems, initiated at the last meeting of the MSWG, indicated a significant YEAR effect in growth, after predator and prey abundance and temperature effects were removed. The existence of this YEAR effect was further investigated at this meeting, through the evaluation of cod feeding data in 6 widely ranging ecosystems (three eastern and three western Atlantic; three boreal and three temperate waters). Results although preliminary, shed significant light on processes feeding, growth, prey availability and environmental variability.
- 7) Within the six cod ecosystems, general linear models were used to investigate factors influencing

total stomach content weight (all prey types aggregated), the total fish component of food, and the fraction of stomachs empty. Stomach content data were length scaled ($1/L^{**3}$) to remove the effect of predator size, and transformed to comply better with assumptions of analyses. Because of the large number of degrees of freedom in these analyses, the MAIN effects of YEAR, QUARTER, TIME OF DAY and PREDATOR LENGTH were generally significant, although the relative significance of these factors varied among systems. Interaction effects examined at the meeting were generally smaller than main effects.

- 8) Multivariate analyses of variance of the effects of YEAR, TEMPERATURE and PREDATOR LENGTH on fraction of empty stomachs and total food were examined for four of the ecosystems where temperature measurements associated with stomach sampling were available (Barents Sea, Iceland, Newfoundland, Northeast USA). In most cases the TEMPERATURE effects explain the greatest residual variance in total food. For the three boreal systems, the YEAR effect was more important than LENGTH. For the temperate water system, length effects were more important in predicting total food than was the residual YEAR effect. Similarly, the fraction of empty stomachs was more related to TEMPERATURE and YEAR effects in the boreal systems than in the temperate ecosystem.
- 9) Principal component analyses of the occurrence of various dietary items, environmental variables (depth, temperature) and predator attributes (CPUE, length) were undertaken to scan these large data sets for associated factors. Several common patterns appeared in analyses of all ecosystems. The ontogenetic pattern of decreasing dependence on invertebrates, particularly crustaceans, with size was clearly apparent in all systems. Increasing representation of fish in the diets was inversely related to invertebrate feeding in the North and Baltic Seas, but was largely independent of the level of feeding on invertebrates in the other ecosystems. The PCA indicated most variation in depth and temperature was not associated with changes in diets. Also, the PCA showed clearly how the feeding 'niche space' of cod increased markedly with fish size.
- 10) Inter-ecosystem comparisons aimed at testing hypotheses set at the meeting of the Study Group on Analysis of Feeding Data were undertaken. Significant and coherent ecosystem effects were found. Ecosystems exhibiting higher average stomach content weights tended to lower proportions of empty stomachs. In four of the systems examined (Barents, Iceland, Newfoundland, USA) there was an inverse relationship between average stomach
- content weight and temperature, and a direct relation between growth and temperature. The effects of temperature need to be examined further when data for all ecosystems are available.
- 11) Significant differences in total food content, fraction of empty stomachs and prey composition were evident among systems. Boreal systems generally had the highest percentage of fish prey, and variation in total stomach content was large. Mean stomach content weight was lowest in the Baltic. The USA cod consumed the largest fraction of non-fish food, and this conclusion was consistent across size intervals. The relative position of the six ecosystems with regards total stomach content was consistent among size classes of cod examined.
- 12) Cod growth data sets were assembled in order to compare feeding levels with measures of incremental change in age-at-length among systems. These comparisons are intriguing, as there are large differences in growth and feeding rates among the systems. However, at present, the relationship between growth and feeding remains confounded by the inter-dependencies of growth, temperature-dependent stomach evacuation, and differences in environmental temperature. Initial ordering of stomach content weights on growth, corrected for temperature effects, suggests a negative relation, consistent with higher MEAN stomach content weights in cooler systems. However, these results are contingent on more thorough analyses unconfounding the above-associated variables.
- 13) The potential for cod to compensate for low capelin abundance in boreal systems with alternate food items was evaluated. The apparent scope for compensation among the systems was different.
- 14) Empirical analyses of cod growth, feeding and recruitment conducted at this and the previous MSWG meeting, suggest that boreal systems are functionally different from highly-networked feeding webs such as the North Sea. Thus, the assumption of constancy of total food consumption, growth, and perhaps predator/prey suitability, which are incorporated into the MSVPA structure, do not seem to apply to boreal systems. Nevertheless, more appropriate models could be developed that incorporate retrospective stock size, F, and predation mortality (M2) estimation and allow for prey-mediated predator growth and environmentally-induced variation in predator/prey overlap. Development of such a retrospective model may capture the MAIN features of cod-capelin interactions, and allow testing of MAJOR assumptions. Thus, the development and testing of a simple retrospective analysis of fishing

and predation mortalities for boreal systems is a promising approach.

- 15) The Working Group considered aspects of the statistical treatment of stomach sampling data, but a comprehensive evaluation of the subject was beyond the scope of the meeting. Proper estimators of precision of stomach content and prey composition are contingent on accounting for the effects of sampling design from which abundance is estimated, the sampling scheme for the selection of stomachs, and the treatment of zero stomach content observations. Trial analyses indicate that the development of logit models of the fraction of empty stomachs was feasible. The fraction of empty stomachs generally varied inversely with (time since lunch) [was it good!] food content, consistent with a negative binomial model. A more thorough treatment of this topic is necessary, particularly as the complete feeding data set for the 1991 stomach sampling program becomes available.
- 16) The Working Group is confronted with the practical problem of estimating catch-at-age for one year of the industrial fish catch for which sampling was inadequate (1990). Given that these estimates are important for determining stock sizes of prey species/ages in 1991 (the year of intensive stomach sampling), the 'fix-up' of missing data takes on added significance. Three potential approaches, including integrated models and a general linear model were tested.
- 17) Estimates of the total amount of sprat and herring (by length group) eaten by Baltic cod was compared to prey stock sizes by length group. Preliminary analyses of predator/prey size ratios suggest that large cod select relatively smaller fish prey compared to their size, than do smaller cod.
- 18) The effect of changes in recruitment level on MSFOR forecasts was again investigated through simulation methods. A factorial design of recruitment variation ($\pm 50\%$) combinations of all MSVPA species was simulated, along with a 30% effort reduction scenario for the roundfish human consumption fishery. The distribution of percentage changes in spawning stock biomass of each stock in 512 model runs (combinations of species recruitment changes) was assessed. The range of SSB outcomes from the predictions was more variable for some species (e.g., haddock) than for others (cod, whiting). However, no probabilities can be associated with long-term recruitment prospects for any stock forecasts, either single- or Multi-species.

- 19) A food-web analysis was applied to MSVPA results and data on lower trophic levels gathered from the literature. The analysis allows tracking of the trophic linkages among species (as the MSWG has undertaken in the past) but including a wider spectrum of producers and consumers. Initial results indicated discrepancies in the production characteristics among some MSVPA species. The value of the approach as an alternative check on fishery-based models of commercial components of the ecosystem is clear.

Recommendations

- 1) The next meeting of the Multispecies Assessment Working Group should be convened in 18 month's time (November, 1993) at the ICES headquarters for 10 days with suggested terms of references to include:
 - a) continue the development of multispecies methods of assessment, and report on progress in development, testing and distribution of updated software for multi-species, multi-fleet assessments;
 - b) integrate the results of the 1991 Stomach Sampling Program and produce an updated MSVPA for the North Sea, including further testing of the assumption of constant suitability;
 - c) evaluate the statistical properties of stomach sampling schemes, and continue the statistical analysis of feeding data;
 - d) initiate data preparation and model construction to apply retrospective multispecies assessment techniques to boreal systems, including variable predator growth and spatial overlap in predators and prey.
- 2) It is recommended that a set of two Cooperative Research Reports be prepared, under the editorships of J. Pope and S. Murawski, documenting progress made in advancing multispecies assessments at the seven meetings of the Multispecies Assessment Working Group.
- 3) The Multispecies Assessment Working Group endorses the recommendation of the Planning Group for the 1991 Stomach Sampling Program to hold a meeting in September, 1993 to prepare the feeding data, in advance of the next meeting of the Multispecies Assessment Working Group.
- 4) Incorporation of a fully-tested tuning algorithm in the current version of MSVPA is considered critical to the next meeting of the Multispecies Assessment Working Group, and completing the testing is a

priority for the development of new software. Therefore, it is recommended that work on the development of tuning algorithms continue, with appropriate exchanges of personnel, at national expense. This work should be completed well in advance of the next meeting of the Multispecies Assessment Working Group.

- 5) The development of new software packages to extend multi-species, multi-fleet assessment tools, and to deliver such products in "user friendly" formats to area-based Working Groups is considered a priority, not only by ACFM, but by the Working Group as well. To this end, the Working Group sees great utility in the establishment of a Coordinating Group for the Development of Multi-Species, Multi-Fleet Assessment Tools (COGMAT). Composition of COGMAT should include members of the Multispecies Assessment and the Long-Term Management Measures Working Groups, with representation from the ultimate users of products: the area-based working groups. The establishment of COGMAT is recommended to ACFM. It is proposed that the Coordinating Group meet for four days in March, 1993 (one month after the first meeting of the Long-Term Management Measures Working Group).
- 6) The Working Group was able to complete its computations utilizing the UNIX workstations of the ICES headquarters with networked PC's. Additional computing was accomplished at DIFMAR, and at various national institutes using internet protocols. The Working Group foresees great difficulty in completing its tasks at its next meeting with but one UNIX workstation at the ICES headquarters. Re-programming of the Multi-species Multi-fleet analysis models will be accomplished so that working groups can run these models on the ICES workstation. Therefore, the Multispecies Assessment Working Group strongly recommends that ICES purchase a second UNIX workstation and additional PCs for scientific computing.
- 7) The scheduling of another assessment working group meeting coinciding for four days with that of the Multispecies WG was problematic for both. In the future such practices should be strongly discouraged, since the MSWG has the nasty habit of laying waste to almost all computing resources and support services available to it.

11 REFERENCES

Alvarez, J. and S. Tjelmeland. 1989. MULTSPEC og oseanografi. IMR int. doc. (in Norwegian). 17pp.

Anon. 1974. Methodical manual on the study of feeding and feeding relations of fish in natural conditions. - Moscow, Nauka Press, 1974. 254pp.

Anon. 1980. Report of the *ad hoc* Working Group on Multispecies Model Testing. ICES, Doc. C.M. 1980/G:2

Anon. 1981. Draft manual for the Stomach Sampling Project. Netherlands Institute for Fishery Investigations, Ijmuiden. 43pp.

Anon. 1984. Report of the *ad hoc* Multispecies Assessment Working Group. ICES, Doc. C.M.1984/Assess:20.

Anon. 1986. Report of the *ad hoc* Multispecies Assessment Working Group. ICES, Doc. C.M.1986/Assess:9.

Anon. 1989a. Report of the Multispecies Assessment Working Group. ICES, Doc. C.M.1989/Assess:20.

Anon. 1989b. Report of the Study Group on Cod Stomach Data for the Baltic, Gdynia, 23-27 January 1989. ICES, Doc. C.M.1989/J:2.

Anon. 1990a. Report of the industrial fisheries working group. ICES, Doc. C.M.1990/Assess:13.

Anon. 1990b. Report of the Working Group on the Multispecies Assessment of Baltic Fish, Gdynia, 6-10 August 1990. ICES, Doc. C.M.1990/Assess:25.

Anon. 1991. Report of the Multispecies Assessment Working Group. ICES, Doc. C.M.1991/Assess:7.

Anon. 1992a. Report of the Study Group on the Analysis of Feeding Data, St. John's, 17-19 March 1992. ICES, Doc. C.M.1992/G:4. 21pp.

Anon. 1992b. Progress report on the ICES 1991 North Sea stomach sampling project. ICES, Doc. C.M. 1992/G:12. 35pp.

Anon. 1992c. The international cod stomach data base for the Baltic Sea. Some comments for ICES MSWG meeting in June 1992. Working Paper No. 2. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 3pp.

Anon. 1992d. Report of the Study Group on the Ecosystem Effects of Fishing. ICES, Doc. C.M. 1992/Assess: (in prep.)

Anon. 1992e. Report of the Industrial Fisheries Working Group. ICES, Doc. C.M.1992/Assess:9

- Anon. 1992f. Report of the Working Group on Multispecies Assessment of Baltic Fish. ICES, Doc. C.M. 1992/Assess:7.
- Anon. 1992g. Reports of the Advisory Committee on Fishery Management. ICES Coop. Res. Rep. No. 179.
- Baden, S.P. 1986. Recent changes in the Kattegat and Skagerrak ecosystem and their possible interdependence. Nat. Swedish Environ. Protection Board Rep. 3157. 91pp.
- Bogstad, B. and S. Mehl. 1992. Description of the Norwegian/Russian stomach data set. Working Paper No. 3. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 7pp.
- Bogstad, B., M. Pennington, and J.H. Volstad. 1991. An evaluation of survey design for estimating the food consumption by fish. ICES, Doc. C.M.1991/D:15.
- Bowman, R.E. 1982. Preliminary evaluation of results of analyses of the stomach contents of silver hake (*Merluccius bilinearis*) aboard ship and in the laboratory ashore. Nat. Mar. Fish Serv., Woods Hole Lab., Ref. Doc. 82-25. 13pp.
- Bundgaard, I. and H. Sparholt. 1992. Length-based multispecies model for estimation of predation mortalities of herring and sprat. Working Paper #12. ICES Multispecies Assessment Working Group, June, 1992, Copenhagen, Denmark. 22pp.
- Chesson, J. 1978. Measuring preference in selective predation. Ecology 59(2): 211-215.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64(5): 1297-1304.
- Chesson, P.L. 1984. Variable predators and switching behavior. Theor. Pop. Biol. 26: 1-26.
- Christensen, V., and D. Pauly. 1992. ECOPATH II - A software for balancing steady state models and calculating network characteristics. Ecol. Modelling, 00: 000-000.
- Cook, R.M. 1992b. Assessment of North Sea fish stocks when data are missing. Working Paper No. 7. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 25 pp.
- Cook, R.M. 1992a. Appendix 1 in Anon. (1992)
- Daan, N. (ed.) 1989. Data base report of the stomach sampling project 1981. ICES Coop. Res. Rep. No. 164. 144pp.
- Daan, N, P.J. Bromley, J.R.G. Hislop, and N.A. Nielsen. 1990. Ecology of North Sea fish. Nether. J. Sea Res. 26(2-4): 343-386.
- Dahl, K. and E. Kirkegaard. 1987. The diet and consumption of horse mackerel (*Trachurus trachurus*) in the Eastern North Sea, August 1986. ICES, Doc. C.M. 1987/H:43. 23pp.
- Deriso, R.B., T.J. Quinn, II and P.R. Neal. 1985. Catch at age analysis with auxiliary information. Can. J. Fish. Aquat. Sci. 42: 815 - 824.
- DeSilva, S.S. 1973. Foods and feeding habits of the herring *Clupea harengus* and sprat *C. sprattus* in inshore waters of the west coast of Scotland. Mar. Biol. 20: 282-290.
- Degnbol, P. 1992. Description of data set: whiting stomachs sampled with "Dana" in the North Sea 1988-89. Working Paper No.1. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 2pp.
- Doubleday, W.G. 1981. A method for estimating the abundance of survivors of an exploited fish population using commercial catch-at-age and research vessel abundance indices. Can. Spec. Pub. Fish. Aquat. Sci. 58:164-178.
- Doubleday, W.G. (ed.) 1981. Manual on groundfish surveys in the Northwest Atlantic. NAFO Sci. Coun. Studies, 2: 7-55.
- Finn, J.T., Idoine, J.S., and Gislason, H. 1991. Sensitivity analysis of multispecies assessments and predictions for the North Sea. ICES, Doc. C.M. 1991/D:7.
- Fransz, H.G. and W.W.C. Gieskes. 1984. The unbalance of phytoplankton and copepods in the North Sea. Rapp. P.-v. Reun. Cons. int. Explor. Mer, 183: 218-225.
- Gislason, H. 1991. The influence of variations in recruitment on multispecies yield predictions in the North Sea. ICES mar. Sci. Symp., 193:50-59.
- Gislason, H. 1992. The multispecies equivalent to the yield per recruit model of Beverton and Holt. Working Paper No.10. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 32pp.

- Hilden, M. 1988. Significance of the functional response of predators to changes in prey abundance in multispecies virtual population analysis. *Can. J. Fish. Aquat. Sci.* 45: 89-96.
- Jones, R. 1982. Species interactions in the North Sea, p. 48-63 in Mercer, M.C. (Ed.) *Multispecies approaches to fisheries management advice*. *Can. Spec. Publ. Fish. Aquat. Sci.* 59: 169 p.
- Jones, R. 1984. Some observations on energy transfer through the North Sea and Georges Bank food webs. *Rapp. P.-v. Reun. Cons. int. Explor. Mer*, 183: 204-217.
- Langton, R.W. and R.E. Bowman. 1980. Food of fifteen northwest Atlantic gadiform fishes. NOAA Technical Rep., NMFS SRRF-740. 23pp.
- Lilly, G.R. 1987. Interactions between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review. *Can. Tech. Rep. Fish. Aquat. Sci.*, 1567: 37pp.
- Lilly, G.R. 1991. Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland. *ICES mar. Sci. Symp.*, 193: 133-146.
- Lilly, G. and P. Shelton. 1992. The cod stomach data set from southern Labrador and northeastern Newfoundland. Working Paper No.5. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 9pp.
- Magnússon, K. and O. Pálsson. 1989. On the trophic ecological relationships of Iceland cod. *Rapp. P.-v. Réun. Cons. int. Explor. Mer.* 188:206-224.
- Magnússon, K. and O. Pálsson. 1991. Predator-prey interactions of cod and capelin in Icelandic waters. *ICES mar. Sci. Symp.*, 193:153-170.
- Manly, B.F.J. 1974. A model for certain types of selection experiments. *Biometrics* 30: 281-294.
- Mehl, S. 1986. Revised and modified programs for storing, analysis and presentation of taxonomic and quantitative stomach content data. *Rapp. Havforskningsinstituttet, BN 8601*. 62pp. (unpubl.).
- Mehl, S. and N.A. Yaragina. 1991. Methods and results in the joint PINRO-IMR stomach sampling program. *Contr. Fifth Soviet-Norwegian Symp.* "Interrelations between fish populations in the Barents Sea", Murmansk 11-17 August 1991. 12 pp.
- Murawski, S.A. and D.G. Mountain. 1990. Climate change and marine fish distributions: analogies from seasonal and annual variability. *ICES, Doc. C.M.1990/C:36 24 pp.*
- Murdoch, W.W. 1969. Switching in general predators; experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39: 335-354.
- Oaten, A. and W.W. Murdoch. 1975. Switching, functional response and stability in predator-prey systems. *Amer Natur.* 109:299-308.
- Overholtz, W.J. and S.A. Murawski. 1992. Analysis of Atlantic cod and silver hake stomach sampling from the northeast USA shelf, 1981-1988. Working Paper No.6. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 14pp.
- Penttila, J.A. and V.M. Gifford. 1976. Growth and mortality rates for cod from Georges Bank and Gulf of Maine areas. *Int. Commn. Northw. Atl. Fish. Res. Bull.* 12:29-36.
- Pálsson, O.K. 1984. Studies on recruitment of cod and haddock in Icelandic waters. *ICES C.M. Doc.*, No. G:6, 18pp.
- Pálsson, O.K., E. Jonsson, S.A. Schopka, G. Stefansson, and B.Æ. Steinarrson. 1989. Icelandic ground-fish survey data used to improve precision in stock assessments. *J. Northw. Atl. Fish. Sci.*, Vol.: 53-72.
- Pálsson, O. 1992. The Icelandic cod stomach data base. Working Paper No. 4. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 4pp.
- Pope, J.G. 1979. Stock assessment in multispecies fisheries, with special reference to the trawl fishery in the Gulf of Thailand. *FAO South China Sea Fisheries Development and Coordination Program SCS/DEV/79/19* 106pp.
- Shepherd, J. 1992. Extended survivors' analysis: an improved method for the analysis of catch-at-age data and catch-per-unit-effort data. Working Paper No.11. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 16pp.
- Singh, S. and J.G. Pope. 1992. Approaches to the smoothed estimation of prey/predator suitability. Working Paper No.9. ICES Multispecies Assessment Working Group, June 1992, Copenhagen, Denmark. 22pp.

- Sparholt, H. 1990a. A Stochastic integrated VPA for herring in the Baltic Sea using acoustic estimates as auxiliary information for estimating natural mortality. *J. Cons.Int. Explor. Mer*, 46:325-332.
- Sparholt, H. 1990b. An estimate of the total biomass of fish in the North Sea. *J. du Cons.* 46:200-210.
- Sparholt, H., H. Jensen, and I.B. Jensen. 1991. The international cod stomach data base for the Baltic Sea and some preliminary analyses. *ICES C.M.1991/J:30*.
- Sparre, P. 1984. A computer program for estimation of food suitability coefficients from stomach content data and multi-species VPA. *ICES, Doc. C.M.1984/G:25*.
- Tretyak, V.L., V.A. Korzhev, and N.A. Yaragina. 1990. Methodical recommendations for studying food relations between fish for mathematical modelling of the Barents Sea ecosystem. Murmansk, PINRO. 80pp. (unpubl.).
- Ulanowicz, R.E. and C.J. Puccia. 1990. Mixed trophic impacts in ecosystems. *Coenoses* 5: 7-16.
- Westgard, T. 1982. Programs for handling and analysis of stomach contents data. *ICES, Doc. C.M.1982/-H:21*.

Unreferenced Working Paper:

- Kunzlik, P.A. and S.T. Forbes. 1992. Yet more exploitation scenarios. Working Paper No.8. ICES Multi-species Assessment Working Group, June 1992, Copenhagen, Denmark. 22pp.

	CHANGE
FLEET	
RF-HC	0.5
RF-DIS.	
IND-DEM	0.5
IND-PEL	0.5
HERRING	0.5
SAITHE	0.5
MACKERE	0.5
FLATFIS	0.5

Table 2.4.1. Comparison of spread sheet approximation (left) and MSFOR model (right) predictions of percent differences in spawning stock biomass and yields (from status quo effort patterns) for North Sea fish stocks, contingent on 50% effort reductions by fleet (i.e., the most extreme effort changes allowed in the spread sheet approximation model). Divergent predictions by the two models are shaded and italicized.

	SSB	RF-HC	IND-DEM	IND-PEL	HERRING	SAITHE	MACKEREL	FLATFISH	DISCARDS	CATCH
Cod	129	140	-30							-31
whi	23	21	-12	-50	-51				-45	-35
sai	160	251	19	-33	-24	-17	4			-13
mac	92	141					-27			-27
had	-4	-51	-73	-60	-79				-62	-85
her	35	30		-35	-27	-31				-31
spr	28	29		-40	-38					-40
nop	-15	-44	-61	-86						-61
amm	34	49	-35	-27						-35
ple	41	91						-22	7	-22
sol	61	126						-17	6	-17

Table 2.4.2. Approximate directions of fleet effort change resulting in maximum rates of spawning stock biomass increase, in the steady-state (i.e., Roundfish-Human Consumption effort of 0.75 times current effort, and effort levels as given in the first column, result in greatest increases in SSB for cod).

	cod	whi	sai	mac	had	her	spr	nop	amm	ple	sol
FLEET											
RF-HC	0.750	0.802	0.750	1.000	0.870	1.095	1.009	1.340	1.008	1.000	1.000
IND-DEM	0.997	0.750	0.985	1.000	0.936	1.027	1.009	0.750	0.750	1.000	1.000
IND-PEL	0.997	0.928	1.000	1.000	0.969	0.750	0.750	1.000	1.000	1.000	1.000
HERRING	1.000	1.000	1.000	1.000	1.000	0.819	1.000	1.000	1.000	1.000	1.000
SAITHE	1.011	1.024	0.782	1.000	1.271	1.018	1.000	1.222	0.992	1.000	1.000
MACKEREL	1.006	1.000	1.000	0.750	1.016	1.018	1.009	1.000	1.030	1.000	1.000
FLATFISH	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	1.000	0.750	0.750

Table 4.1. An hypothetical example of the effect of prey biomass on estimates of overall suitability in the case where the predator does not share the same distribution area as the prey. Half the predator population is found in each area. Suitability of prey = 0.5 and suitability of other food = 0.5 within each area.

Situation 1

Area	Prey biom.	Biom. Oth. food	Rel. St. cont.
north	1	1	.5
south	0	1	.0
Average prop. of prey in stom cont.:			.25
Estimate of overall suitability of prey from observed av. stomach content $(.25/ (.25+.75/2))=$:			.40

Situation 2

Area	Prey biom.	Biom. Oth. food	Rel. St. cont.
north	2	1	.67
south	0	1	.0
Average prop. of prey in stom cont.:			.33
Estimate of overall suitability of prey from observed av. stomach content $(.33/2/ (.33/2+.67/2))=$:			.33

Table 4.3. Correlation between age 1 stock sizes estimated using MSVPA, with varying levels of the switching coefficient, and the IYFS abundance indices for the North Sea. The model tested is: $\ln(\text{MSVPA}) = a \cdot \ln(\text{IYFS}) + b$. Data are R^2 values for various species and degrees of switching (-0.6 to +0.4).

	-0.6	-0.4	-0.2	0.0	0.2	0.4
Cod	0.56	0.54	0.52	0.50	0.46	0.44
Whiting	0.57	0.60	0.62	0.63	0.65	0.66
Haddock	0.79	0.84	0.87	0.88	0.86	0.81
Herring	0.77	0.80	0.79	0.78	0.78	0.79
N. pout	0.70	0.73	0.75	0.77	0.78	0.70

Table 5.1. Characteristics of cod feeding data sets analyzed, by ecosystem.

Characteristic	North Sea	Baltic Sea	Barents Sea	Iceland	Newf'dland	N.E. USA	Total
Number of samples	7,871	8,966	35,753	9,364	26,273	8,501	96,728
Number of fish	41,161	50,737	35,753	38,210	26,273	8,501	200,635
Mean predator length (cm)	37.48	41.05	47.43	54.27	51.53	53.75	45.87
Mean total food weight (g)	30.39	13.44	21.55	45.40	33.73	27.74	27.70
Proportion of empty stomachs	.1385	.2055	.2175	.1589	.0295	.1562	.1599

Table 5.2.1. Distribution of North Sea cod samples used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
	1	2	3	4	
80	378 4.80 36.45 12.85	198 2.52 19.09 10.14	349 4.43 33.65 14.56	112 1.42 10.80 19.31	1037 13.17
81	608 7.72 35.98 20.67	380 4.83 22.49 19.46	329 4.18 19.47 13.73	373 4.74 22.07 64.31	1690 21.47
82	249 3.16 34.30 8.47	173 2.20 23.83 8.86	209 2.66 28.79 8.72	95 1.21 13.09 16.38	726 9.22
84	0 0.00 0.00 0.00	1202 15.27 100.00 61.55	0 0.00 0.00 0.00	0 0.00 0.00 0.00	1202 15.27
85	612 7.78 61.94 20.81	0 0.00 0.00 0.00	376 4.78 38.06 15.69	0 0.00 0.00 0.00	988 12.55
86	539 6.85 49.91 18.33	0 0.00 0.00 0.00	541 6.87 50.09 22.57	0 0.00 0.00 0.00	1080 13.72
87	555 7.05 48.34 18.87	0 0.00 0.00 0.00	593 7.53 51.66 24.74	0 0.00 0.00 0.00	1148 14.59
Total	2941 37.37	1953 24.81	2397 30.45	580 7.37	7871 100.00

Table 5.2.2. Distribution of North Sea cod (as individual fish, excluding regurgitated stomachs) used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
Frequency Percent Row Pct Col Pct	1	2	3	4	
80	2653 6.45 29.43 17.94	2864 6.96 31.77 36.35	2562 6.22 28.42 17.38	937 2.28 10.39 24.97	9016 21.90
81	3872 9.41 36.94 26.19	2202 5.35 21.01 27.94	2019 4.91 19.26 13.70	2390 5.81 22.80 63.68	10483 25.47
82	1000 2.43 23.82 6.76	1612 3.92 38.39 20.46	1161 2.82 27.65 7.88	426 1.03 10.15 11.35	4199 10.20
84	0 0.00 0.00 0.00	1202 2.92 100.00 15.25	0 0.00 0.00 0.00	0 0.00 0.00 0.00	1202 2.92
85	2496 6.06 54.91 16.88	0 0.00 0.00 0.00	2050 4.98 45.09 13.91	0 0.00 0.00 0.00	4546 11.04
86	2547 6.19 42.59 17.22	0 0.00 0.00 0.00	3433 8.34 57.41 23.29	0 0.00 0.00 0.00	5980 14.53
87	2219 5.39 38.69 15.01	0 0.00 0.00 0.00	3516 8.54 61.31 23.85	0 0.00 0.00 0.00	5735 13.93
Total	14787 35.92	7880 19.14	14741 35.81	3753 9.12	41161 100.00

Table 5.2.3. Distribution of North Sea cod (as individual fish, including regurgitated stomachs) used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
Frequency Percent Row Pct Col Pct	1	2	3	4	
80	2653 5.98 29.43 16.41	2864 6.46 31.77 35.27	2562 5.78 28.42 15.83	937 2.11 10.39 24.14	9016 20.33
81	4181 9.43 36.43 25.86	2437 5.49 21.24 30.01	2345 5.29 20.43 14.49	2513 5.67 21.90 64.75	11476 25.88
82	1085 2.45 25.21 6.71	1618 3.65 37.59 19.92	1170 2.64 27.18 7.23	431 0.97 10.01 11.11	4304 9.70
84	0 0.00 0.00 0.00	1202 2.71 100.00 14.80	0 0.00 0.00 0.00	0 0.00 0.00 0.00	1202 2.71
85	2705 6.10 51.36 16.73	0 0.00 0.00 0.00	2562 5.78 48.64 15.83	0 0.00 0.00 0.00	5267 11.88
86	2977 6.71 44.36 18.42	0 0.00 0.00 0.00	3734 8.42 55.64 23.08	0 0.00 0.00 0.00	6711 15.13
87	2565 5.78 40.24 15.87	0 0.00 0.00 0.00	3809 8.59 59.76 23.54	0 0.00 0.00 0.00	6374 14.37
Total	16166 36.45	8121 18.31	16182 36.49	3881 8.75	44350 100.00

Table 5.3.1. Distribution of Baltic Sea cod samples used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
	1	2	3	4	
77	28	28	5	20	81 0.90
	0.31	0.31	0.06	0.22	
	34.57	34.57	6.17	24.69	
	0.50	5.32	0.94	0.88	
78	39	32	12	40	123 1.37
	0.43	0.36	0.13	0.45	
	31.71	26.02	9.76	32.52	
	0.69	6.08	2.26	1.76	
79	23	23	20	41	107 1.19
	0.26	0.26	0.22	0.46	
	21.50	21.50	18.69	38.32	
	0.41	4.37	3.77	1.80	
80	29	26	18	21	94 1.05
	0.32	0.29	0.20	0.23	
	30.85	27.66	19.15	22.34	
	0.51	4.94	3.40	0.92	
81	35	169	31	903	1138 12.69
	0.39	1.88	0.35	10.07	
	3.08	14.85	2.72	79.35	
	0.62	32.13	5.85	39.69	
82	2012	40	29	1049	3130 34.91
	22.44	0.45	0.32	11.70	
	64.28	1.28	0.93	33.51	
	35.71	7.60	5.47	46.11	
83	1165	39	3	46	1253 13.98
	12.99	0.43	0.03	0.51	
	92.98	3.11	0.24	3.67	
	20.67	7.41	0.57	2.02	
Total	5635	526	530	2275	8966
	62.85	5.87	5.91	25.37	100.00

(Continued)

Table 5.3.1 (continued).

YEAR	QUARTER				Total
Frequency Percent Row Pct Col Pct	1	2	3	4	
84	787 8.78 88.63 13.97	38 0.42 4.28 7.22	21 0.23 2.36 3.96	42 0.47 4.73 1.85	888 9.90
85	1103 12.30 95.33 19.57	23 0.26 1.99 4.37	0 0.00 0.00 0.00	31 0.35 2.68 1.36	1157 12.90
86	310 3.46 90.64 5.50	16 0.18 4.68 3.04	0 0.00 0.00 0.00	16 0.18 4.68 0.70	342 3.81
87	21 0.23 4.59 0.37	30 0.33 6.55 5.70	385 4.29 84.06 72.64	22 0.25 4.80 0.97	458 5.11
88	31 0.35 38.27 0.55	23 0.26 28.40 4.37	6 0.07 7.41 1.13	21 0.23 25.93 0.92	81 0.90
89	29 0.32 41.43 0.51	18 0.20 25.71 3.42	0 0.00 0.00 0.00	23 0.26 32.86 1.01	70 0.78
90	23 0.26 52.27 0.41	21 0.23 47.73 3.99	0 0.00 0.00 0.00	0 0.00 0.00 0.00	44 0.49
Total	5635 62.85	526 5.87	530 5.91	2275 25.37	8966 100.00

Table 5.3.2. Distribution of Baltic Sea cod (as individual fish, excluding regurgitated stomachs) used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
	1	2	3	4	
77	1702	942	283	376	3303
	3.35	1.86	0.56	0.74	6.51
	51.53	28.52	8.57	11.38	
	9.09	8.16	6.58	2.33	
78	1583	742	258	1544	4127
	3.12	1.46	0.51	3.04	8.13
	38.36	17.98	6.25	37.41	
	8.45	6.43	6.00	9.56	
79	753	476	563	2209	4001
	1.48	0.94	1.11	4.35	7.89
	18.82	11.90	14.07	55.21	
	4.02	4.12	13.09	13.67	
80	773	797	859	807	3236
	1.52	1.57	1.69	1.59	6.38
	23.89	24.63	26.55	24.94	
	4.13	6.90	19.98	4.99	
81	934	884	843	2153	4814
	1.84	1.74	1.66	4.24	9.49
	19.40	18.36	17.51	44.72	
	4.99	7.66	19.60	13.32	
82	3893	984	763	2802	8442
	7.67	1.94	1.50	5.52	16.64
	46.11	11.66	9.04	33.19	
	20.78	8.52	17.74	17.34	
83	1856	1642	21	2182	5701
	3.66	3.24	0.04	4.30	11.24
	32.56	28.80	0.37	38.27	
	9.91	14.22	0.49	13.50	
Total	18733	11546	4300	16158	50737
	36.92	22.76	8.48	31.85	100.00

(Continued)

Table 5.3.2(continued).

YEAR	QUARTER				Total
	1	2	3	4	
84	1678	659	210	1429	3976
	3.31	1.30	0.41	2.82	7.84
	42.20	16.57	5.28	35.94	
	8.96	5.71	4.88	8.84	
85	1958	639	0	782	3379
	3.86	1.26	0.00	1.54	6.66
	57.95	18.91	0.00	23.14	
	10.45	5.53	0.00	4.84	
86	546	543	0	626	1715
	1.08	1.07	0.00	1.23	3.38
	31.84	31.66	0.00	36.50	
	2.91	4.70	0.00	3.87	
87	507	1860	410	526	3303
	1.00	3.67	0.81	1.04	6.51
	15.35	56.31	12.41	15.92	
	2.71	16.11	9.53	3.26	
88	1165	396	90	326	1977
	2.30	0.78	0.18	0.64	3.90
	58.93	20.03	4.55	16.49	
	6.22	3.43	2.09	2.02	
89	789	688	0	396	1873
	1.56	1.36	0.00	0.78	3.69
	42.12	36.73	0.00	21.14	
	4.21	5.96	0.00	2.45	
90	596	294	0	0	890
	1.17	0.58	0.00	0.00	1.75
	66.97	33.03	0.00	0.00	
	3.18	2.55	0.00	0.00	
Total	18733	11546	4300	16158	50737
	36.92	22.76	8.48	31.85	100.00

Table 5.3.3. Distribution of Baltic Sea cod (as individual fish, including regurgitated stomachs) used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
	1	2	3	4	
77	1702	942	283	376	3303
	3.35	1.86	0.56	0.74	6.51
	51.53	28.52	8.57	11.38	
	9.09	8.16	6.58	2.33	
78	1583	742	258	1544	4127
	3.12	1.46	0.51	3.04	8.13
	38.36	17.98	6.25	37.41	
	8.45	6.43	6.00	9.56	
79	753	476	563	2209	4001
	1.48	0.94	1.11	4.35	7.89
	18.82	11.90	14.07	55.21	
	4.02	4.12	13.09	13.67	
80	773	797	859	807	3236
	1.52	1.57	1.69	1.59	6.38
	23.89	24.63	26.55	24.94	
	4.13	6.90	19.98	4.99	
81	934	884	843	2153	4814
	1.84	1.74	1.66	4.24	9.49
	19.40	18.36	17.51	44.72	
	4.99	7.66	19.60	13.32	
82	3893	984	763	2802	8442
	7.67	1.94	1.50	5.52	16.64
	46.11	11.66	9.04	33.19	
	20.78	8.52	17.74	17.34	
83	1856	1642	21	2182	5701
	3.66	3.24	0.04	4.30	11.24
	32.56	28.80	0.37	38.27	
	9.91	14.22	0.49	13.50	
Total	18733	11546	4300	16158	50737
	36.92	22.76	8.48	31.85	100.00

(Continued)

Table 5.3.3(continued).

YEAR	QUARTER				Total
	1	2	3	4	
84	1678	659	210	1429	3976
	3.31	1.30	0.41	2.82	7.84
	42.20	16.57	5.28	35.94	
	8.96	5.71	4.88	8.84	
85	1958	639	0	782	3379
	3.86	1.26	0.00	1.54	6.66
	57.95	18.91	0.00	23.14	
	10.45	5.53	0.00	4.84	
86	546	543	0	626	1715
	1.08	1.07	0.00	1.23	3.38
	31.84	31.66	0.00	36.50	
	2.91	4.70	0.00	3.87	
87	507	1860	410	526	3303
	1.00	3.67	0.81	1.04	6.51
	15.35	56.31	12.41	15.92	
	2.71	16.11	9.53	3.26	
88	1165	396	90	326	1977
	2.30	0.78	0.18	0.64	3.90
	58.93	20.03	4.55	16.49	
	6.22	3.43	2.09	2.02	
89	789	688	0	396	1873
	1.56	1.36	0.00	0.78	3.69
	42.12	36.73	0.00	21.14	
	4.21	5.96	0.00	2.45	
90	596	294	0	0	890
	1.17	0.58	0.00	0.00	1.75
	66.97	33.03	0.00	0.00	
	3.18	2.55	0.00	0.00	
Total	18733	11546	4300	16158	50737
	36.92	22.76	8.48	31.85	100.00

Table 5.4. Distribution of Barents Sea cod samples used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years). All samples are of individual fish, and no regurgitated stomachs are included in the data.

YEAR	QUARTER				Total
	1	2	3	4	
84	1051	346	2297	0	3694
	2.94	0.97	6.42	0.00	10.33
	28.45	9.37	62.18	0.00	
	6.92	6.12	15.59	0.00	
85	1882	808	1213	0	3903
	5.26	2.26	3.39	0.00	10.92
	48.22	20.70	31.08	0.00	
	12.39	14.28	8.23	0.00	
86	1969	594	2244	0	4807
	5.51	1.66	6.28	0.00	13.45
	40.96	12.36	46.68	0.00	
	12.96	10.50	15.23	0.00	
87	1652	862	3155	124	5793
	4.62	2.41	8.82	0.35	16.20
	28.52	14.88	54.46	2.14	
	10.88	15.24	21.41	71.26	
88	2492	239	2153	50	4934
	6.97	0.67	6.02	0.14	13.80
	50.51	4.84	43.64	1.01	
	16.41	4.22	14.61	28.74	
89	2811	1625	2020	0	6456
	7.86	4.55	5.65	0.00	18.06
	43.54	25.17	31.29	0.00	
	18.51	28.72	13.71	0.00	
90	1724	761	1479	0	3964
	4.82	2.13	4.14	0.00	11.09
	43.49	19.20	37.31	0.00	
	11.35	13.45	10.04	0.00	
91	1607	423	172	0	2202
	4.49	1.18	0.48	0.00	6.16
	72.98	19.21	7.81	0.00	
	10.58	7.48	1.17	0.00	
Total	15188	5658	14733	174	35753
	42.48	15.83	41.21	0.49	100.00

Table 5.5.1. Distribution of Icelandic cod samples used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
	1	2	3	4	
79	73	0	95	66	234
	0.78	0.00	1.01	0.70	2.50
	31.20	0.00	40.60	28.21	
	1.47	0.00	3.25	100.00	
80	152	219	302	0	673
	1.62	2.34	3.23	0.00	7.19
	22.59	32.54	44.87	0.00	
	3.05	15.63	10.34	0.00	
81	172	126	739	0	1037
	1.84	1.35	7.89	0.00	11.07
	16.59	12.15	71.26	0.00	
	3.46	8.99	25.30	0.00	
82	418	216	539	0	1173
	4.46	2.31	5.76	0.00	12.53
	35.64	18.41	45.95	0.00	
	8.40	15.42	18.45	0.00	
83	371	146	224	0	741
	3.96	1.56	2.39	0.00	7.91
	50.07	19.70	30.23	0.00	
	7.46	10.42	7.67	0.00	
84	388	110	0	0	498
	4.14	1.17	0.00	0.00	5.32
	77.91	22.09	0.00	0.00	
	7.80	7.85	0.00	0.00	
85	443	34	184	0	661
	4.73	0.36	1.96	0.00	7.06
	67.02	5.14	27.84	0.00	
	8.90	2.43	6.30	0.00	
Total	4976	1401	2921	66	9364
	53.14	14.96	31.19	0.70	100.00

(Continued)

Table 5.5.1 (continued).

YEAR	QUARTER				Total
	1	2	3	4	
86	515	35	0	0	550
	5.50	0.37	0.00	0.00	5.87
	93.64	6.36	0.00	0.00	
	10.35	2.50	0.00	0.00	
87	403	0	0	0	403
	4.30	0.00	0.00	0.00	4.30
	100.00	0.00	0.00	0.00	
	8.10	0.00	0.00	0.00	
88	477	38	208	0	723
	5.09	0.41	2.22	0.00	7.72
	65.98	5.26	28.77	0.00	
	9.59	2.71	7.12	0.00	
89	495	0	228	0	723
	5.29	0.00	2.43	0.00	7.72
	68.46	0.00	31.54	0.00	
	9.95	0.00	7.81	0.00	
90	597	211	188	0	996
	6.38	2.25	2.01	0.00	10.64
	59.94	21.18	18.88	0.00	
	12.00	15.06	6.44	0.00	
91	472	266	214	0	952
	5.04	2.84	2.29	0.00	10.17
	49.58	27.94	22.48	0.00	
	9.49	18.99	7.33	0.00	
Total	4976	1401	2921	66	9364
	53.14	14.96	31.19	0.70	100.00

Table 5.5.2. Distribution of Icelandic cod (as individual fish) used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years).

YEAR	QUARTER				Total
Frequency Percent Row Pct Col Pct	1	2	3	4	
79	549 1.44 46.64 2.82	0 0.00 0.00 0.00	365 0.96 31.01 3.04	263 0.69 22.34 100.00	1177 3.08
80	727 1.90 27.14 3.74	877 2.30 32.74 13.49	1075 2.81 40.13 8.95	0 0.00 0.00 0.00	2679 7.01
81	853 2.23 15.99 4.39	653 1.71 12.24 10.04	3829 10.02 71.77 31.89	0 0.00 0.00 0.00	5335 13.96
82	1827 4.78 34.64 9.40	1305 3.42 24.74 20.07	2142 5.61 40.61 17.84	0 0.00 0.00 0.00	5274 13.80
83	2099 5.49 54.55 10.80	752 1.97 19.54 11.57	997 2.61 25.91 8.30	0 0.00 0.00 0.00	3848 10.07
84	1413 3.70 68.83 7.27	640 1.67 31.17 9.84	0 0.00 0.00 0.00	0 0.00 0.00 0.00	2053 5.37
85	1792 4.69 61.96 9.22	250 0.65 8.64 3.85	850 2.22 29.39 7.08	0 0.00 0.00 0.00	2892 7.57
Total	19440 50.88	6501 17.01	12006 31.42	263 0.69	38210 100.00

(Continued)

Table 5.5.2(continued).

YEAR	QUARTER				Total
	1	2	3	4	
86	1760	277	0	0	2037
	4.61	0.72	0.00	0.00	5.33
	86.40	13.60	0.00	0.00	
	9.05	4.26	0.00	0.00	
87	1795	0	0	0	1795
	4.70	0.00	0.00	0.00	4.70
	100.00	0.00	0.00	0.00	
	9.23	0.00	0.00	0.00	
88	1721	311	730	0	2762
	4.50	0.81	1.91	0.00	7.23
	62.31	11.26	26.43	0.00	
	8.85	4.78	6.08	0.00	
89	1608	0	751	0	2359
	4.21	0.00	1.97	0.00	6.17
	68.16	0.00	31.84	0.00	
	8.27	0.00	6.26	0.00	
90	1801	663	603	0	3067
	4.71	1.74	1.58	0.00	8.03
	58.72	21.62	19.66	0.00	
	9.26	10.20	5.02	0.00	
91	1495	773	664	0	2932
	3.91	2.02	1.74	0.00	7.67
	50.99	26.36	22.65	0.00	
	7.69	11.89	5.53	0.00	
Total	19440	6501	12006	263	38210
	50.88	17.01	31.42	0.69	100.00

Table 5.6. Distribution of Newfoundland cod samples used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years). All samples are of individual fish, and no regurgitated stomachs are included in the data.

YEAR	QUARTER		YEAR	QUARTER	
Frequency Percent Row Pct Col Pct	4	Total	Frequency Percent Row Pct Col Pct	4	Total
78	1024 3.90 100.00 3.90	1024 3.90	86	2121 8.07 100.00 8.07	2121 8.07
80	1794 6.83 100.00 6.83	1794 6.83	87	2160 8.22 100.00 8.22	2160 8.22
81	1403 5.34 100.00 5.34	1403 5.34	88	1831 6.97 100.00 6.97	1831 6.97
82	3075 11.70 100.00 11.70	3075 11.70	89	2073 7.89 100.00 7.89	2073 7.89
83	2759 10.50 100.00 10.50	2759 10.50	90	1278 4.86 100.00 4.86	1278 4.86
84	2733 10.40 100.00 10.40	2733 10.40	91	1590 6.05 100.00 6.05	1590 6.05
85	2432 9.26 100.00 9.26	2432 9.26	Total	26273 100.00	26273 100.00
Total	26273 100.00	26273 100.00			

Table 5.7. Distribution of Northeast USA cod samples used in feeding analyses studies. Data are numbers of cod samples by year and quarter. Percentages in each cell are the percent of the row total, percent of the annual total, and percent of the quarterly total (over all years). All samples are of individual fish, and no regurgitated stomachs are included in the data.

YEAR	QUARTER				Total
	1	2	3	4	
81	0	324	0	185	509
	0.00	3.81	0.00	2.18	5.99
	0.00	63.65	0.00	36.35	
	0.00	9.90	0.00	10.34	
82	224	436	0	0	660
	2.63	5.13	0.00	0.00	7.76
	33.94	66.06	0.00	0.00	
	19.26	13.32	0.00	0.00	
83	142	0	0	1	143
	1.67	0.00	0.00	0.01	1.68
	99.30	0.00	0.00	0.70	
	12.21	0.00	0.00	0.06	
84	195	33	482	213	923
	2.29	0.39	5.67	2.51	10.86
	21.13	3.58	52.22	23.08	
	16.77	1.01	21.20	11.90	
85	264	661	533	328	1786
	3.11	7.78	6.27	3.86	21.01
	14.78	37.01	29.84	18.37	
	22.70	20.19	23.44	18.32	
86	19	674	486	321	1500
	0.22	7.93	5.72	3.78	17.64
	1.27	44.93	32.40	21.40	
	1.63	20.59	21.37	17.93	
87	0	879	773	336	1988
	0.00	10.34	9.09	3.95	23.39
	0.00	44.22	38.88	16.90	
	0.00	26.85	33.99	18.77	
88	319	267	0	406	992
	3.75	3.14	0.00	4.78	11.67
	32.16	26.92	0.00	40.93	
	27.43	8.16	0.00	22.68	
Total	1163	3274	2274	1790	8501
	13.68	38.51	26.75	21.06	100.00

Table 6.1.1a Comparison of different GLM models to estimate mean amount of total food and amount of fish to length, year and quarter effects (r-squared and variance ratio's).

1. NORTH SEA

LENGTH				NOT TRANSFORMED					LOG TRANSFORMED				
Main	Nested	Scaled	Fixed cat	r**2	F-Year	F-Quar	F-Main	F-Nest/ F-Y*L	r**2	F-Year	F-Quar	F-Main	F-Nest/ F-Y*L
Total food; continuous length													
no	yes	no	—	0.182	5.42	5.84	-	226.41	0.434	35.3	45.2	-	764.69
			df		6	3		7		6	3		7
yes	yes	no	—	0.182	5.42	5.84	1145.6	21.53	0.434	35.3	45.2	4713.22	8.03
			df		6	3	1	6		6	3	1	6
no	yes	yes	—	not available					not available				
			df										
yes	yes	yes	—	0.005	NS	NS	14.39	NS	0.086	45.1	33.3	86.79	5.93
			df		6	3	1	6		6	3	1	6
Total food; categorized length													
yes	no	no	6	0.153	13.1	NS	110.60	4.25	0.376	27.4	21.1	384.20	2.10
			df		6	3	5	26		6	3	5	26
yes	no	no	3	0.132	13.2	NS	339.3	6.73	0.348	47.0	22.2	1224.40	3.80
			df		6	3	2	12		6	3	2	12
yes	no	yes	6	0.060	21.6	12.5	4.93	2.51	0.082	27.5	20.1	6.26	2.17
			df		6	3	5	26		6	3	5	26
yes	no	yes	3	0.055	32.6	12.3	6.41	4.03	0.078	43.5	20.5	11.88	3.49
			df		6	3	2	12		6	3	2	12
Fish food; Continuous length													
no	yes	no	—	0.183	6.42	3.77	-	229.32	0.384	6.91	8.15	-	466.23
			df		6	3		7		6	3		7
yes	yes	no	—	0.183	6.42	3.77	1172.1	20.85	0.384	6.91	8.15	2757.04	7.89
			df		6	3	1	6		6	3	1	6
no	yes	yes	—	not available					not available				
			df										
yes	yes	yes	—	0.002	NS	NS	NS	NS	0.031	NS	12.4	28.37	NS
			df		6	3	1	6		6	3	1	6
Fish food; categorized length													
yes	no	no	6	0.157	10.3	NS	144.80	5.10	0.338	16.2	15.9	302.00	NS
			df		6	3	5	26		6	3	5	26
yes	no	no	3	0.127	8.7	5.3	320.16	6.93	0.317	14.0	16.5	837.61	2.52
			df		6	3	2	12		6	3	2	12
yes	no	yes	6	0.051	12.2	10.3	5.86	2.31	0.044	12.4	12.7	3.56	NS
			df		6	3	5	26		6	3	5	26
yes	no	yes	3	0.046	15.6	10.4	17.94	2.99	0.040	11.3	12.6	8.73	NS
			df		6	3	2	12		6	3	2	12

Table 6.1.1b Comparison of different GLM models to estimate mean amount of total food and amount of to length, year and quarter effects (r-squared and variance ratios)

5. NEWFOUNDLAND

LENGTH				Fixed	NOT TRANSFORMED				LOG TRANSFORMED			
Main	Nested	Scaled	cat		r**2	F-Year	F-Main	F-Nest/ F-Y*L	r**2	F-Year	F-Main	F-Nest/ F-Y*L
Total food; continuous length												
no	yes	no	—	df	0.171	9.89	-	388.1	0.279	16.46	-	627.25
						12		13		12		13
yes	yes	no	—	df	0.171	9.89	380.1	11.34	0.279	16.46	726.0	18.29
						12	1	12		12	1	12
no	yes	yes	—	df	0.045	13.7	-	28.9	0.022	8.7	-	6.2
						12		13		12		13
yes	yes	yes	—	df	0.046		139	14.66	not available			
						12	1	12				
Total food; categorized length												
yes	no	no	6	df	0.173	53.5	601.6	11.44	0.324	22.97	853.3	3.74
						12	5	60		12	5	60
yes	no	no	3	df	0.109	9.1	933.7	10.79	0.198	10.9	1742.1	3.47
						12	2	24		12	2	24
yes	no	yes	6	df	0.056	44.3	15.5	5.7	0.033	25.2	11.2	3.6
						12	5	60		12	5	60
yes	no	yes	3	df	0.052	24.8	27.9	10.3	0.029	13.1	26.3	5.24
						12	2	24		12	2	24
Fish food; Continuous length												
no	yes	no	—	df	0.120	7.9	-	250.7	0.172	12.5	-	116.92
						12		13		12		13
yes	yes	no	—	df	0.120	7.9	245.4	11.36	0.172	12.5	188.7	9.74
						12	1	12		12	1	12
no	yes	yes	—	df	0.054	12.58	-	393.23	0.089	15.17	-	16.47
						12		13		12		12
yes	yes	yes	—	df	0.054	12.58	329	20.4	0.089	15.2	34.6	7.7
						12	1	12		12	1	12
Fish food; categorized length												
yes	no	no	6	df	0.124	61.6	350.6	12.97	0.158	39.3	183.4	3.91
						12	5	60		12	5	60
yes	no	no	3	df	0.078	12.7	491	13.9	0.127	14.1	337.9	4.3
						12	2	24		12	2	24
yes	no	yes	6	df	0.064	56.3	23.8	5.9	0.127	42.3	42.7	3.9
						12	5	60		12	5	60
yes	no	yes	3	df	0.059	30.55	40.5	10.76	0.118	18.7	96.4	6.4
						12	2	24		12	2	24

Table 6.1.4 Results of core GLM models to estimate year, quarter, time of day and predator length effects on total food and total fish for the 6 ecosystems (r-squared and variance ratios).

		TOTAL FOOD					F-Nest	FISH FOOD					F-Nest
		r**2	F-Year	F-Quar	F-Time	F-Length	F-Y*L	r**2	F-Year	F-Quar	F-Time	F-Length	F-Y*L
1. NORTH SEA													
1980/1981/ 1982/1985/ 1986/1987	Cont	0.068	15.51	51.37	-	-	9.20	0.088	9.44	51.85	-	-	51.74
	df		5	3			6		5	3			6
	6 cat	0.099	7.99	48.95	-	5.99	9.32	0.118	10.49	57.28	-	45.82	6.04
	df		5	3		5	21		5	3		5	21
1984	Cont	0.040	-	-	NS	-	4.37	0.133	-	-	NS	-	32.53
	df				3		4				3		4
	6 cat	0.060	-	-	NS	4.90	NS	0.174	-	-	6.35	32.81	NS
	df				3	5	15				3	5	15
2. BALTIC													
1977-1990	Cont	0.168	21.67	77.08	-	-	20.60	0.165	16.17	73.68	-	-	29.30
	df		13	3			14		13	3			14
	6 cat	0.252	25.57	69.54	-	77.52	11.52	0.272	23.97	73.85	-	147.64	7.63
	df		13	3		4	52		13	3		4	52
3. BARENTS SEA													
1984-1991	Cont	0.054	20.59	120.10	24.17	-	19.92	0.084	38.89	205.83	7.55	-	30.02
	df		6	3	5		8		7	3	3		8
	6 cat	0.055	87.09	125.51	22.38	18.8	7.27	0.095	98.24	192.71	6.64	29.08	12.48
	df		7	3	3	5	35		7	3	3	5	35
4. ICELAND													
1979-1991	Cont	0.165	16.40	33.73	4.56	-	16.54	0.149	10.32	10.77	NS	-	7.11
	df		12	3	3		13		12	3	3		13
	6 cat	0.197	55.31	33.54	4.33	42.03	3.01	0.192	54.9	13.09	NS	44.87	2.48
	df		12	3	3	5	60		12	3	3	5	60
5. NEWFOUNDLAND													
1978, 1980- 1991	Cont	0.030	7.94	-	18.91	-	10.91	0.065	19.18	-	4.45	-	26.63
	df		12		3		13		12		3		13
	6 cat	0.036	25.91	-	18.84	11.23	3.62	0.078	60.0	-	4.82	31.59	6.70
	df		12		3	5	60		12		3	5	60
6. USA EAST COAST													
1981-1988	Cont	0.041	2.86	19.46	6.83	-	18.32	0.058	11.17	57.67	12.62	-	11.94
	df		7	3	3		8		7	3	3		8
	6 cat	0.052	2.59	20.12	6.72	18.76	2.35	0.066	9.21	52.58	11.8	13.32	2.24
	df		7	3	3	5	34		7	3	3	5	34

Table 6.1.5. Results of MANOVA models to estimate year, temperature and predator length effects on fraction empty for the 6 ecosystems (r-squared and variance ratios).

		FRACTION EMPTY				TOTAL FOOD				MANOVA					
		r**2	F-Year	F-Temp	F-Lngth	r**2	F-Year	F-Temp	F-Lngth	r**2Y	F-Year	r**2T	F-Temp	r**2L	F-Lngth
1. NORTH SEA 1980-1987															
Temp.	df														
Stc. T	df														
Cat. T	df														
2. BALTIC 1977-1990															
Temp.	df														
Stc. T	df														
Cat. T	df														
3. BARENTS SEA 1984-1991															
Temp.	df	0.030	65.29	488.78	394.67	0.033	165.07	705.2	31.66	0.043	109.82	0.023	419.97	0.011	203.34
			7	1	1		7	1	1		14		2		2
Stc. T	df	0.017	20.10	42.07	383.75	0.018	69.00	143.90	38.43	0.025	61.93	0.004	72.73	0.011	195.99
			7	1	1		7	1	1		14		2		2
Cat. T	df	0.020	16.74	48.09	383.47	0.025	48.64	124.20	32.45	0.020	51.55	0.011	64.32	0.011	197.02
			7	3	1		7	3	1		14		6		2
4. ICELAND 1979-1991															
Temp.	df	0.060	18.35	64.66	NS	0.219	79.51	115.23	135.70	0.177	44.54	0.028	65.66	0.032	74.92
			10	1	1		10	1	1		20		2		2
Stc. T	df	0.063	20.92	77.90	NS	0.212	78.68	76.35	134.21	0.180	45.15	0.023	54.75	0.032	76.1
			10	1	1		10	1	1		20		2		2
Cat. T	df	0.049	23.34	13.17	NS	0.174	75.96	16.18	227.88	0.149	48.56	0.011	11.41	0.040	126.19
			10	3	1		10	3	1		20		6		2
5. NEWFOUNDLAND 1978, 1980-1991															
Temp.	df	0.023	21.70	333.65	17.23	0.112	68.83	2709.5	21.23	0.040	43.64	0.097	1399.2	0.001	16.42
			12	1	1		12	1	1		24		2		2
Stc. T	df	0.023	22.08	327.12	17.62	0.114	47.94	2759.3	23.65	0.031	33.86	0.099	1421.6	0.001	17.64
			12	1	1		12	1	1		24		2		2
Cat. T	df	0.027	23.03	144.07	17.21	0.113	50.65	921.06	19.46	0.032	35.59	0.100	463.02	0.001	15.68
			12	3	1		12	3	1		24		6		2
6. USA EAST COAST 1981-1988															
Temp.	df	0.016	4.41	16.21	NS	0.046	11.05	40.30	38.38	0.023	6.51	0.011	20.91	0.011	22.10
			7	1	1		7	1	1		14		2		2
Stc. T	df	0.014	6.79	6.21	NS	0.039	15.39	12.85	30.87	0.031	8.84	0.003	NS	0.009	18.68
			7	1	1		7	3	34		14		2		2
Cat. T	df	0.013	14.00	4.47	NS	0.028	13.77	4.93	115.95	0.016	10.00	0.002	NS	0.015	64.90
			7	3	1		7	3	1		14		6		2

Table 6.1.6 Summary of highly correlated factors within ecosystems according to PCA.

	1. North Sea	2. Baltic	3. Barents S	4. Iceland	5. Newfndld	6. USA
Capelin	X	X	3\1	2\ -1	3	X
Unidentified fish	X	4	3\1	4	3	3
Other fish	1	-2	4	4	3	2
Crustaceans	-1	2	2	3	-1	-1
Molluscs	3\2	3	1	2	2	2
Polychaetes	3	-3	1	2	2	4\3
Echinoderms	2	X	1	2	2	4
Other food	2	1	1\2	4	4	3
Depth	X	X	'-3\1	1	1	'-2\1
Temperature	X	X	3	1	1	X
CPUE	4	X	4	2	-4	X
Length	1	-1	'-2\4	-3	-2	1
Nr of eigenvalues > 1	3	3	4	4	4	4

Notes:

Entries designate correlation coefficients $>|0.3|$ between variable (row) and principal component (nr in table)

Negative signs designate negative correlations.

When a variable was correlated with more than one component, these are listed in descending order of correlation.

An X indicates the variable was missing in the data set.

Table 6.1.7. Results of P.C.A. for 6 ecosystems. Subtables include:

- i) Eigenvalues of first 4 principal components, cumulative variance explained by eigenvalues, and variance explained by each rotated factor (where an orthogonal variable has a value of 1.0).
- ii) Correlations of each variable with Varimax rotated axes, and communality of each variable given the 4 retained factors.

6.1.7a - North Sea

i) Structure

Component	Eigenvalue	Cumulative variance	Variance Explained by rotated PC.
I	1.408	0.176	1.340
II	1.223	0.329	1.213
III	1.032	0.458	1.071
IV	0.973	0.580	1.012

ii) Pattern

Variable	Factor I	II	III	IV	Communality
Other Fish	.718	-.014	.076	.091	.529
Crustacean	-.614	-.284	.135	.012	.477
Mollusc	-.107	.424	.517	.147	.480
Polychaete	.024	-.127	.873	-.075	.785
Echinoderm	-.009	.714	-.103	-.103	.531
Other Food	.060	.635	.077	.033	.414
CPUE	-.049	-.047	-.006	.967	.939
Length	.655	-.141	-.023	-.174	.480

6.1.7b - Baltic Sea

i) Structure

Component	Eigenvalue	Cumulative variance	Variance Explained by rotated PC.
I	1.463	0.209	1.246
II	1.039	0.358	1.232
III	1.031	0.505	1.029
IV	0.998	0.647	1.023

ii) Pattern

Variable	Factor I	II	III	IV	Communality
Unident. Fish	-.018	.018	.009	.951	.905
Other Fish	-.155	-.717	.083	-.226	.596
Crustacean	.024	.821	.069	-.179	.711
Mollusc	.162	-.105	.721	-.031	.557
Polychaete	.177	-.096	-.704	-.035	.537
Other Food	.793	.015	.029	.119	.644
Length	-.731	-.154	.044	.141	.580

6.1.7c - Barents Sea

i) Structure

Component	Eigenvalue	Cumulative variance	Variance Explained by rotated PC.
I	1.511	0.126	1.453
II	1.272	0.232	1.279
III	1.205	0.332	1.198
IV	1.138	0.427	1.194

ii) Pattern

Variable	Factor I	II	III	IV	Communality
Capelin	.417	-.239	.479	.049	.463
Unident. Fish	.357	.317	.495	.106	.483
Other Fish	-.033	.229	.018	.607	.422
Crustacean	-.148	.751	-.073	.085	.598
Mollusc	.405	-.092	.011	-.070	.177
Polychaete	.646	-.040	-.112	-.070	.437
Echinoderm	.367	.111	.005	-.029	.148
Other Food	.426	.364	-.038	.290	.400
Temperature	-.235	-.163	.696	.050	.569
Depth	.372	-.179	-.467	.304	.482
CPUE	.051	.096	-.026	-.626	.404
Length	-.185	-.531	-.013	.474	.542

6.1.7d - Iceland

i) Structure

Component	Eigenvalue	Cumulative variance	Variance Explained by rotated PC.
I	1.915	0.160	1.709
II	1.563	0.290	1.405
III	1.241	0.393	1.352
IV	1.020	0.478	1.272

ii) Pattern

Variable	Factor I	II	III	IV	Communality
Capelin	-.366	.522	-.161	.222	.482
Unident. Fish	-.026	.166	.061	.653	.458
Other Fish	.208	-.025	-.008	.400	.204
Crustacean	.104	-.014	.837	-.056	.714
Mollusc	.062	.568	.012	.046	.329
Polychaete	.291	.603	.028	.035	.450
Echinoderm	.061	.451	.131	.096	.234
Other Food	-.043	.126	.070	.668	.469
Temperature	.816	.134	-.036	.129	.701
Depth	.838	.091	.004	.056	.714
CPUE	-.202	.381	.125	-.359	.331
Length	.131	-.165	-.763	-.163	.654

6.1.7e - Newfoundland

i) Structure

Component	Eigenvalue	Cumulative variance	Variance Explained by rotated PC.
I	2.027	0.169	1.867
II	1.543	0.298	1.510
III	1.182	0.396	1.319
IV	1.061	0.484	1.116

ii) Pattern

Variable	Factor I	II	III	IV	Communality
Capelin	-.006	.110	.599	.110	.383
Unident. Fish	-.022	.179	.621	.175	.449
Other Fish	-.115	-.064	.598	-.138	.393
Crustacean	-.588	.127	-.140	.156	.406
Mollusc	-.009	.648	.106	-.119	.444
Polychaete	.117	.583	.130	.151	.394
Echinoderm	-.055	.517	.135	-.133	.307
Other Food	-.187	.003	.056	.723	.561
Temperature	.842	-.012	-.226	-.020	.761
Depth	.851	.096	-.113	.062	.750
CPUE	-.061	.023	-.055	-.643	.420
Length	.140	-.640	.284	-.187	.545

6.1.7f - Eastern USA

i) Structure

Component	Eigenvalue	Cumulative variance	Variance Explained by rotated PC.
I	1.459	0.162	1.417
II	1.104	0.285	1.113
III	1.082	0.405	1.082
IV	1.040	0.520	1.073

ii) Pattern

Variable	Factor I	II	III	IV	Communality
Unident. Fish	.255	.044	.668	-.162	.539
Other Fish	.278	.601	.037	-.091	.448
Crustacean	-.727	.052	-.044	.016	.534
Mollusc	-.013	.541	-.049	.285	.376
Polychaete	-.114	-.011	.356	.616	.519
Echinoderm	.075	.027	-.200	.735	.585
Other Food	-.230	-.021	.676	.133	.529
Depth	.380	-.671	-.045	.142	.617
Length	.727	.062	-.063	-.000	.537

Table 6.1.2 Parameter estimates and standard errors of estimates for YEAR and PREDLEN effects from fit to model with 6 categories for predator size, with North Sea and Newfoundland data sets.

NORTH SEA

Year/Predlen	ln TOTAL FISH		ln TOTAL FOOD	
	Estimate	Std. Error	Estimate	Std. Error
80	0.83	0.26	0.79	0.26
81	-0.10	0.28	0.35	0.23
82	0.17	0.32	0.33	0.28
85	0.21	0.31	0.19	0.27
86	0.39	0.33	0.08	0.29
87	reference			
2	0.15	0.28	0.57	0.23
3	0.72	0.27	0.86	0.23
4	0.67	0.28	0.70	0.25
5	0.35	0.33	0.19	0.29
6	0.49	0.34	0.15	0.30
7	reference			

NEWFOUNDLAND

78	-0.60	0.36	-0.47	0.28
80	-1.44	0.32	-0.65	0.24
81	-1.10	0.32	-0.46	0.25
82	-1.58	0.30	-0.63	0.23
83	-1.01	0.31	-0.32	0.24
84	-1.12	0.30	-0.33	0.24
85	-0.34	0.31	-0.01	0.24
86	0.19	0.32	0.30	0.25
87	-0.20	0.33	0.02	0.26
88	0.26	0.34	0.34	0.27
89	0.53	0.42	-0.51	0.32
90	0.23	0.50	-0.17	0.41
91	reference			
2	-3.88	0.40	-3.86	0.25
3	-2.34	0.32	-2.50	0.23
4	-1.87	0.31	-2.03	0.23
5	-1.05	0.35	-1.43	0.25
6	-0.91	0.35	-0.93	0.26
7	reference			

Table 6.1.3 Statistics of fit to the GLM model with predator length as continuous covariate nested under years, fit to Newfoundland data scaled and transformed BEFORE and AFTER bulking to mean value per haul.

STATISTIC	ln TOTAL FISH		ln TOTAL FOOD	
	BEFORE	AFTER	BEFORE	AFTER
SumSquare Total	23573.2	23991.8	20171.9	20584.9
r^2	0.086	0.101	0.024	0.038
Type III MS_{year}	17.564	16.543	6.427	6.104
" $MS_{predlen}$	29.557	58.425	6.109	31.748

Table 6.2.1 Cod growth data available for analysis.

Area	Period	Ages	Quarter	Source
i) Length at age for all years				
Iceland	85-91	1-9	I	Iceland; national data
Barents Sea	79-92	1-8	I	Norway; national data
North Sea	77-91	0-9	III	England; national data
Newfoundland	78-89	2-11	IV	Canada; national data
ii) Mean length at age across years:				
Baltic Sea	81-88	0-9	I-IV	Anon. 1990a
Gulf of Maine	70-74	1-17	I, IV	Penttila <i>et al.</i> 1976
Georges Bank	70-74	1-15	I, IV	Penttila <i>et al.</i> 1976

Table 6.2.2 Mean age at length (mid-length of 10 cm class interval) by area.

Area	Mid-length (cm)	Mean age (years)
Baltic Sea	25	2.05
	35	3.05
	45	4.05
	55	5.17
	65	6.67
	75	8.55
Iceland	25	2.12
	35	2.62 *
	45	3.12
	55	4.12
	65	5.62
	75	7.12
Barents Sea	25	2.12
	35	3.12
	45	4.12
	55	5.12
	65	6.12
	75	7.12
Newfoundland (2J & 3K)	25	2.92
	35	3.92
	45	4.92
	55	6.42
	65	8.42
	75	10.42
North Sea	25	1.67
	35	2.17 *
	45	2.67
	55	3.17 *
	65	3.67
	75	4.67
Gulf of Maine	25	2.08
	35	3.08
	45	3.58 *
	55	4.08
	65	5.08
	75	6.58
Georges Bank	25	1.25
	35	1.80
	45	2.18
	55	3.05
	65	4.05
	75	5.44

*Interpolated value.

Table 8.4. Results of eight GLM analyses, one for each combination of prey species and quarter, for comparing the M2 estimates from the LBMS with those from the MSVPA.

GLM model for analysis:

$\ln(M2) = \text{Model } \ln(\text{length})$
by quarter species

Parameters	1.Quarter	2.Quarter	3.Quarter	4.Quarter
Sprat:				
R2	0.40	0.43	0.07	0.73
Intercept	3.572	4.372	-0.695	5.225
MSVPA (25,26,28)	0.057 n.s.	0.334 n.s.	-0.049 n.s.	-0.360 n.s.
LBMS	0.000	0.000	0.000	0.000
Slope	-2.273	-2.560	-0.634	-3.202
Herring:				
R2	0.80	0.75	0.75	0.74
Intercept	8.296	6.214	4.665	3.910
MSVPA (25-27)	-0.801	0.071 n.s.	-0.496	-0.858
MSVPA (28-29s)	0.143	0.435 n.s.	0.253	-0.075
LBMS	0.000	0.000	0.000	0.000
Slope	-3.997	-3.412	-2.465	-2.318

Table 8.6.1. Percentage change in long term equilibrium yield predicted by the MSFOR by reducing the fishing mortality generated by the roundfish fishery by 30%. Recruitment kept constant at average 1974-1988 level.

Species	Landings	Discards
Cod	-8	0
Whiting	-11	-25
Saithe	-9	0
Haddock	-16	-37
Total	-11	-33

Table 8.6.2. Percentage change in long term equilibrium biomass, spawning stock biomass, catch and value of landings predicted by the MSFOR following a 30 % reduction of the fishing mortality generated by the roundfish fishery. Recruitment kept constant at average 1974-1988 level.

Species	Total Biom.	SSB	Catch	Value
Cod	21	61	-8	-4
Whiting	2	3	-11	-9
Saithe	13	34	3	3
Mackerel	0	0	0	0
Haddock	-8	4	-24	-13
Herring	-5	-6	-7	-8
Sprat	0	0	0	0
Norway pout	-8	-12	-21	-21
Sandeel	0	0	0	0
Plaice	0	0	0	0
Sole	0	0	0	0
Total	-1	0	-7	-4

Table 8.6.3. Distribution of percentage long term changes in landings and discards from the North Sea roundfish fleet subject to changes in levels of recruitment. Status quo compared to 30% reduction in fishing mortality. Results from 512 comparisons.

Species % Change	Landings				Discards	
	Cod	Whiting	Saithe	Haddock	Whiting	Haddock
60 - 70	0	0	0	0	0	0
50 - 60	0	0	0	0	0	0
40 - 50	0	0	0	0	0	0
30 - 40	0	0	0	0	0	0
20 - 30	0	0	0	0	0	0
10 - 20	0	0	0	0	0	0
.01 - 10	6.4	0	0	4.3	0	0
-.01 - .01	0	0	0	0	0	0
-10 - -.01	66.2	46.3	100.0	34.2	0	0
-20 - -10	27.3	53.7	0	19.7	0	0
-30 - -20	0	0	0	16.8	100.0	25.8
-40 - -50	0	0	0	13.3	0	33.4
-50 - -60	0	0	0	11.7	0	18.8
-60 - -70	0	0	0	0	0	22.1
Sum	100.0	100.0	100.0	100.0	100.0	100.0

Table 8.6.4. Distribution of percentage long term changes in spawning stock biomass subject to changes in levels of recruitment. Status quo compared to 30% reduction in the fishing mortality generated by the North Sea roundfish fleet. Results from 512 comparisons.

Species % Change	Cod	Whiting	Saithe	Mack.	Haddock	Herring	Sprat	N. Pout	Sandeel	All species
80 - 90	0	0	0	0	0	0	0	0	0	0
70 - 80	24.0	0	0	0	0	0	0	0	0	0
60 - 70	33.8	0	0	0	0	0	0	0	0	0
50 - 60	36.1	0	0	0	0	0	0	0	0	0
40 - 50	6.1	0	0	0	0	0	0	0	0	0
30 - 40	0	0	100.0	0	0	0	0	0	0	0
20 - 30	0	0	0	0	16.0	0	0	0	0	0
10 - 20	0	0	0	0	27.5	0	0	0	0	0
.01 - 10	0	100.0	0	0	13.7	0	21.5	0	30.1	53.7
-.01 - .01	0	0	0	100.0	0	0	1.6	0	1.0	0
-10 - -.01	0	0	0	0	17.4	94.1	77.0	48.8	68.9	46.3
-20 - -10	0	0	0	0	3.9	5.9	0	51.2	0	0
-30 - -20	0	0	0	0	19.7	0	0	0	0	0
-40 - -50	0	0	0	0	1.8	0	0	0	0	0
-50 - -60	0	0	0	0	0	0	0	0	0	0
-60 - -70	0	0	0	0	0	0	0	0	0	0
-70 - -80	0	0	0	0	0	0	0	0	0	0
-80 - -90	0	0	0	0	0	0	0	0	0	0
Sum	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0

Table 8.6.5. Results of an ANOVA of the percentage change in landings and discards from the roundfish fleet upon a 30% reduction in the fishing mortality generated by the North Sea roundfish fleet at high and low levels of recruitment. The intercept is the expected change if all recruitments are at a high level.

Species	Landings			Discards	
	Cod	Whiting	Haddock	Whiting	Haddock
Parameter					
Intercept	-9.7	-11.8	-24.0	-25.6	-41.9
Recruitment low for:					
Cod	6.8	4.0	2.7	0.7	0.3
Whiting	-0.2	0.3	2.9	0.5	1.9
Saithe	4.4	1.3	24.3	0.8	16.2
Mackerel	-0.1	0.1	0.4	0.6	0.2
Haddock	-0.8	-0.4	-1.8	-0.1	-0.9
Herring	-1.1	-0.4	-1.2	-0.1	-0.7
Sprat	-0.2	-0.2	-0.7	-0.1	-0.4
Norway pout	-2.9	-1.0	-12.5	-0.6	-8.0
Sandeel	-0.8	-0.7	-2.7	-0.3	-1.5
R ²	0.99	0.97	0.96	0.93	0.96

Table 8.6.6. Results of an ANOVA of the percentage change in spawning stock biomass upon a 30% reduction in the fishing mortality generated by the North Sea roundfish fleet at high and low levels of recruitment. The intercept is the expected change if all recruitments are at a high level. Only species for which a change in recruitment level produces a change in the percentage increase/decrease of spawning stock biomass has been included.

Species	COD	WHITING	HADDOCK	HERRING	SPRAT	N. POUT	SANDEEL
Parameter							
Intercept	57.1	2.9	-5.3	-6.9	-0.6	-11.9	0.3
Recruitment low for:							
Cod	13.4	2.0	3.1	-1.2	-0.5	-0.6	-0.9
Whiting	-0.4	0.6	3.6	1.0	-0.8	0.1	-0.8
Saithe	7.7	1.4	30.1	2.5	0.3	5.0	-0.4
Mackerel	-0.1	0.1	0.5	0.0	-0.0	-0.0	-0.1
Haddock	-1.3	-0.3	-2.2	-0.1	0.2	0.1	-0.4
Herring	-2.0	-0.2	-1.4	-0.4	0.1	-0.1	0.3
Sprat	-0.4	-0.2	-0.9	-0.2	0.3	-0.0	0.1
Norway pout	-5.0	-1.0	-15.4	-1.6	0.5	-0.8	0.6
Sandeel	-1.3	-0.6	-3.4	0.3	0.1	-0.3	-0.1
R ²	0.99	0.96	0.96	0.95	0.53	0.80	0.52

Table 8.7. Parameters used for describing the North Sea food web in 1981. All estimates are expressed in t wet weight km⁻² year⁻¹. P/B is the production/biomass ratio, Q/B is the consumption/biomass ratio, both on an annual basis. The ecotrophic efficiency expresses the proportion of the production that is utilized for predation or catches, while the gross efficiency is the ratio between production and consumption.

GROUP	CATCHES	BIOMASS	P/B	Q/B	ECOTROPH. EFF.	GROSS EFF.
COD	0.57	0.57	1.43	3.15	0.75	0.45
WHITING	0.37	0.66	1.15	3.56	0.70	0.32
SAITHE	0.21	0.65	0.62	3.29	0.51	0.19
MACKEREL	0.11	0.46	0.24	5.79	0.99	0.04
HADDOCK	0.38	0.83	1.53	3.79	0.60	0.40
HERRING	0.29	0.84	0.73	4.87	0.80	0.15
SPRAT	0.34	0.55	1.48	9.87	0.85	0.15
NORWAY POUT	0.81	1.94	2.18	14.53	0.56	0.15
SANDEEL	1.16	2.58	1.93	12.87	0.65	0.15
PLAICE	0.22	0.64	0.86	8.60	0.40	0.10
SOLE	0.03	0.08	0.84	8.40	0.39	0.10
RAY	0.00	0.53	0.43	4.30	0.00	0.10
O. PRED. FISH	0.00	1.48	0.20	1.98	0.00	0.10
O PREY FISH	0.00	4.35	1.17	11.70	0.95	0.10
ANNELIDA	0.00	2.99	5.00	33.33	0.95	0.15
CEPHALOPODA	0.00	0.12	1.79	11.90	0.95	0.15
COPEPODA	0.00	6.44	30.00	200.00	0.95	0.15
EUPHAUSIACEA	0.00	2.36	5.00	33.33	0.95	0.15
O. CRUSTACEA	0.00	5.03	5.00	33.33	0.95	0.15
ECHINODERMATA	0.00	7.82	5.00	33.33	0.95	0.15
O. INVERTS.	0.00	10.50	5.00	33.33	0.95	0.15
PLANTS	0.00	100.00	15.14	0.00	0.82	
DETRITUS	0.00				0.80	

Table 9.1.1 Results from probit analysis. Regression coefficients are given for the effect of the SMSCFOOD as a continuous variable on the proportion of empty stomachs in the same bulked sample. SMSCFOOD = mean stomach content of non empty stomach contents, scaled ($S/L^{**3} * 100,0000$).

20 - 30 cm						40 - 50 cm					
Year Quart.	81	85	86	87	mean	Year Quart.	81	85	86	87	mean
1	-0.5	-0.3	-0.8	-0.2	-0.4	1	-0.8	-0.6	-0.0	/	-0.3
2	-0.4				-0.4	2	-0.4				-0.4
3	0.3	/	-0.2	0.1	0.1	3	0.5	-0.9	-0.1	-0.5	-0.3
4	0.2				0.2	4	0.1				0.1
mean	-0.07	-0.14	-0.51	-0.06	-0.14	mean	-0.16	-0.75	-0.08	-0.26	-0.24

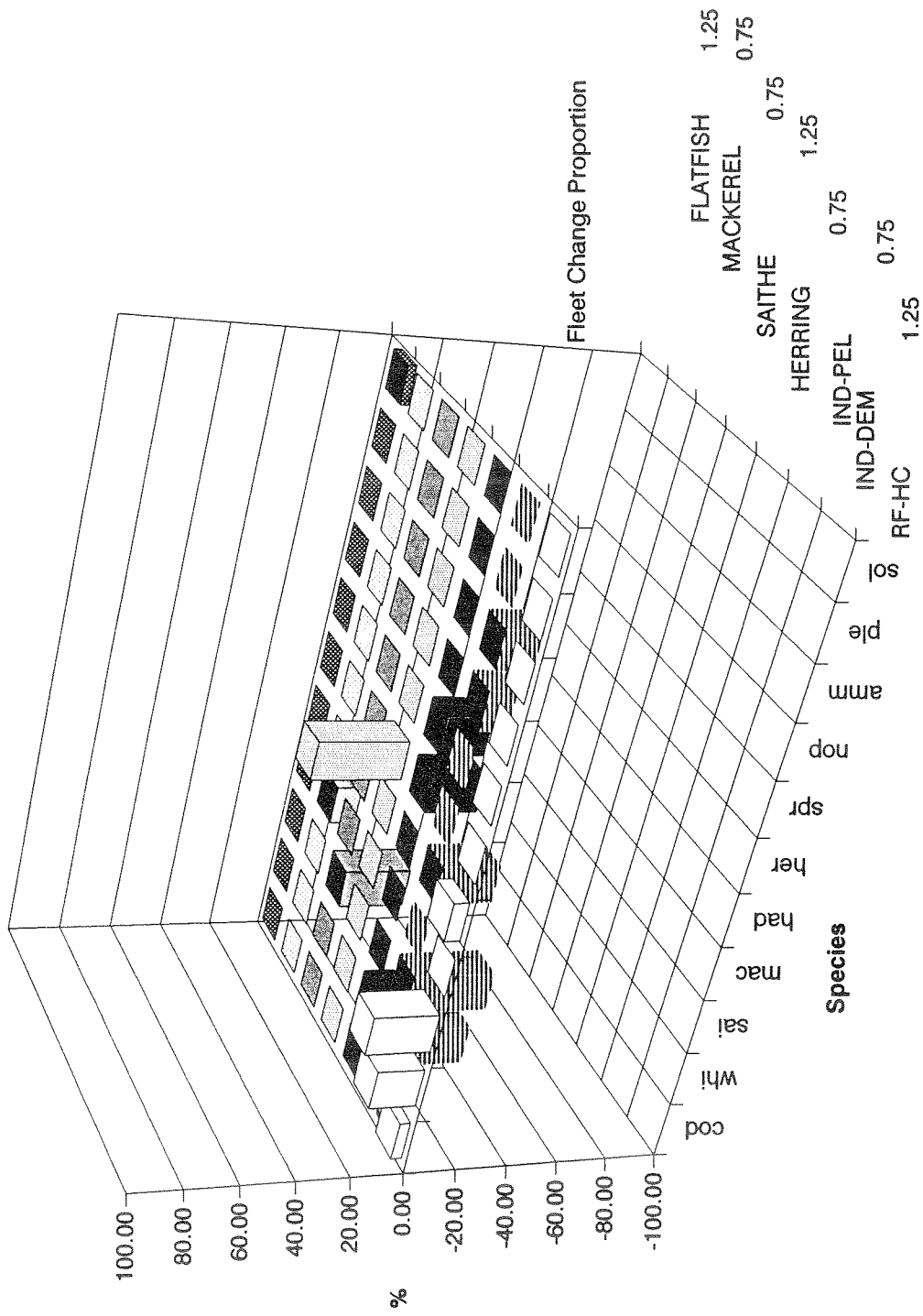
30 - 40 cm						50 - 60 cm					
Year Quart.	81	85	86	87	mean	Year Quart.	81	85	86	87	mean
1	-0.7	-0.3	-0.4	-0.5	-0.5	1	-0.2	/	/	/	-0.0
2	-0.1				-0.1	2	0.3				0.3
3	0.7	0.2	-0.6	-0.5	-0.1	3	0.4	0.0	-0.9	-0.1	-0.1
4	-1.0				-1.0	4	-1.9				-1.9
mean	-0.28	-0.06	-0.51	-0.52	-0.41	mean	-0.36	0.016	-0.43	0.04	-0.45

60 - 70 cm				
Year Quart.	81	85	86	87
1	-0.1	X	X	X
2	-3.0			
3	0.0	X	X	X
4	-0.1			
mean	-0.78			

Table 9.1.2 Results from probit analysis. The effect of predator length and SMSCFOOD on the proportion of empty stomachs is analysed. SMSCFOOD = mean stomach content of non empty stomachs in one bul sample.

regress. coeff. for the effect of SMSCFOOD					
Year Quart.	81	85	86	87	mean
1	-0.4	-0.3	-0.2	-0.4	-0.3
2	-0.3				-0.3
3	0.2	-0.2	-0.3	-0.2	-0.1
4	-0.4				-0.4
mean	-0.02	-0.3	-0.3	-0.3	-0.3

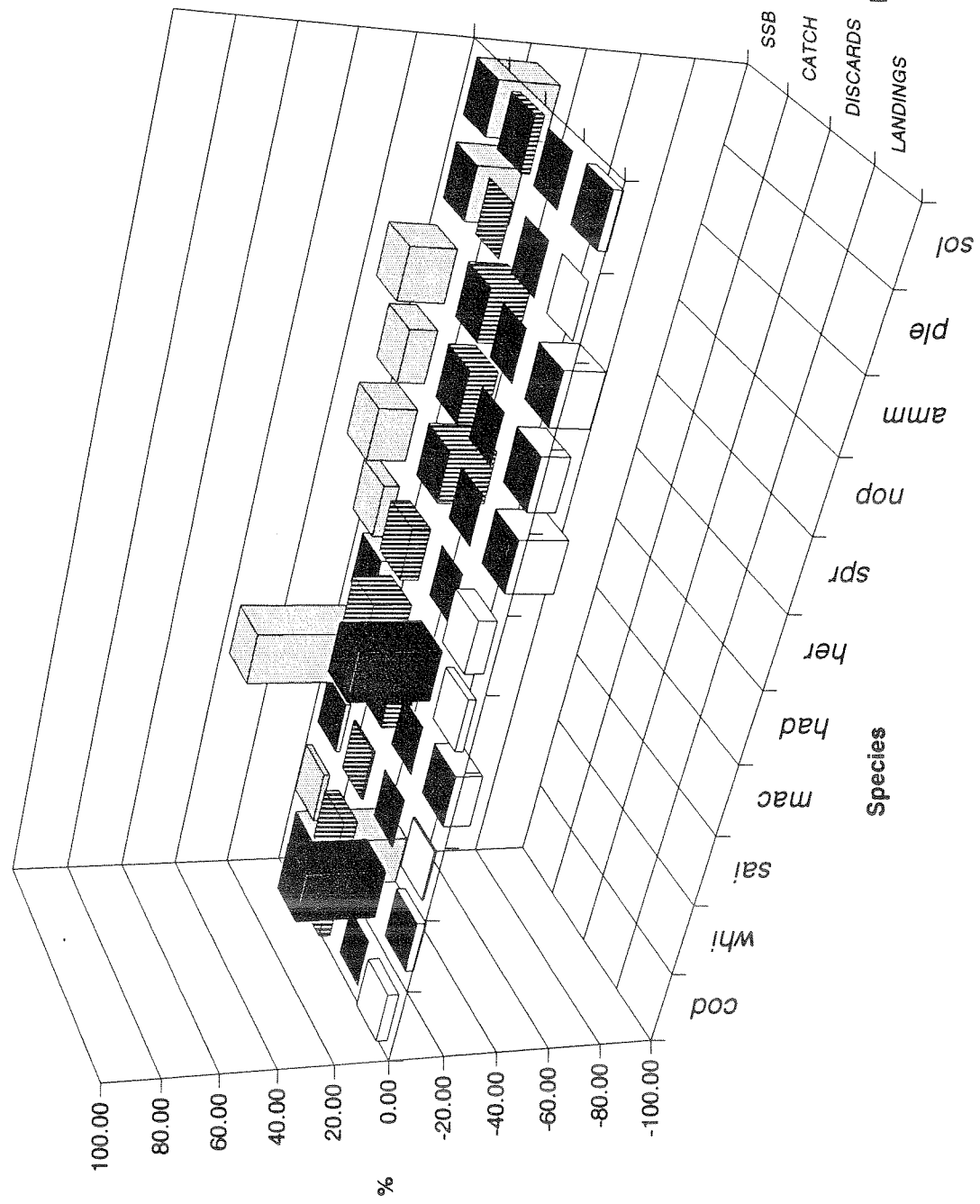
Year Quart.	81	85	86	87	mean
1	0.5	0.1	0.0	0.1	0.2
2	-0.8				-0.8
3	0.5	0.3	-0.9	0.3	0.0
4	-0.8				-0.8
mean	-0.4	0.03	-0.9	0.3	-0.2



% Yield Change from Status Quo

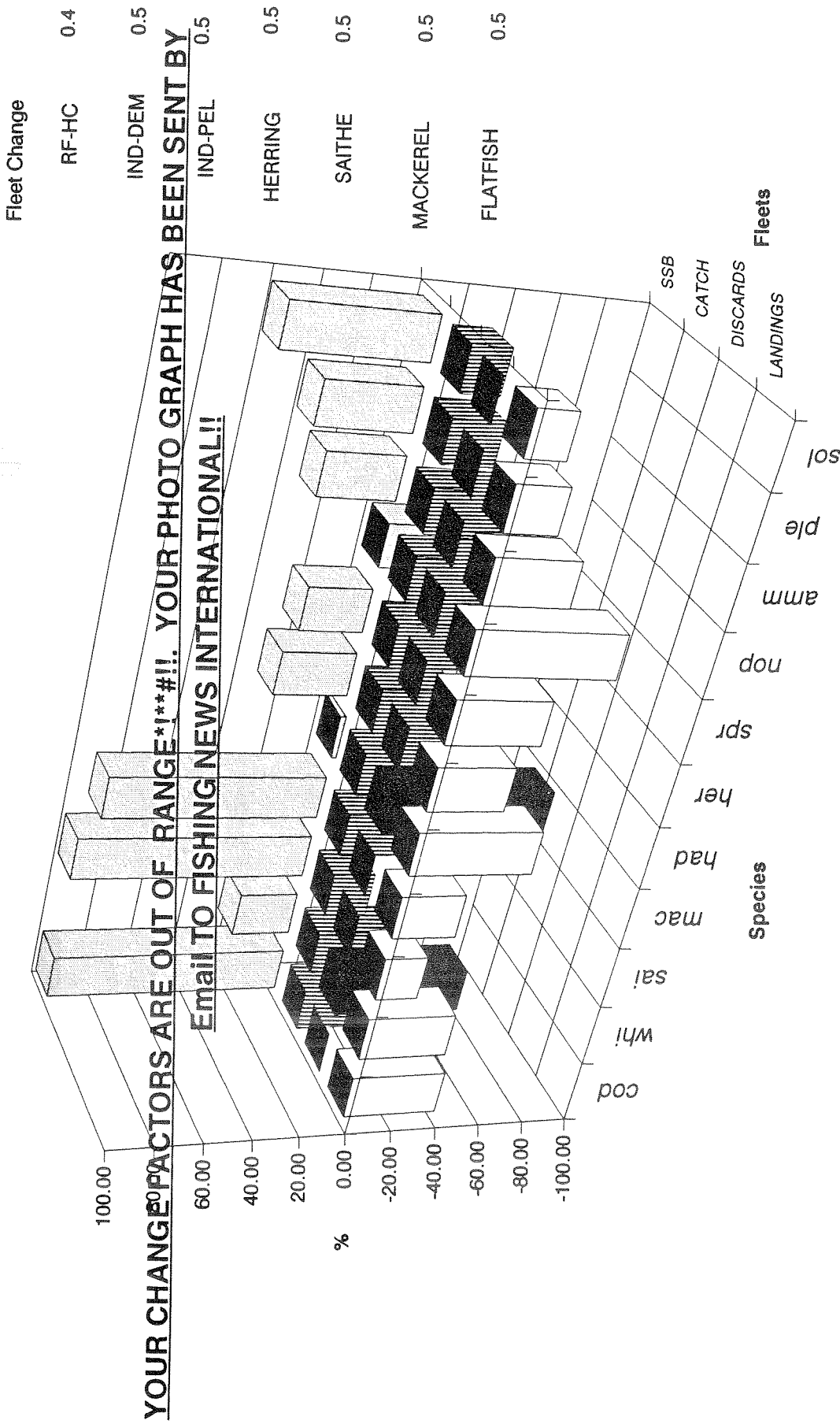
Figure 2.4.1. Percentage differences in long-term average yields (from status quo) for 11 species and seven nominal fleets in the North Sea, contingent on effort changes given along the right axis (i.e., Roundfish-Human Consumption effort 1.25 times current effort, etc.).

Fleet Change	
RF-HC	1.25
IND-DEM	0.75
IND-PEL	0.75
HERRING	1.25
SAITHE	0.75
MACKEREL	0.75
FLATFISH	1.25



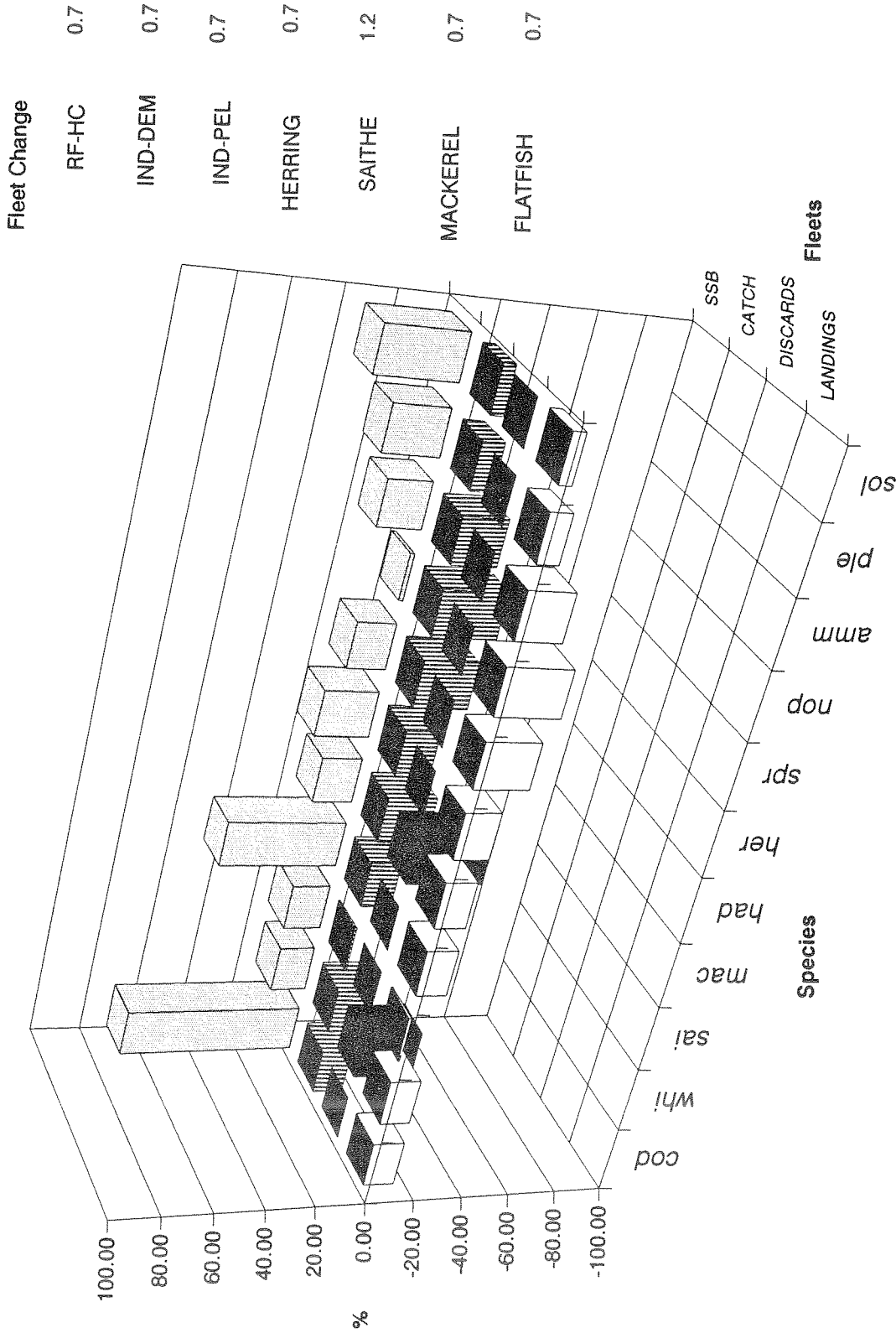
%SSB, Landings, Discards and Catch:- Change from Status Quo

Figure 2.4.2. Percentage differences in long-term average landings, discards, catch (landings + discards) and spawning stock biomass (from status quo) for 11 North Sea species, contingent on fleet effort changes given at right (i.e., Roundfish-Human Consumption fleet effort 1.25 times current, etc.).



%SSB, Landings, Discards and Catch:- Change from Status Quo

Figure 2.4.3. Percentage differences in long-term average landings, discards, catch (landings + discards) and spawning stock biomass (from status quo) for 11 North Sea species, contingent on fleet effort changes given at right (i.e., Roundfish-Human Consumption fleet effort 0.4 times current, etc.). Note, the MSWG has advised that effort changes > 50% from status quo in any fleet component are beyond the range of predictability of forecast models currently in use.



%SSB, Landings, Discards and Catch:- Change from Status Quo

Figure 2.4.4. Percentage differences in long-term average landings, discards, catch (landings + discards) and spawning stock biomass (from status quo) for 11 North Sea species, contingent on fleet effort changes given at right (i.e., Roundfish-Human Consumption fleet effort 0.7 times current, etc.). The combination of effort change factors at right results in increased SSB for all stocks considered in the analysis.

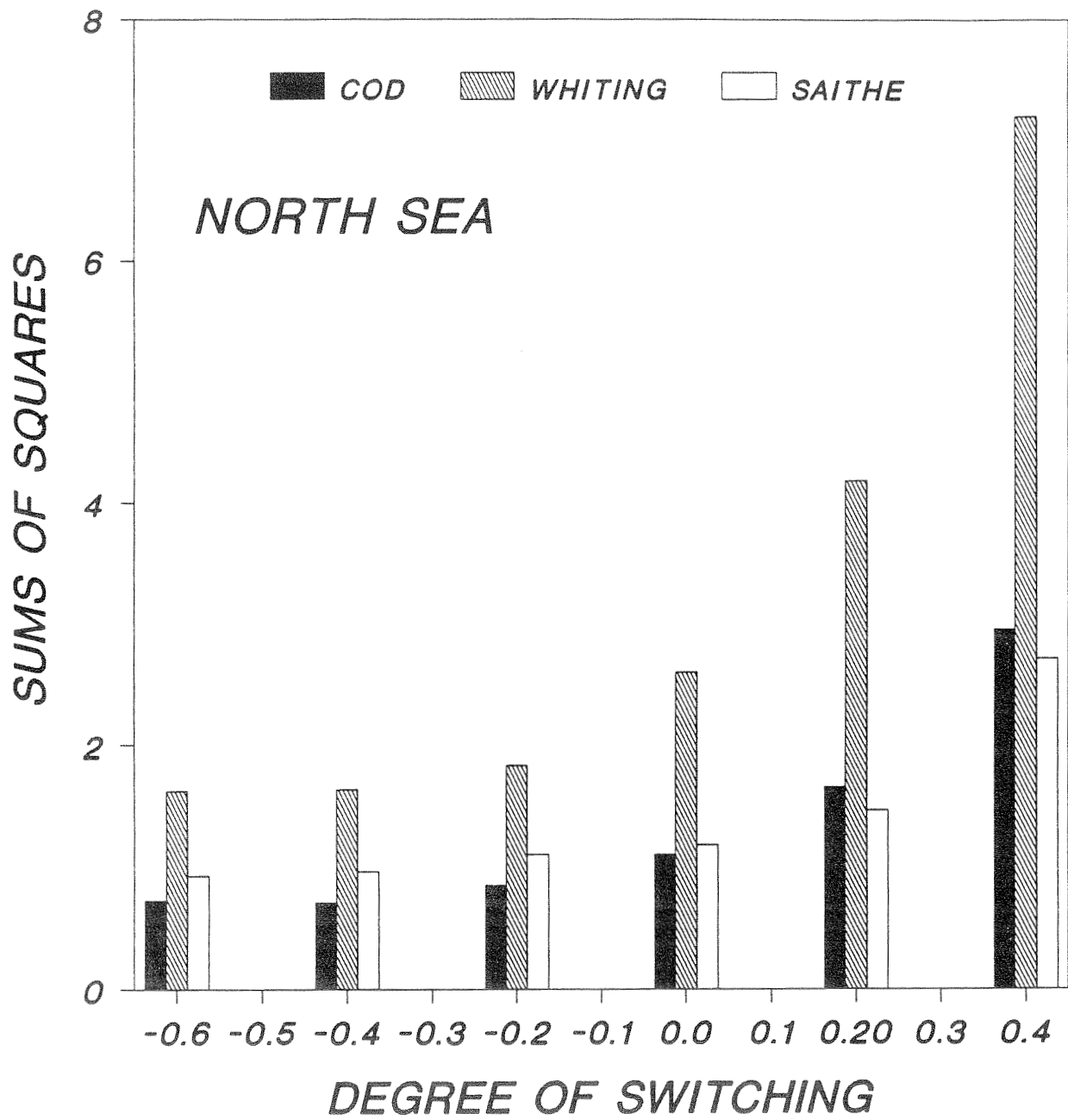


Figure 4.1. Sums of squared deviations between observed and estimated stomach content for three predator species in the North Sea, for various levels of prey switching coefficients (deviations are between absolute weight values).

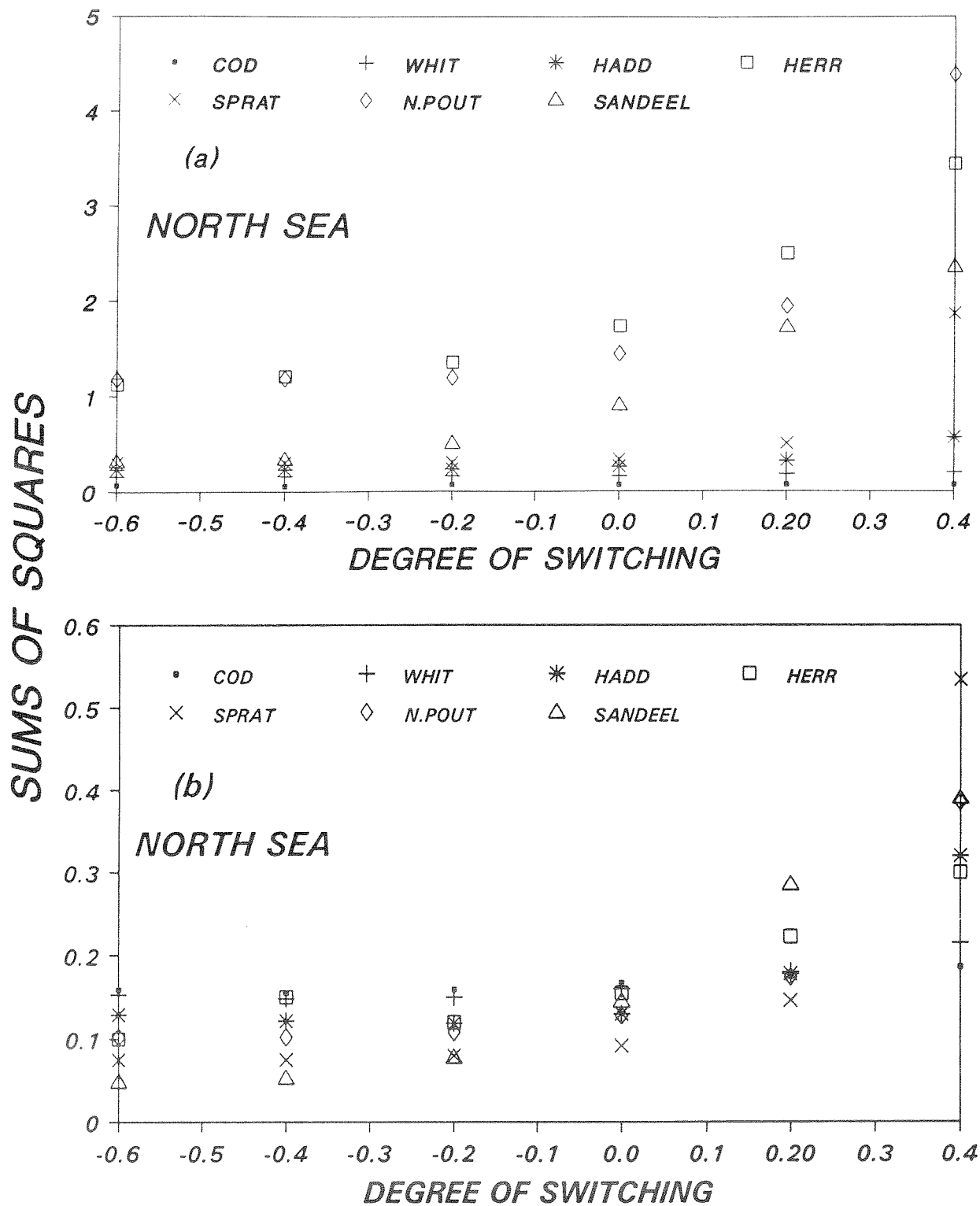


Figure 4.2. Sums of squared deviations between observed and estimated stomach content for each prey species in the North Sea (a). Results are for all predator species combined. In plot (b) the contribution of each prey species is normalized by dividing by the contribution over all values of the switching coefficient.

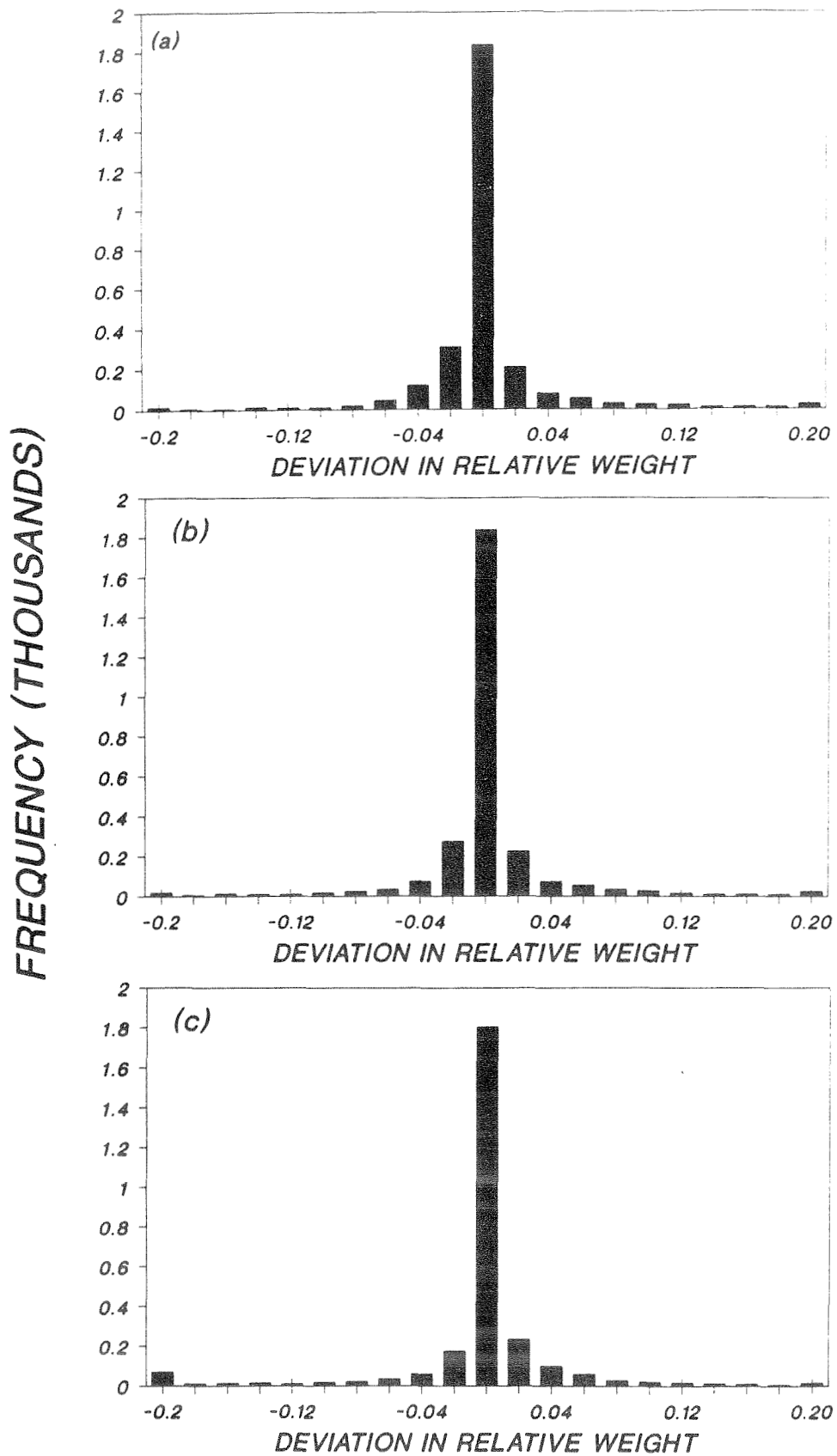


Figure 4.3. Distribution of relative deviations between estimated and observed stomach content weight for all North Sea predators. Data are presented for three values of the switching coefficient: (a) -0.4, (b) 0.0, (c) 0.4.

SUMS OF SQUARES

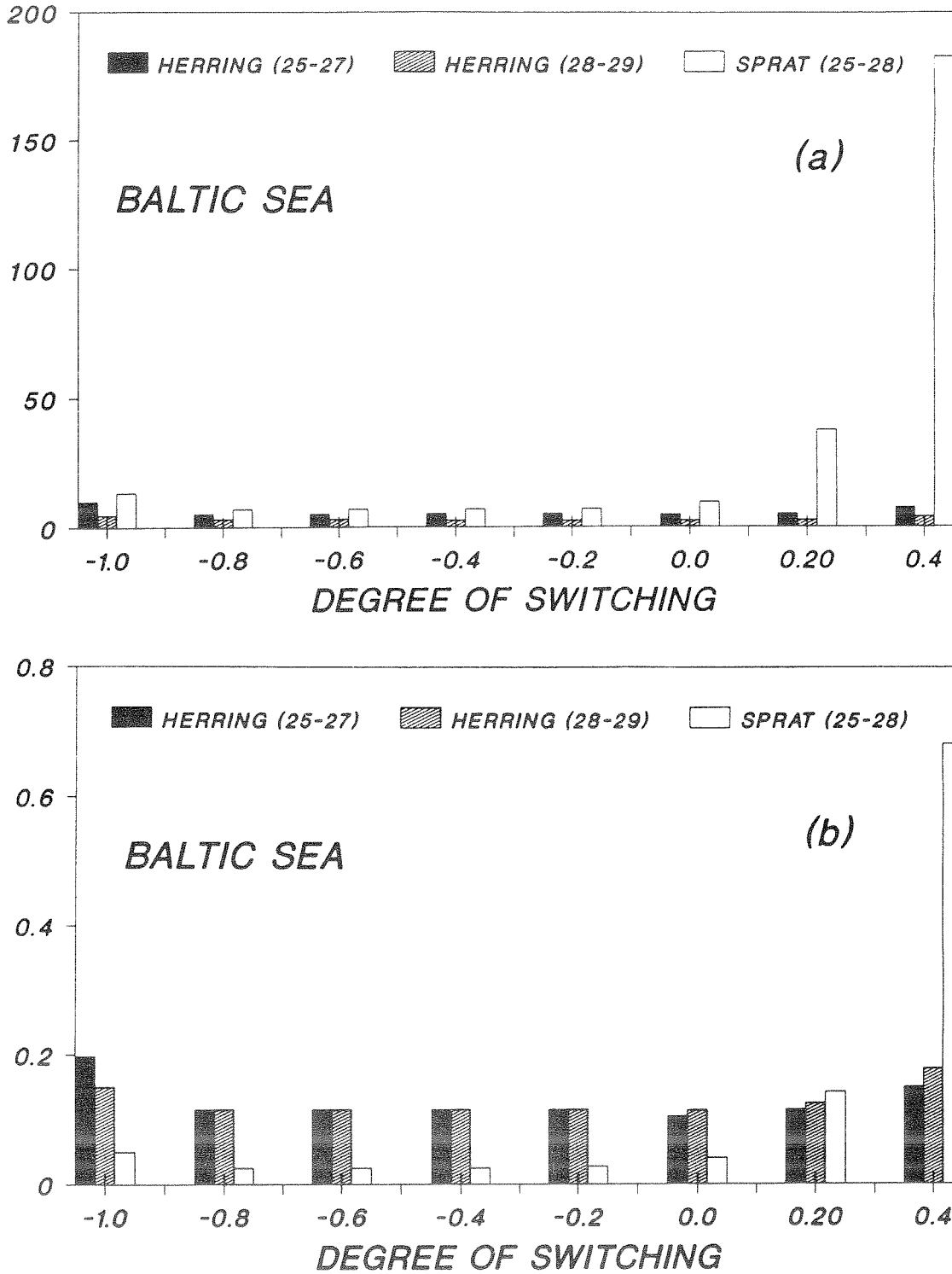


Figure 4.4. Sums of squared deviations between observed and estimated stomach content for each prey species in the Baltic Sea (a). Results are for cod as predator. In plot (b) the contribution of each prey species is normalized by dividing by the contribution over all values of the switching coefficient.

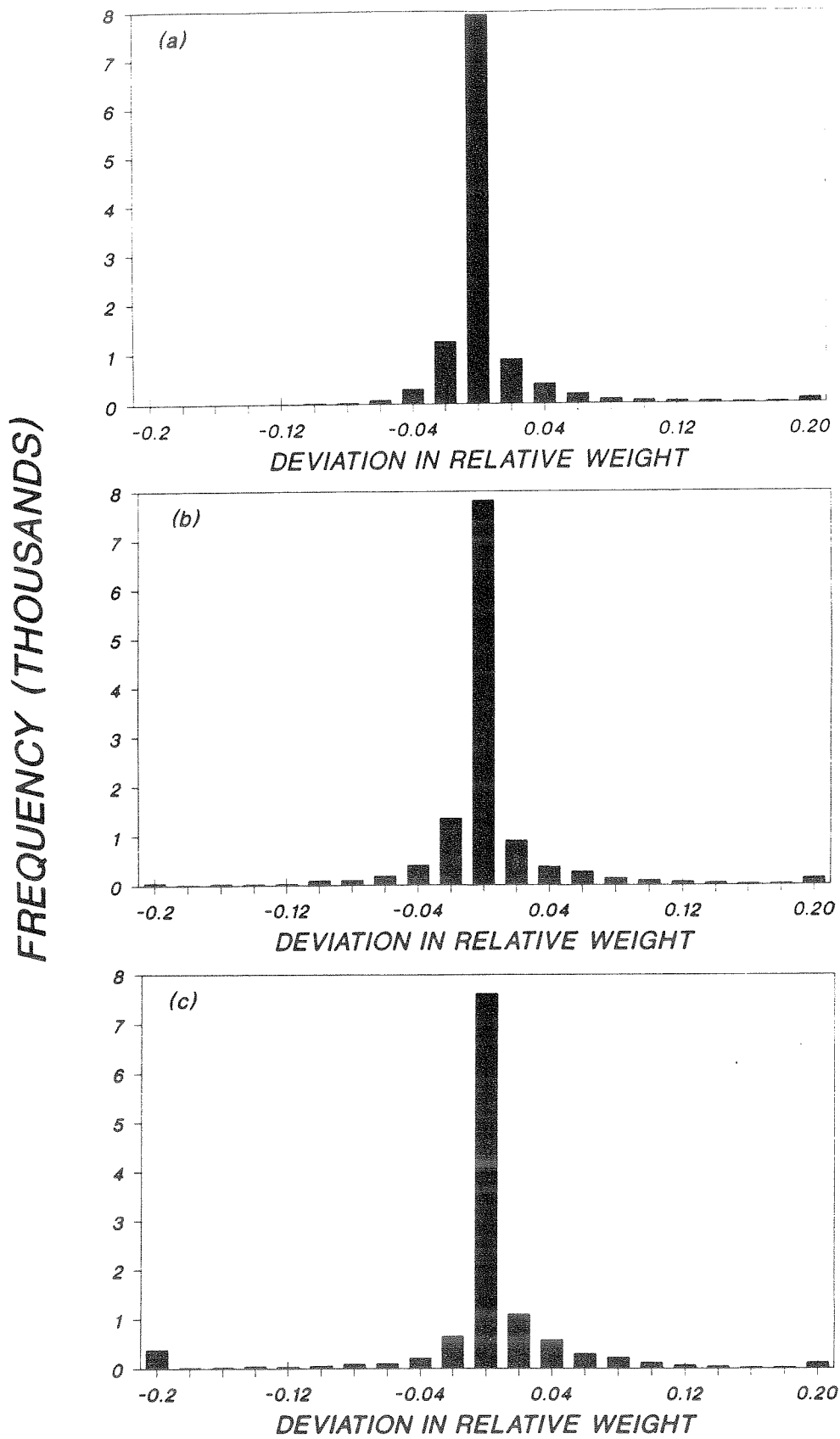


Figure 4.5. Distribution of relative deviations between estimated and observed stomach content weight for Baltic Sea cod as predator. Data are presented for three values of the switching coefficient: (a) -0.4, (b) 0.0, (c) 0.4.

Figure 5.1. Geographic distributions of cod feeding data sets, and numbering sequence used in statistical analyses.

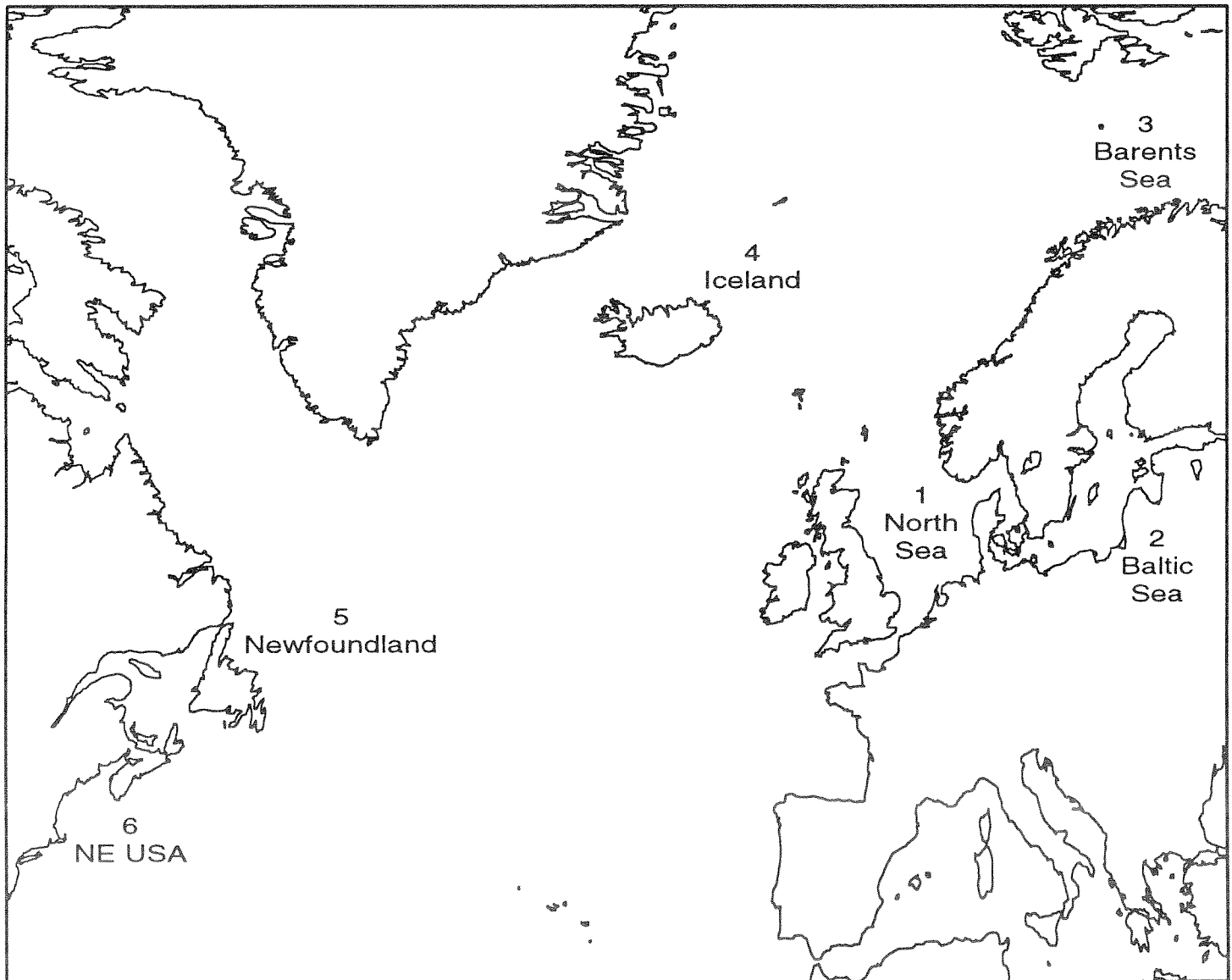


Fig.5.2. Length frequency distribution (%) of cod sample for feeding studies for North sea.

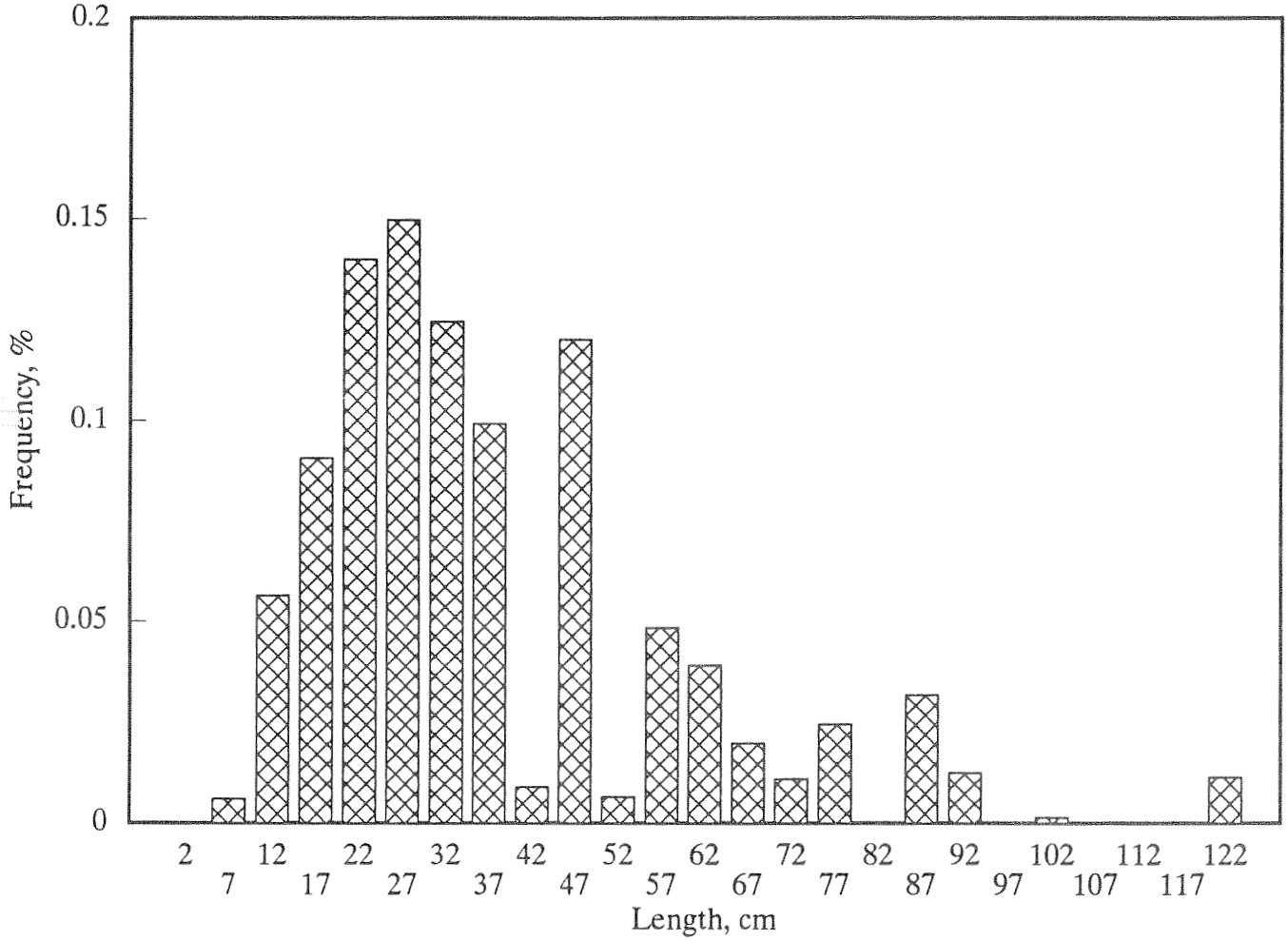


Fig.5.3. Length frequency distribution (%) of cod sample for feeding studies for Baltic sea.

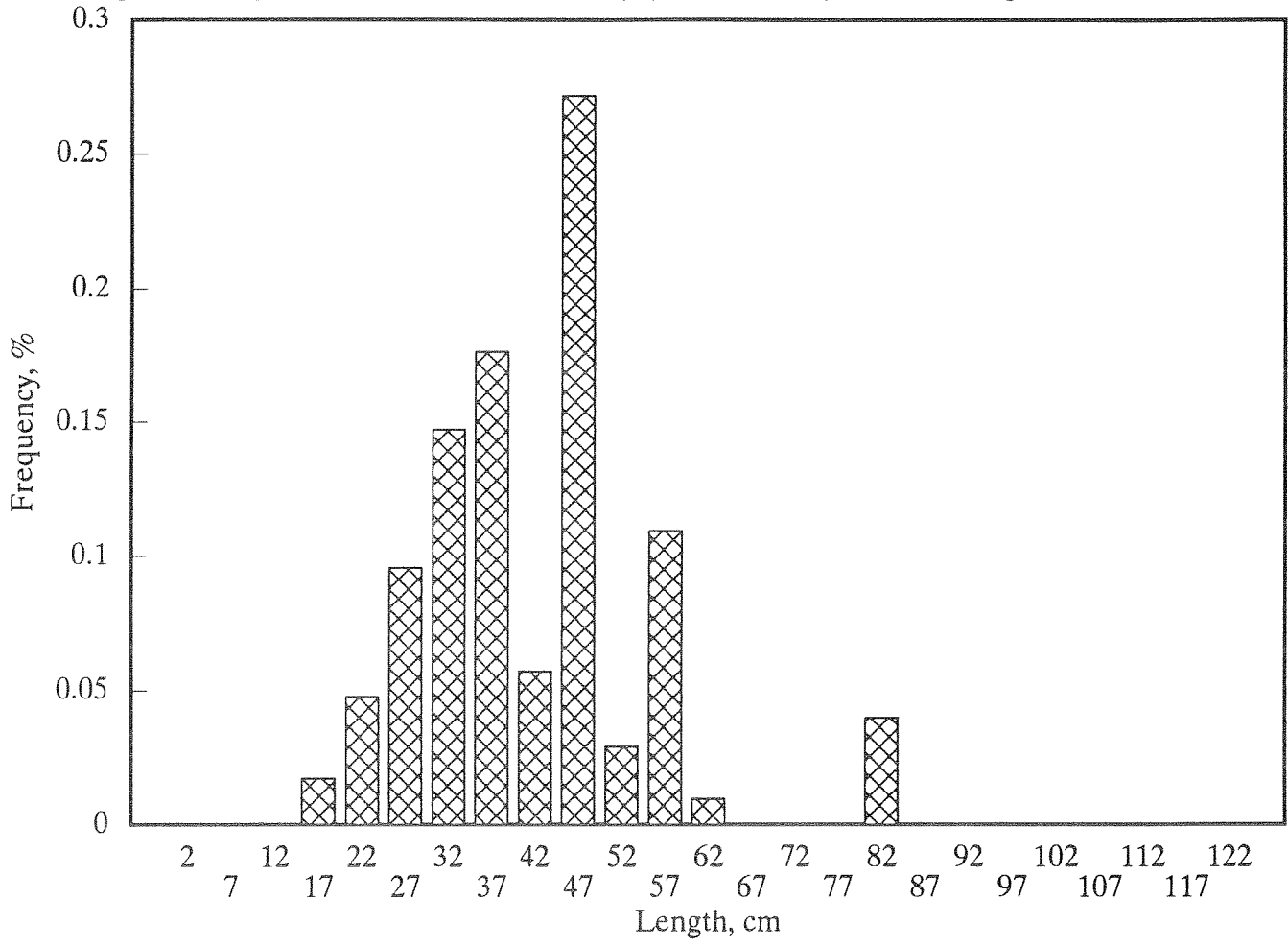


Fig.5.4. Length frequency distribution (%) of cod sample for feeding studies for Barents sea.

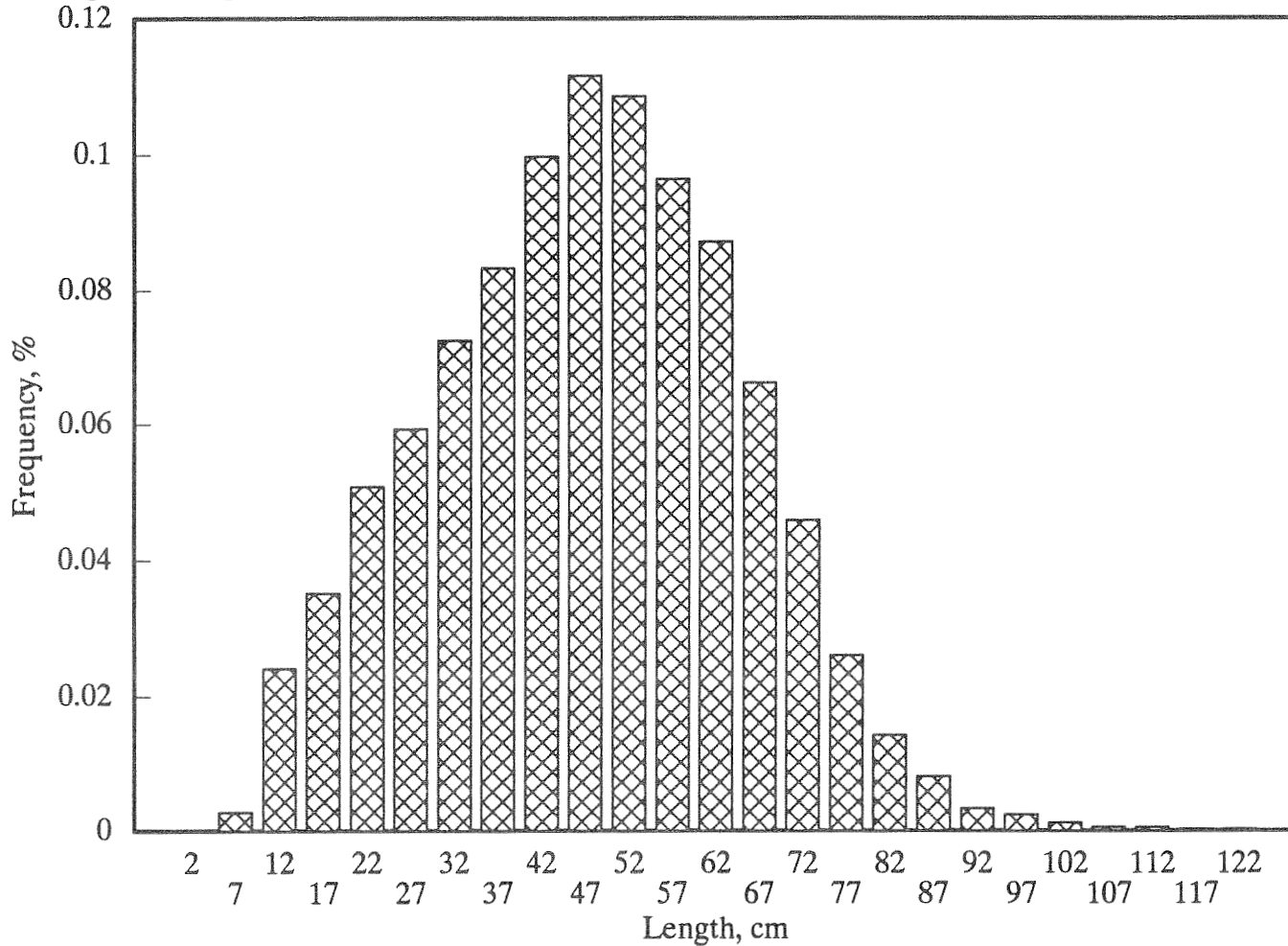


Fig.5.5. Length frequency distribution (%) of cod sample for feeding studies for Iceland ecosystem.

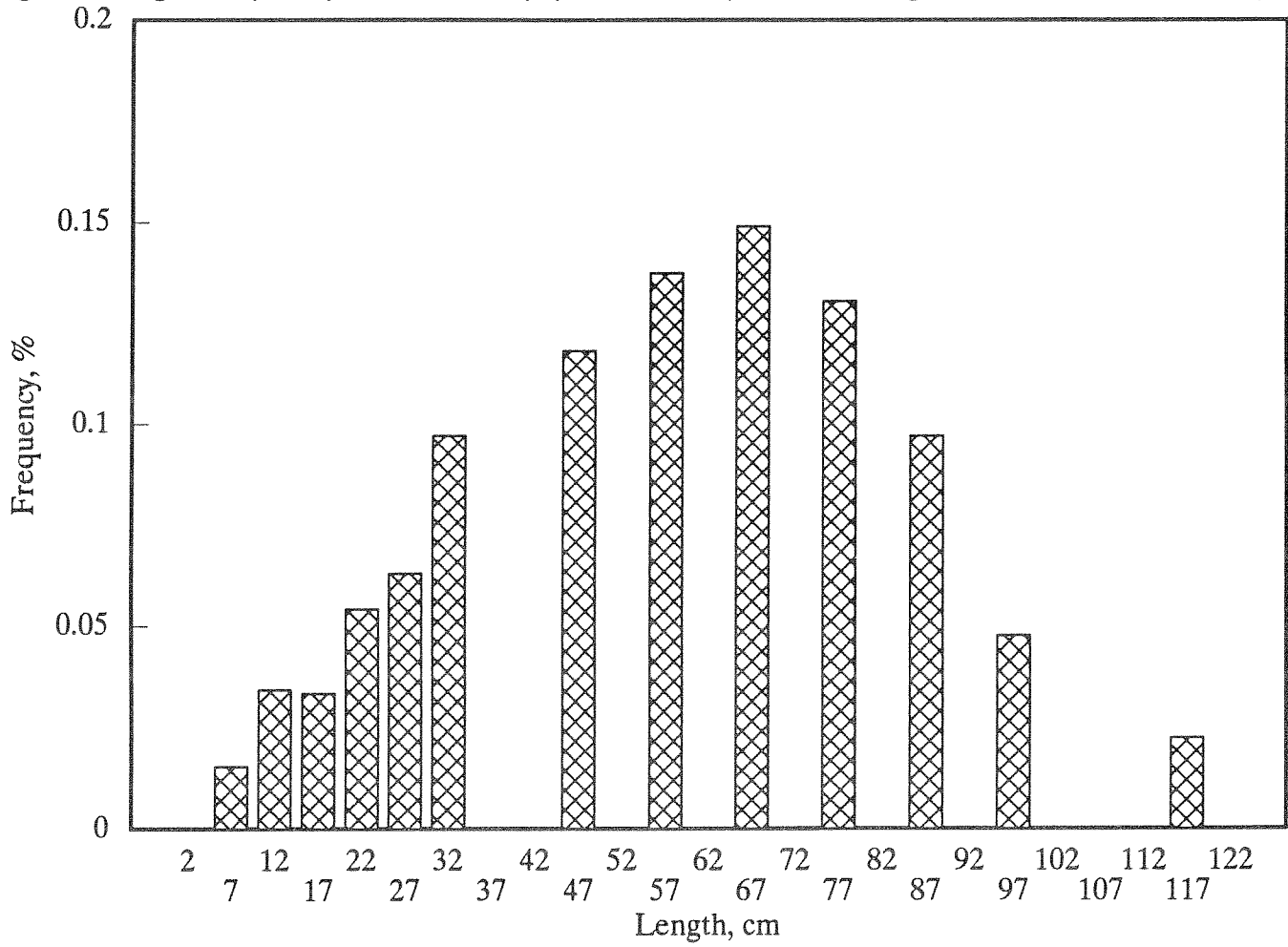


Fig.5.6. Length frequency distribution (%) of cod sample for feeding studies for Newfoundland.

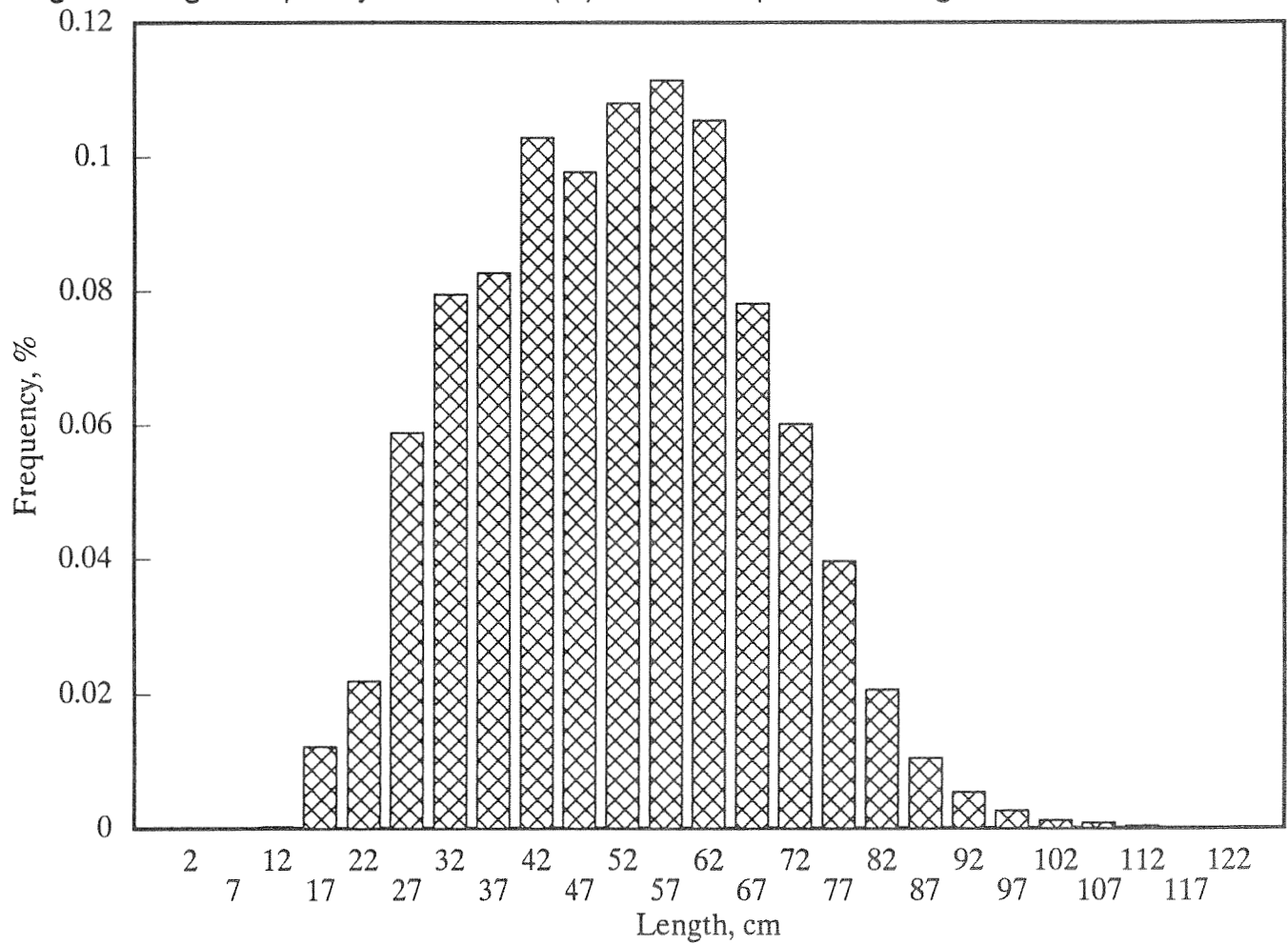
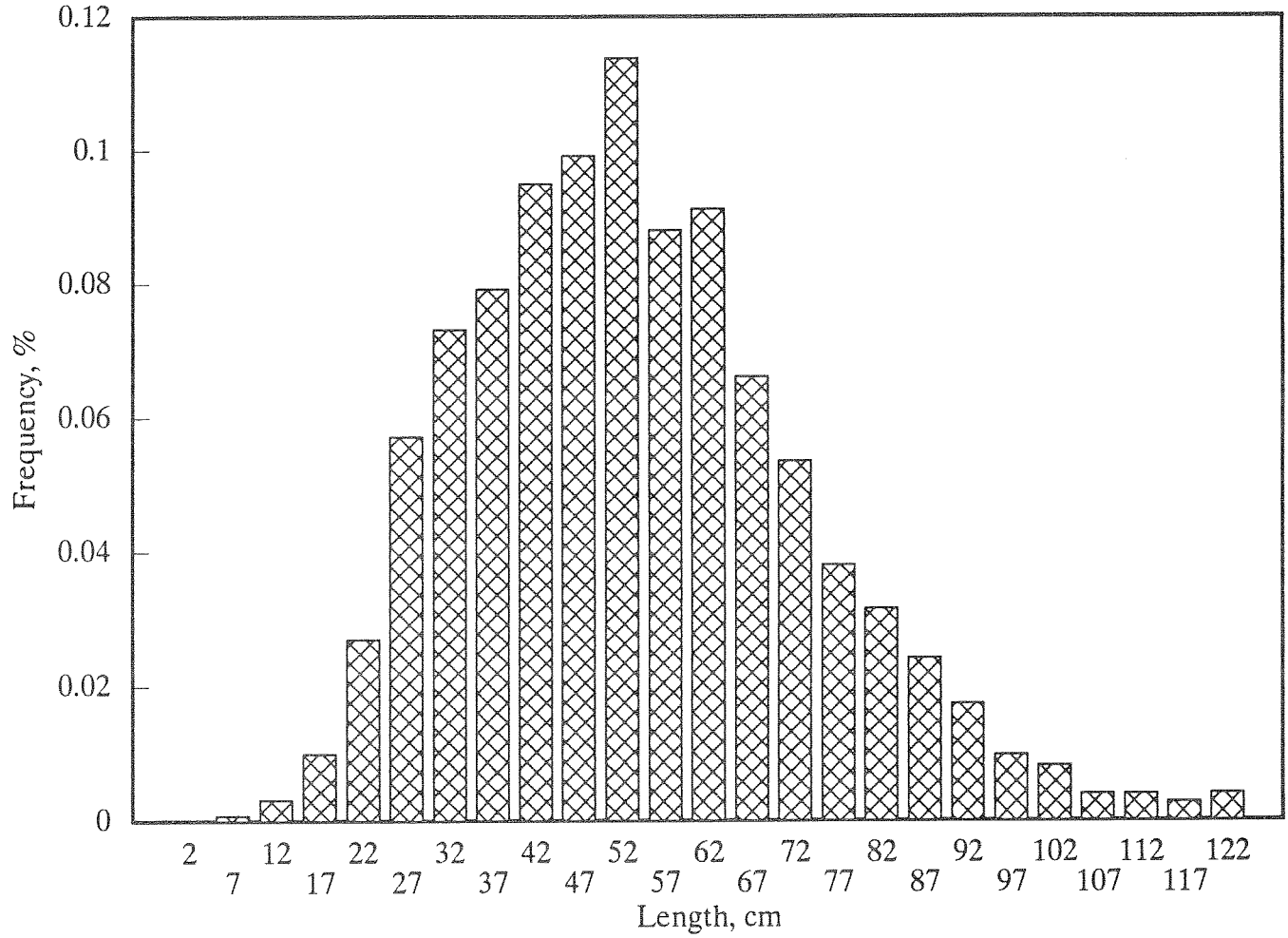


Fig.5.7. Length frequency distribution (%) of cod sample for feeding studies for USA ecosystem.



HAKE LENGTH COMPOSITION ICES AREA VIII AND USA

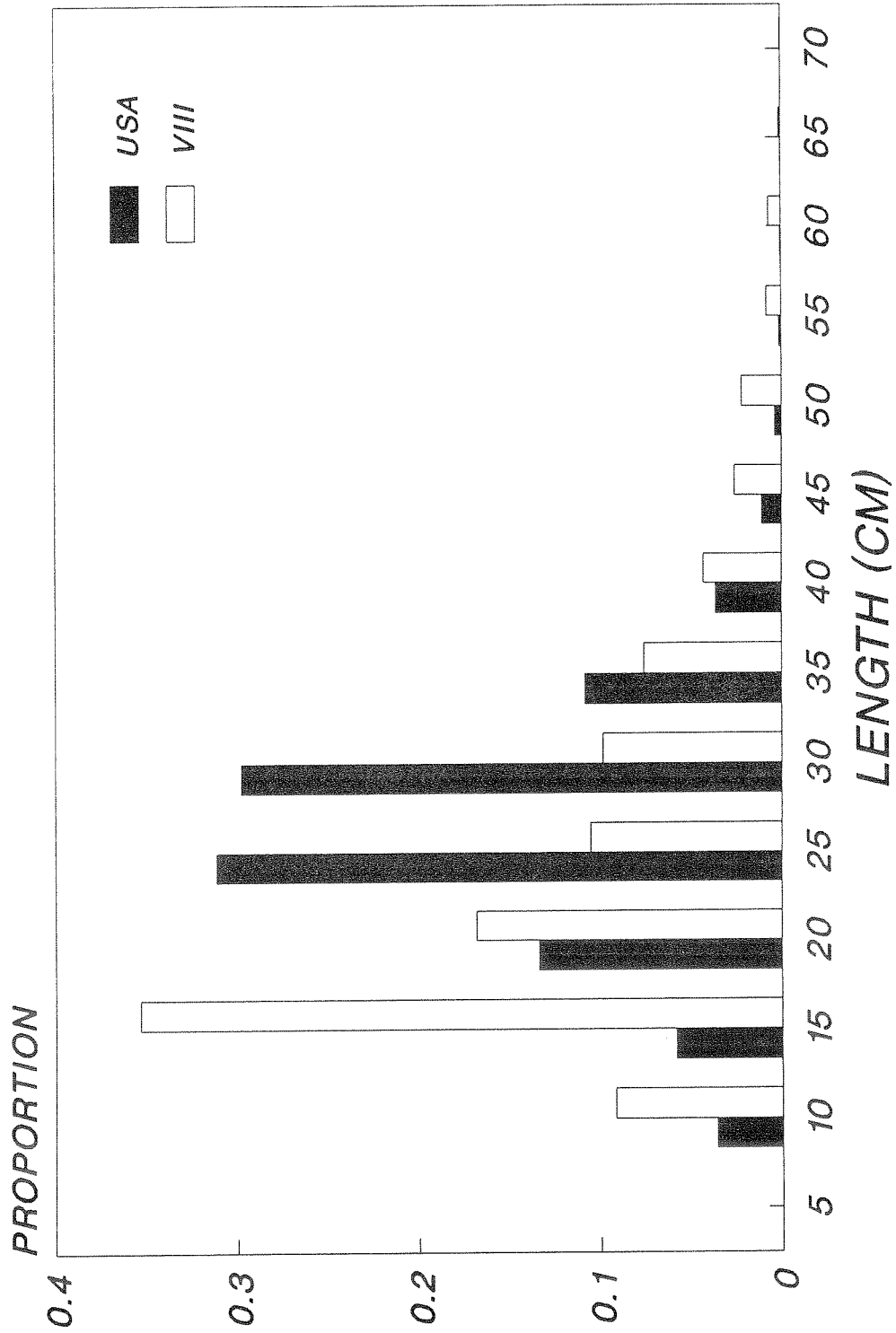


Figure 5.8. Size composition of hake sampled from the northeast USA and in ICES Area VIII for stomach content analysis.

Figure 6.1.1a. Plot of mean PCA score by predator size category for six ecosystems.

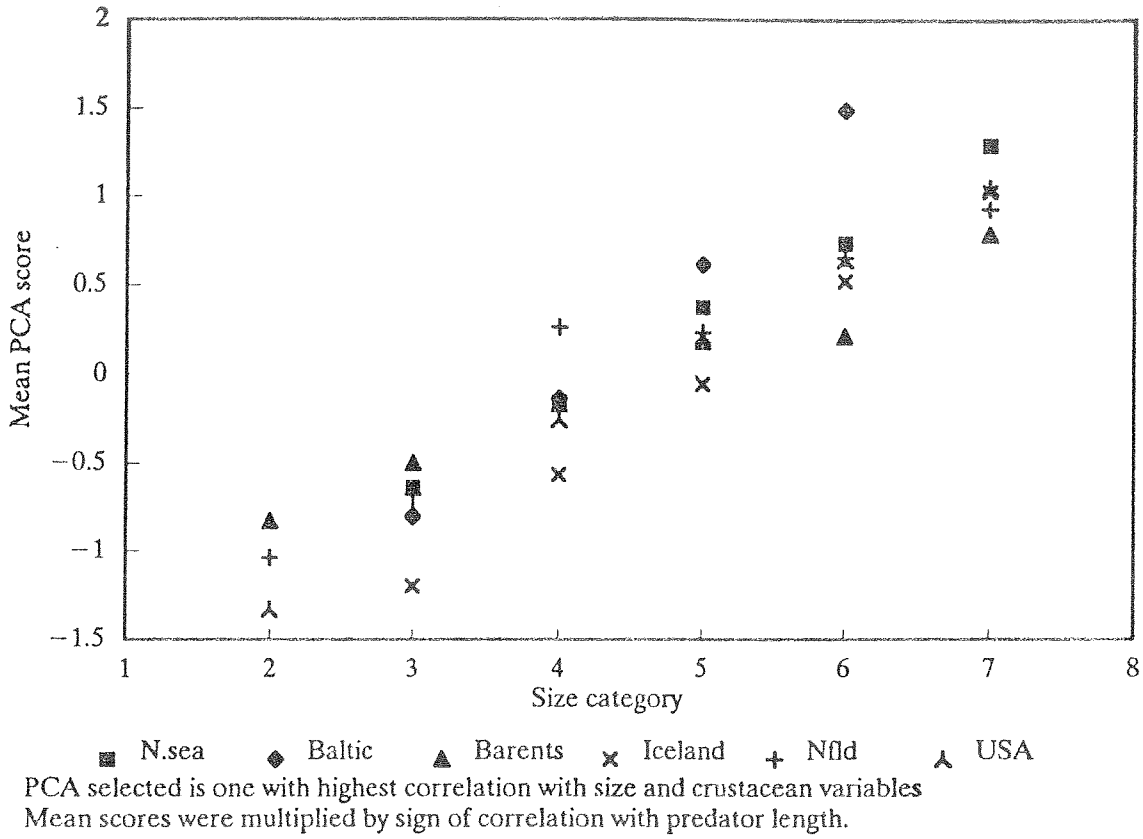


Figure 6.1.1b. Plot of standard deviation of PCA score by predator size category for six ecosystems.

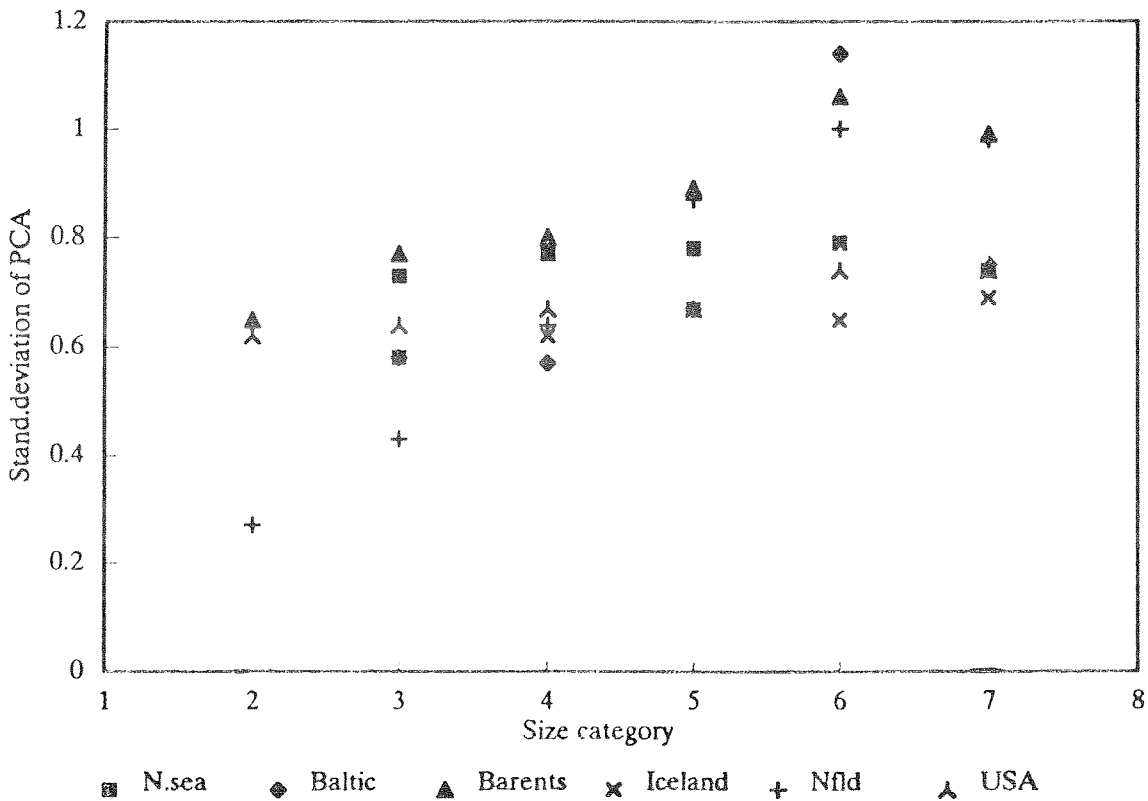


Figure 6.1.1c. Plot of mean PCA score by predator size category for six ecosystems.

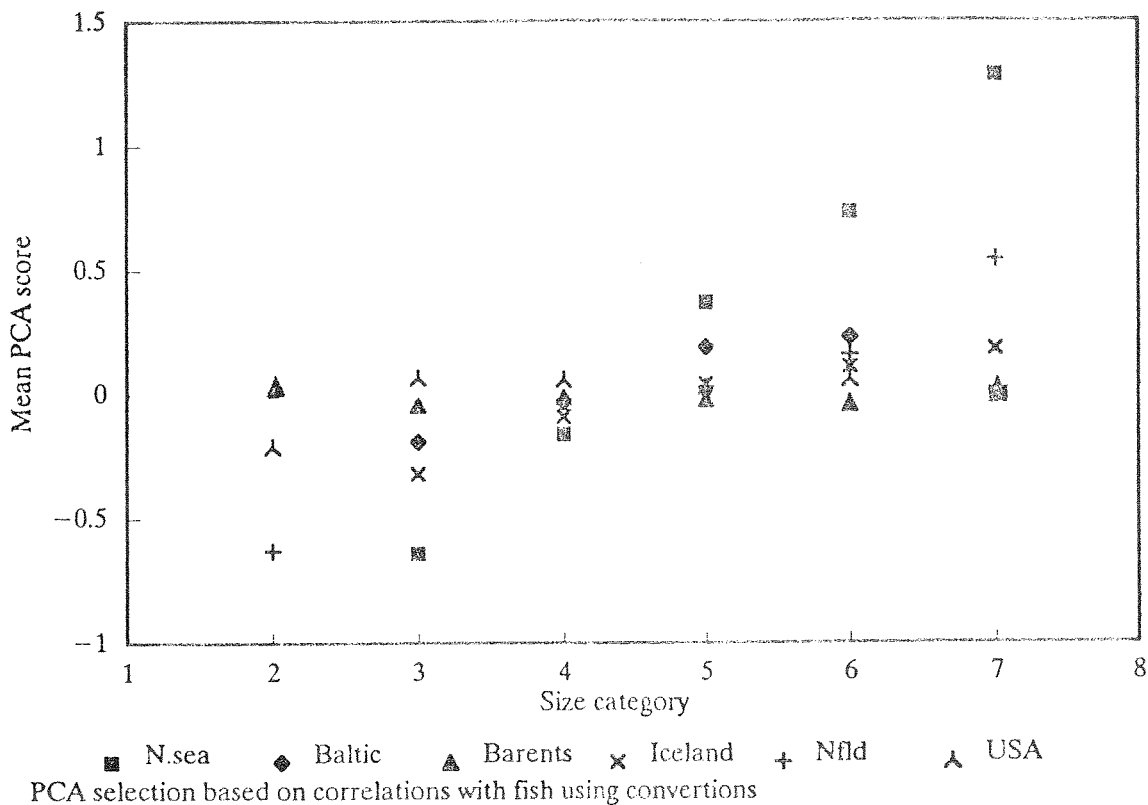
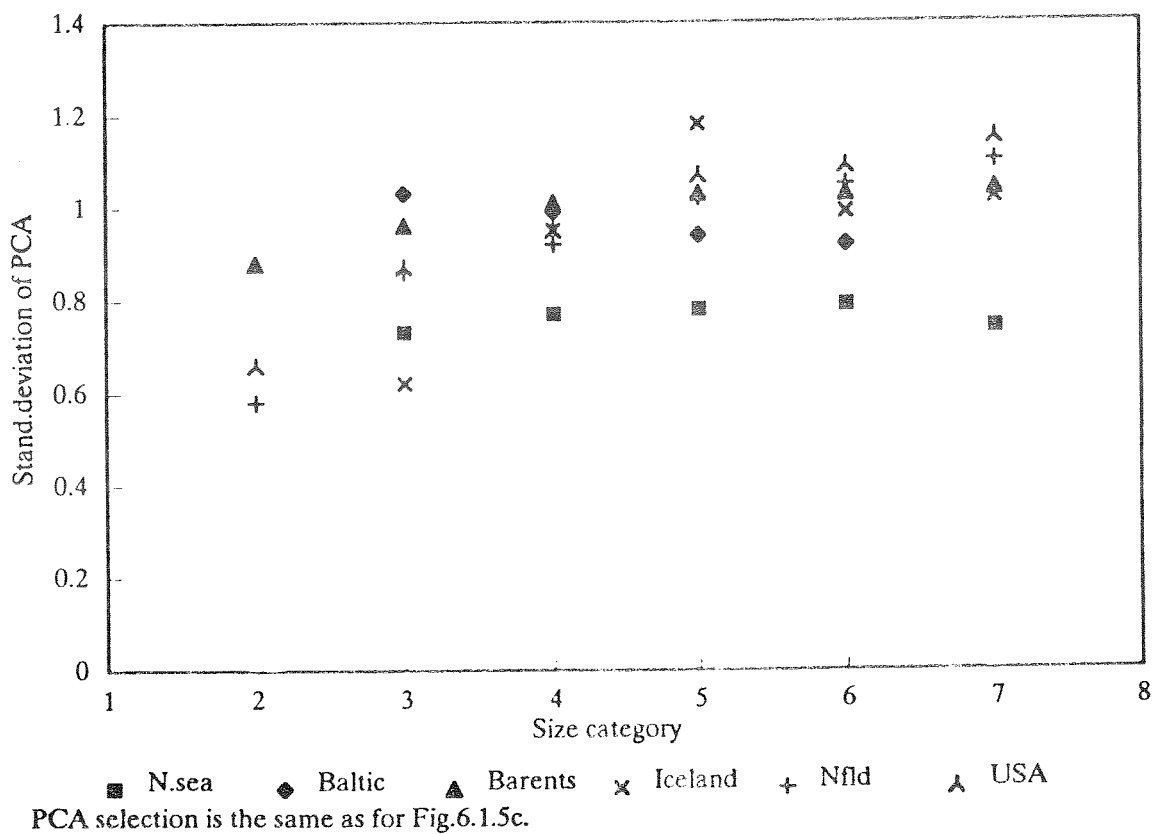
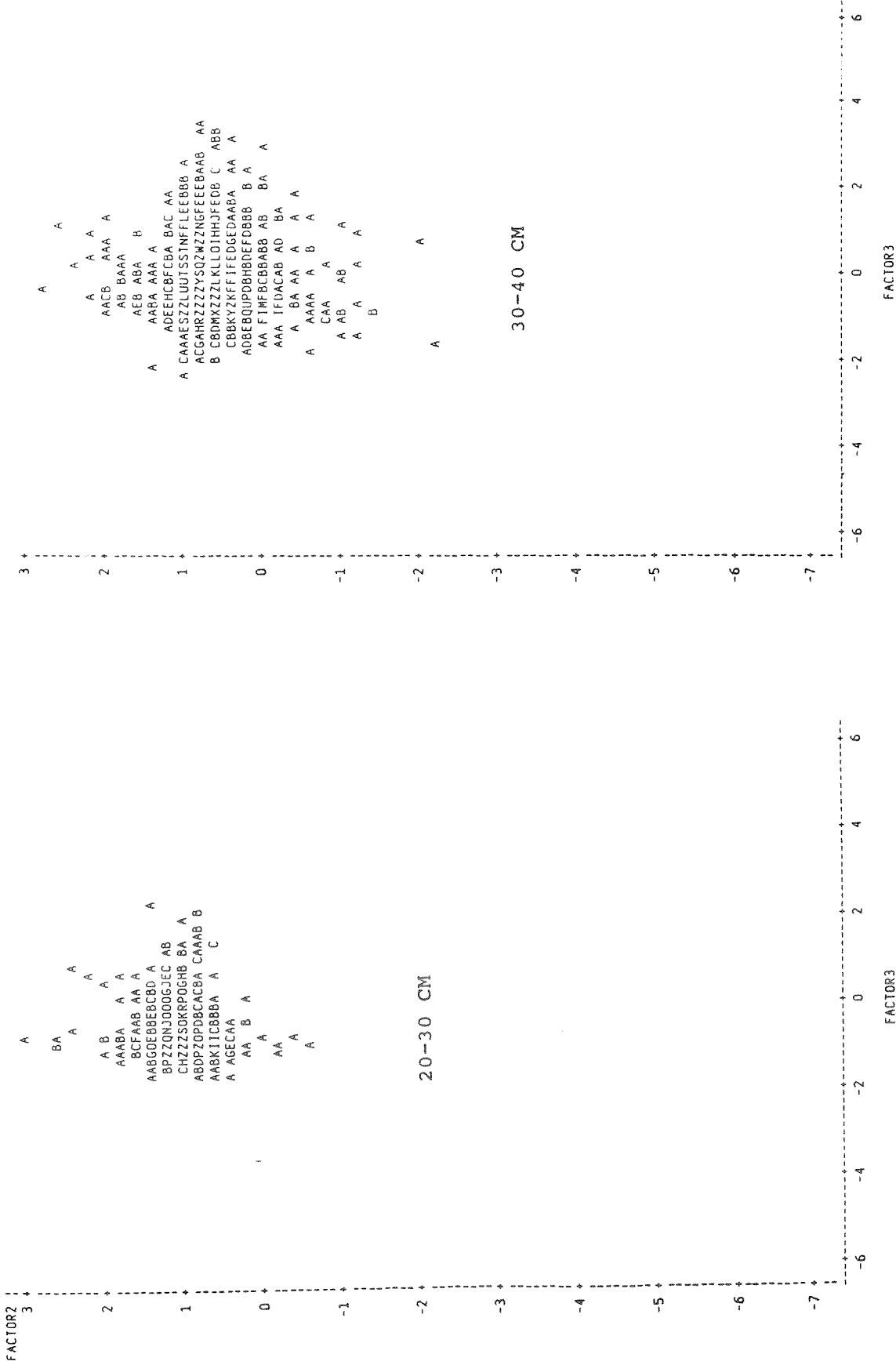


Figure 6.1.1d. Plot of standard deviation of PCA score by predator size category for six ecosystems.

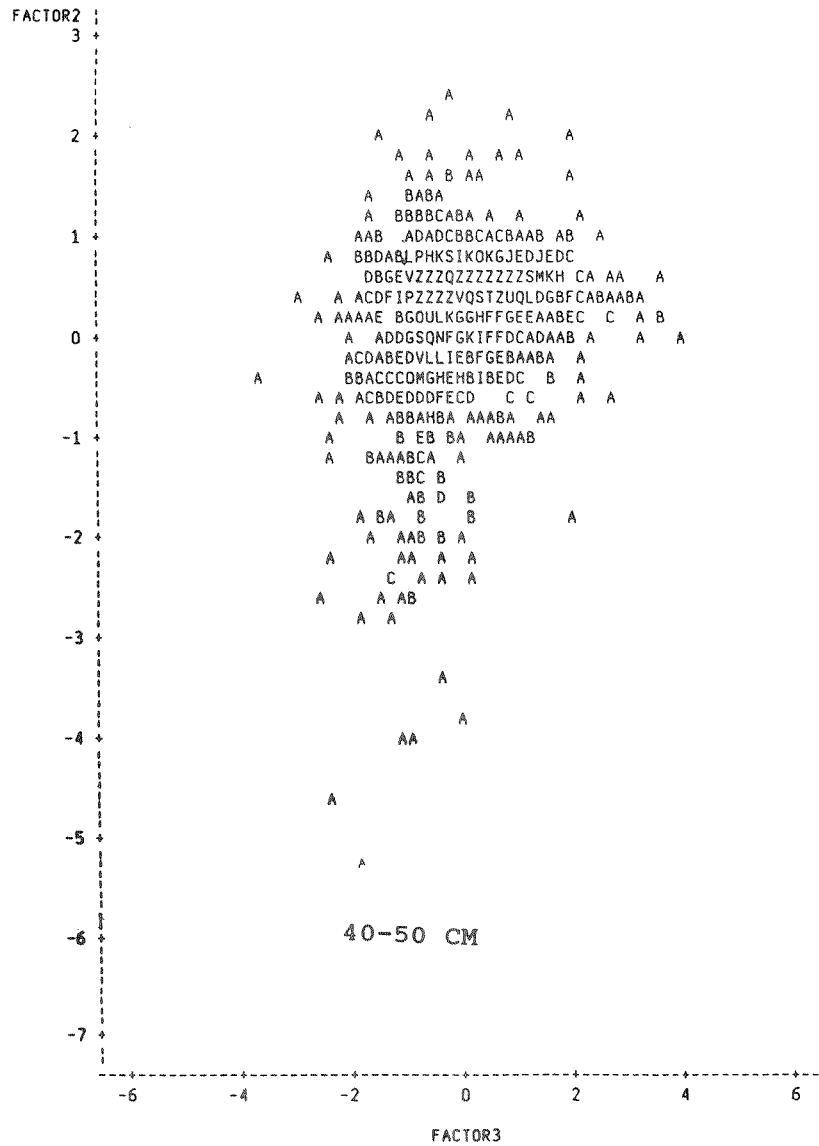




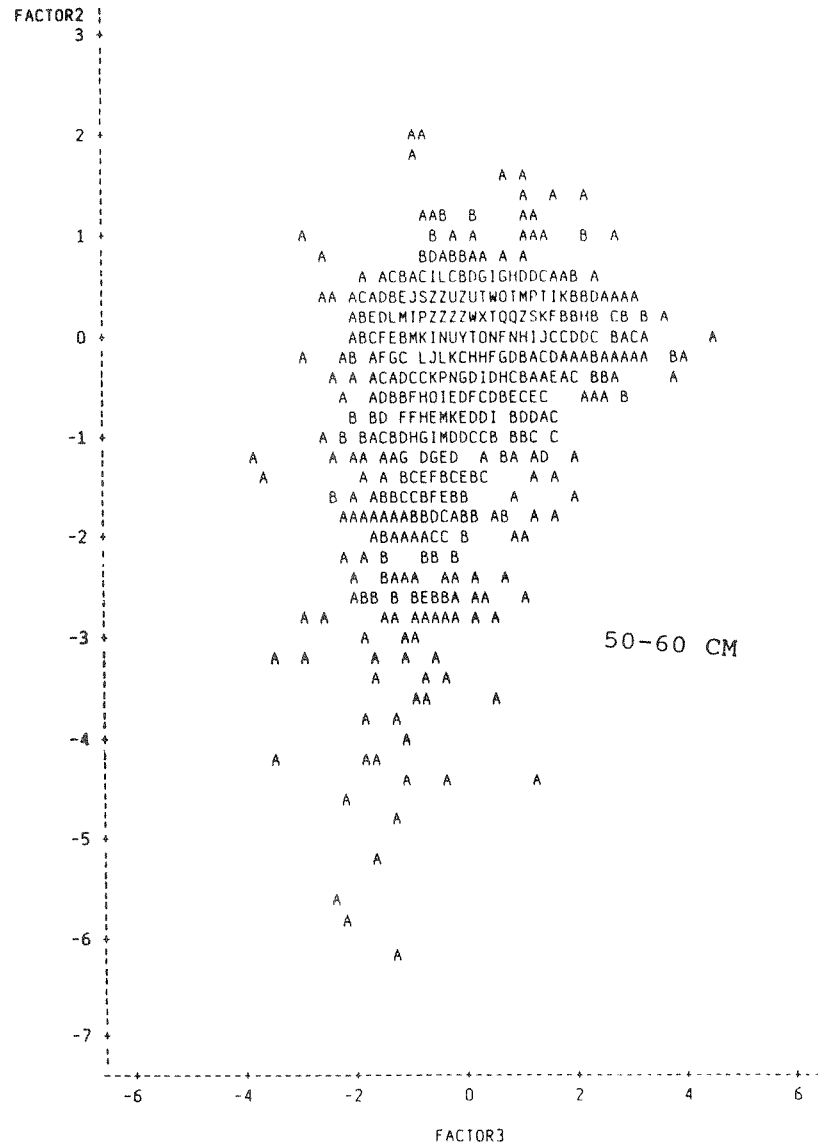
NOTE: 8 obs had missing values. 358 obs hidden.

NOTE: 23 obs had missing values. 648 obs hidden.

Figure 6.1.2. Scatterplot of scores of bulked cases on PC 3 (tendency to feed on fish) vs. PC 2 (tendency to feed on invertebrates), stratified by 10 cm length interval, from PCA of Newfoundland data set. Note trajectory of mean scores and increasing variance over size intervals.



NOTE: 46 obs had missing values. 881 obs hidden.



NOTE: 71 obs had missing values. 1025 obs hidden.

Figure 6.1.2 (continued).

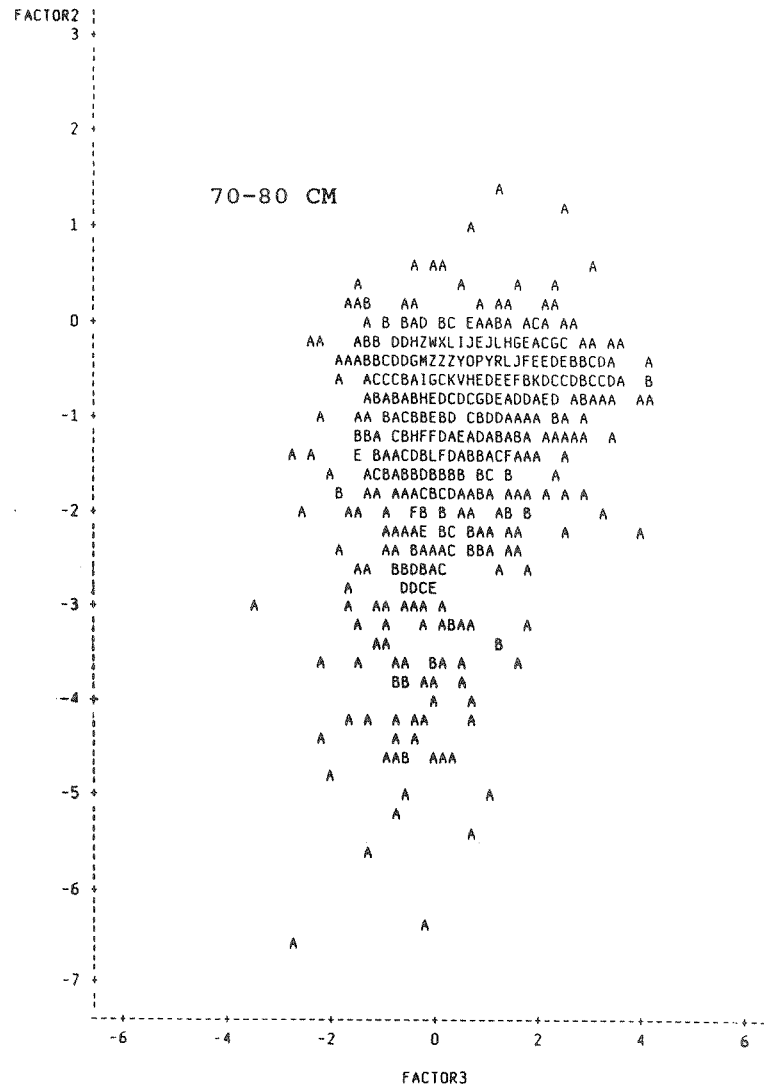
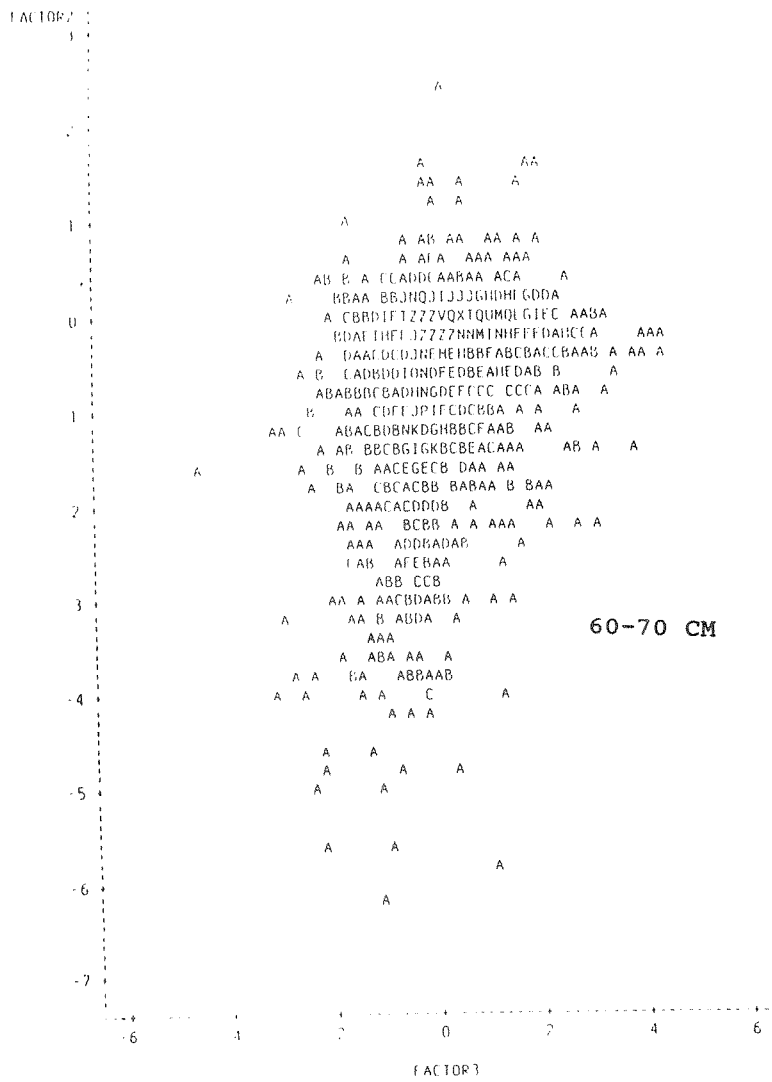


Figure 6.1.2 (continued).

Fig 6.1.3 Mean PCA score by year by ecosystem. A. Selected components are ones correlated with fish consumption.

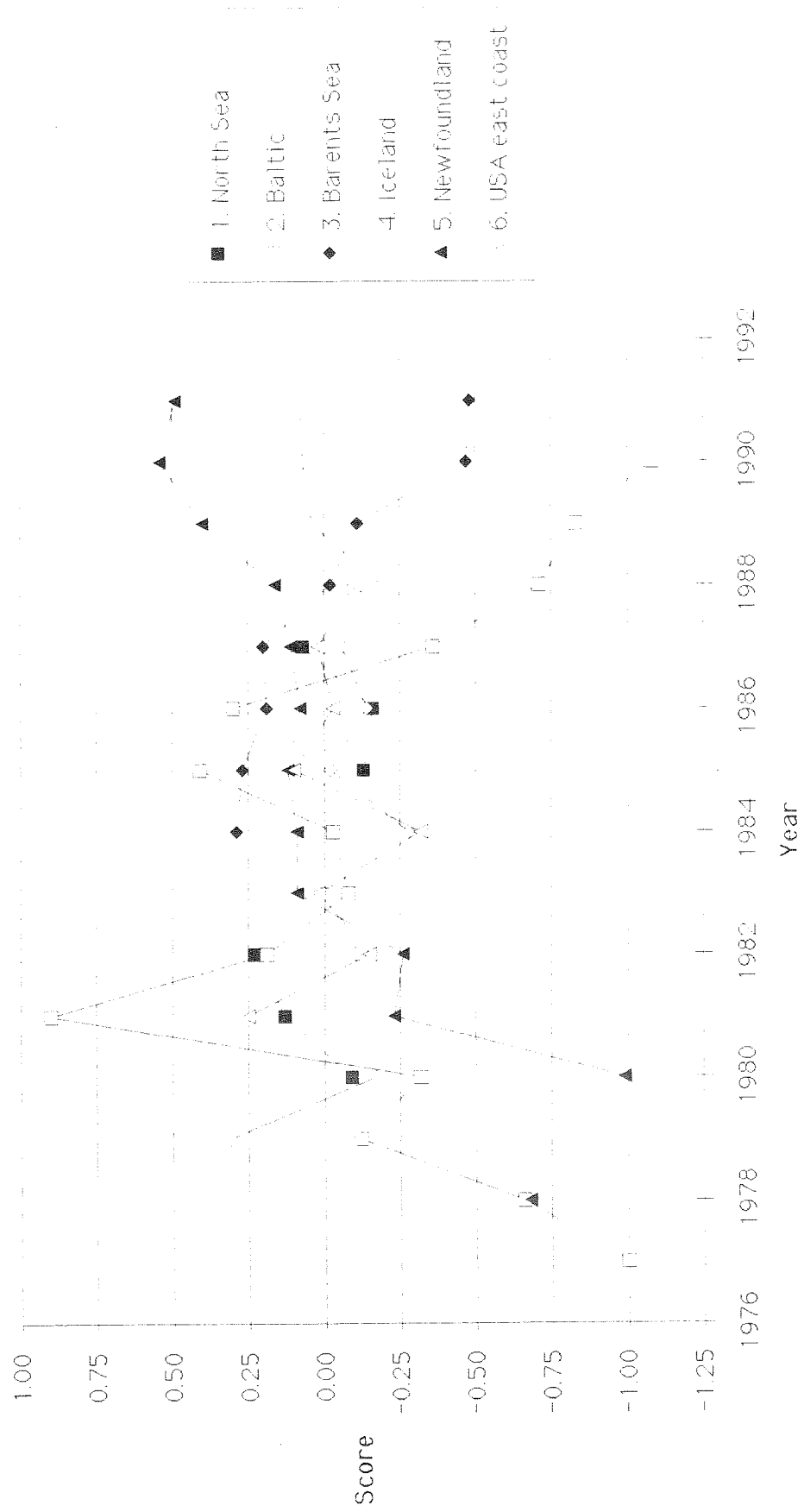
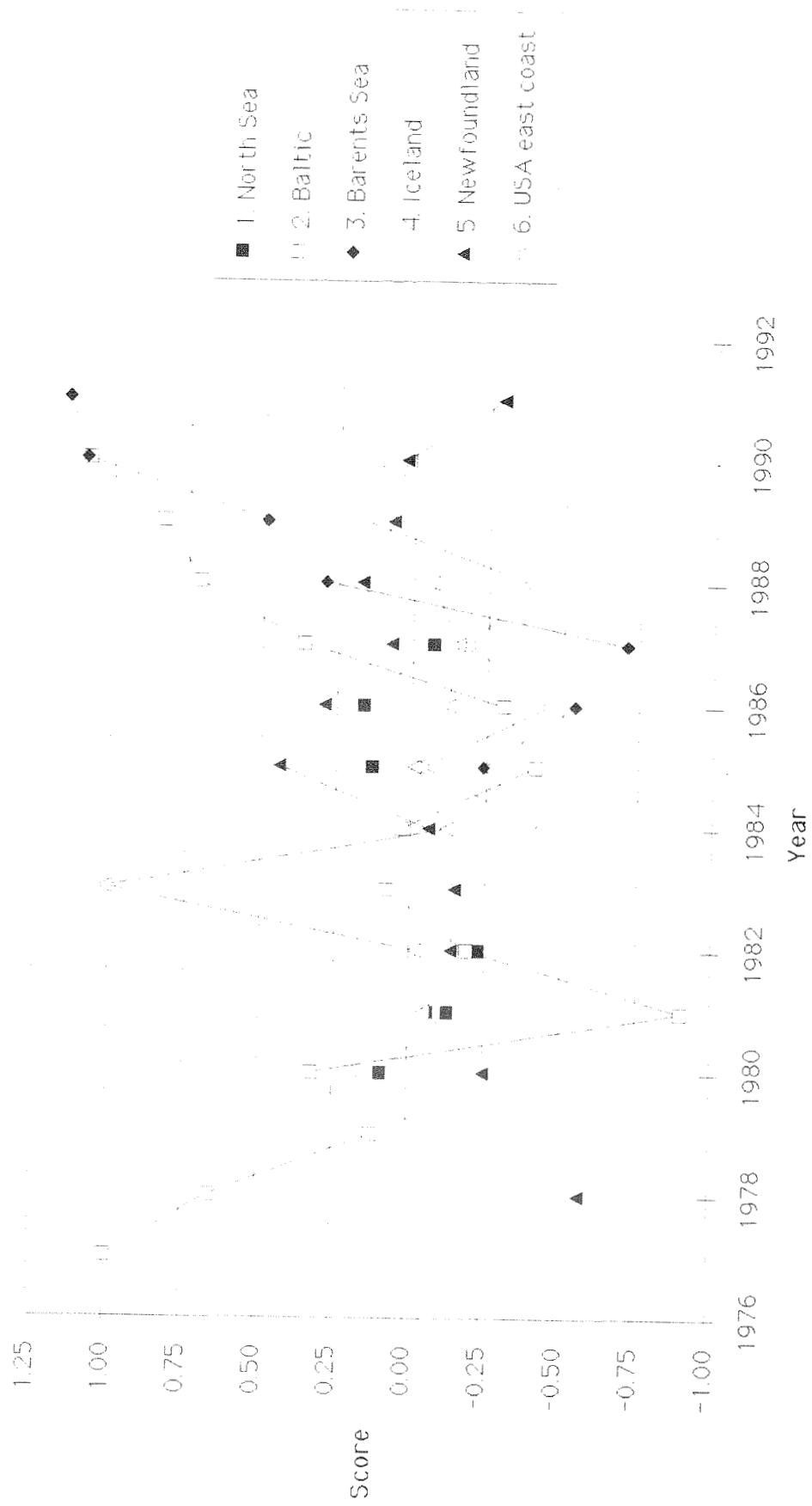


Fig 6.1.3 Mean PCA score by year by ecosystem. B. Selected components are ones correlated with invertebrate consumption (especially crustaceans).



Cod growth across systems

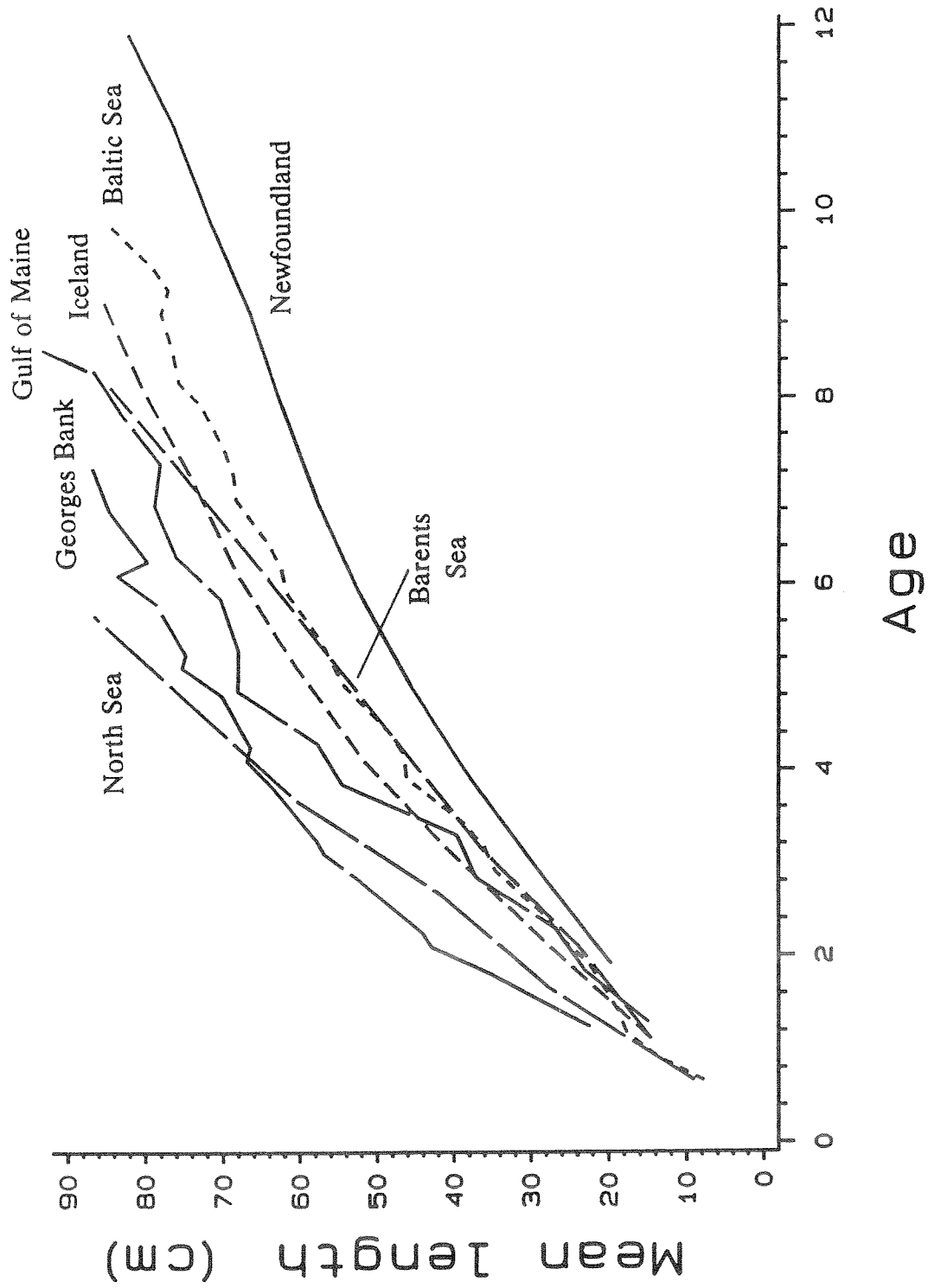


Figure 6.2.1. Comparative cod growth rates among ecosystems.

Distribution of scaled stomach weight

ECOSYS=1

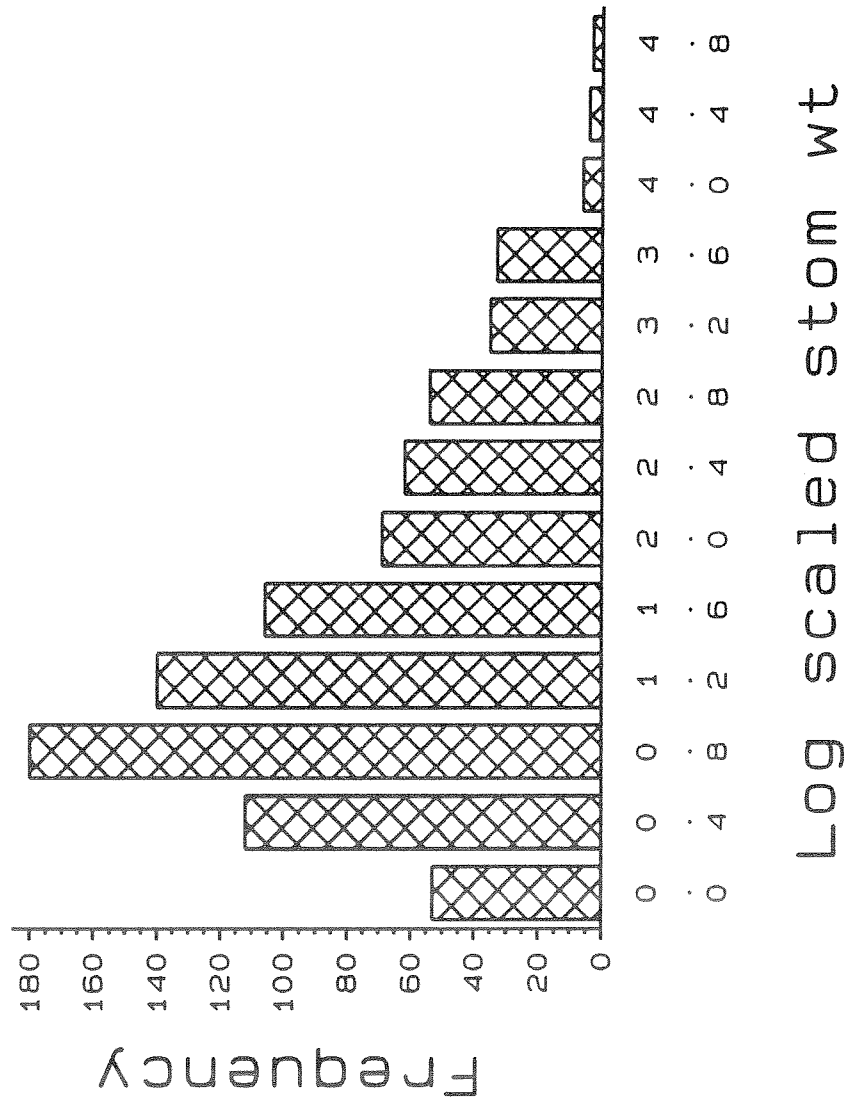
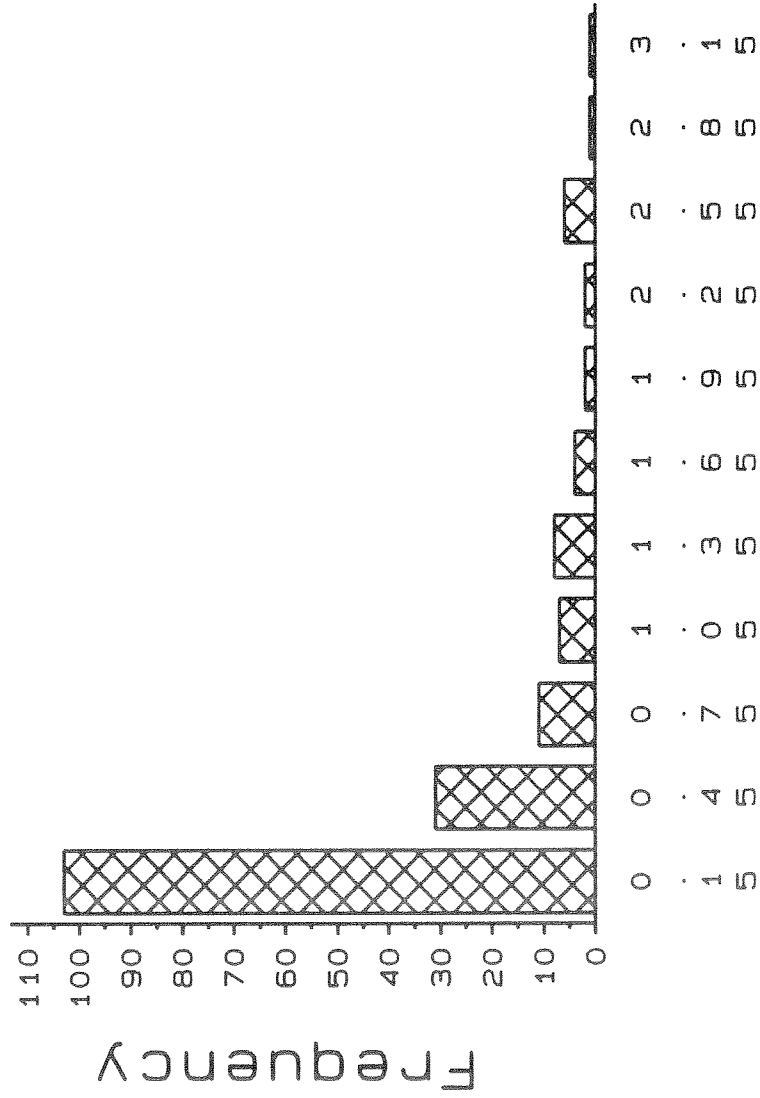


Figure 6.2.2. Frequency distribution of log scaled mean total stomach weight in the 40-50cm cod length class for the bulked (within stratum samples) for the North Sea.

Distribution of scaled stomach weight

ECOSYS=2



Log scaled stom wt

Figure 6.2.3. Frequency distribution of log scaled mean total stomach weight in the 40-50cm cod length class for the bulked (within stratum) for the Baltic Sea.

Distribution of scaled stomach weight

ECOSYS=3

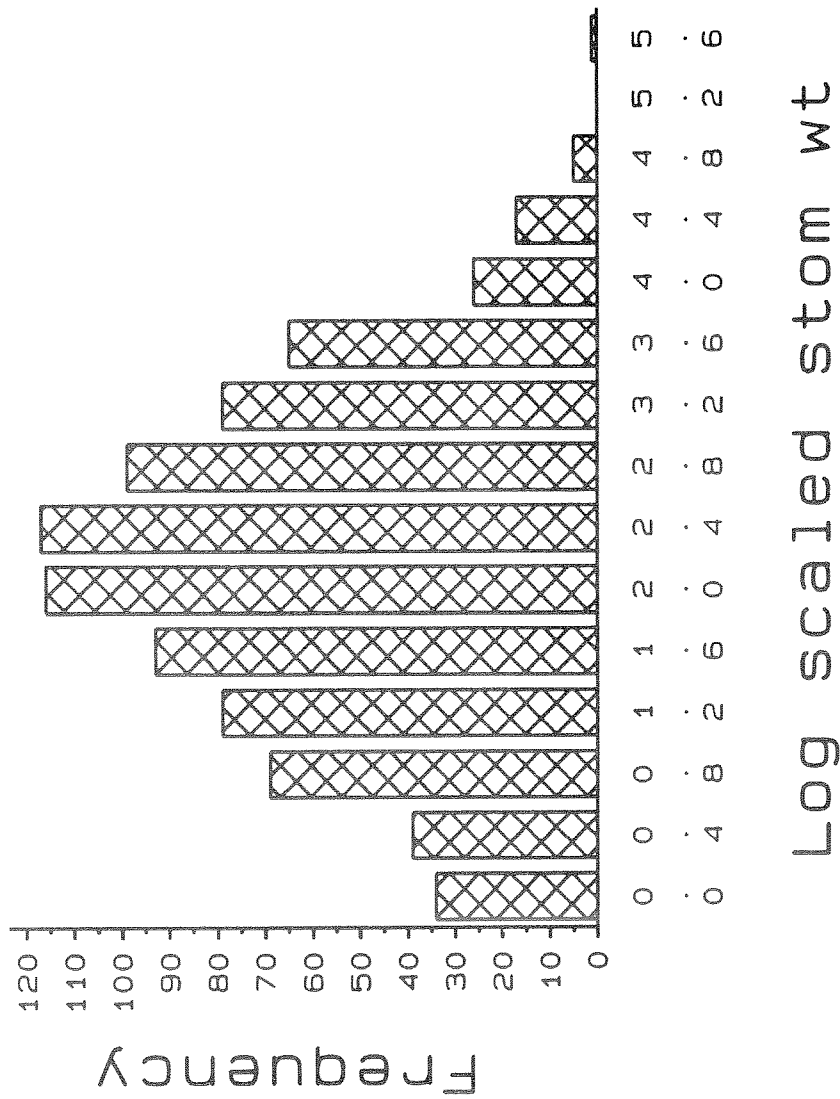


Figure 6.2.4. Frequency distribution of log scaled mean total stomach weight in the 40-50cm length class bulked within hauls for the Barents Sea.

Distribution of scaled stomach weight

ECOSYS=4

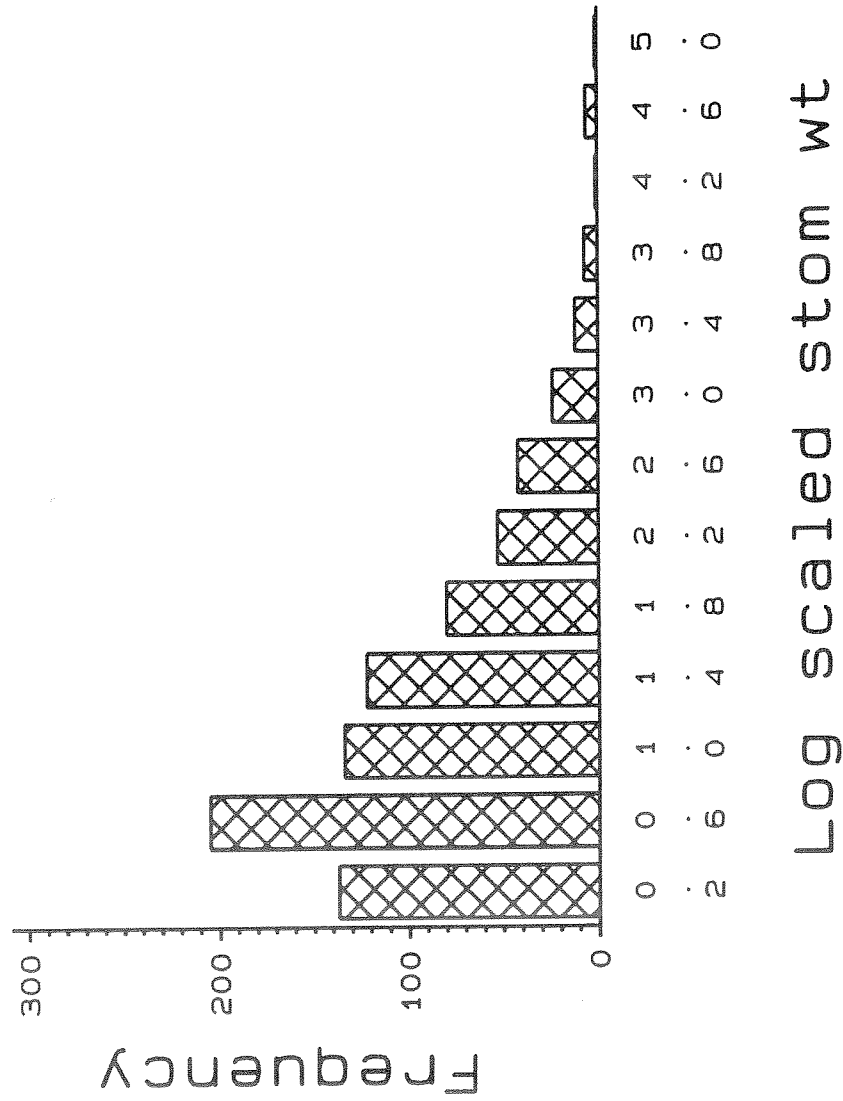


Figure 6.2.5. Frequency distribution of log scaled mean total stomach weight in the 40-50 cm length class bulked within hauls for Iceland (note, data initially bulked by haul prior to meeting).

Distribution of scaled stomach weight

ECOSYS=5

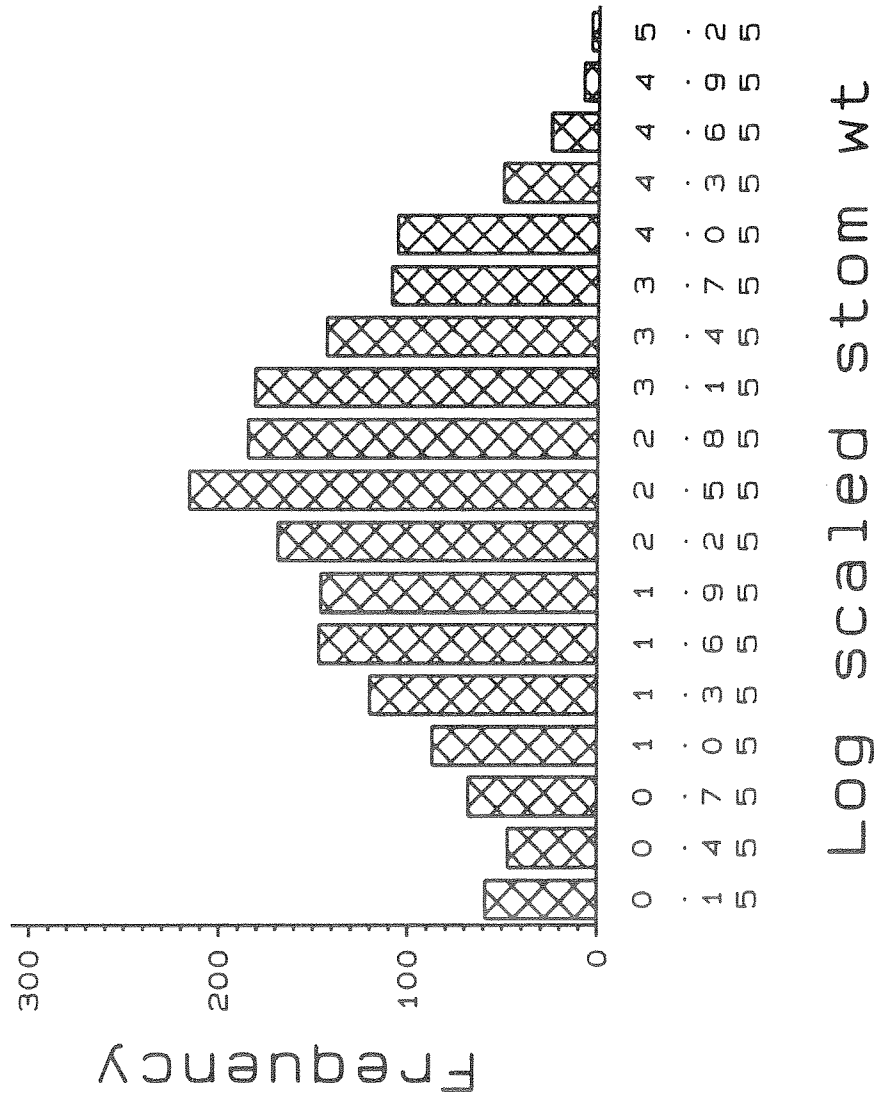


Figure 6.2.6. Frequency distribution of log scaled mean total stomach weight in the 40-50cm length class bulked within hauls for Newfoundland.

Distribution of scaled stomach weight

ECOSYS=6

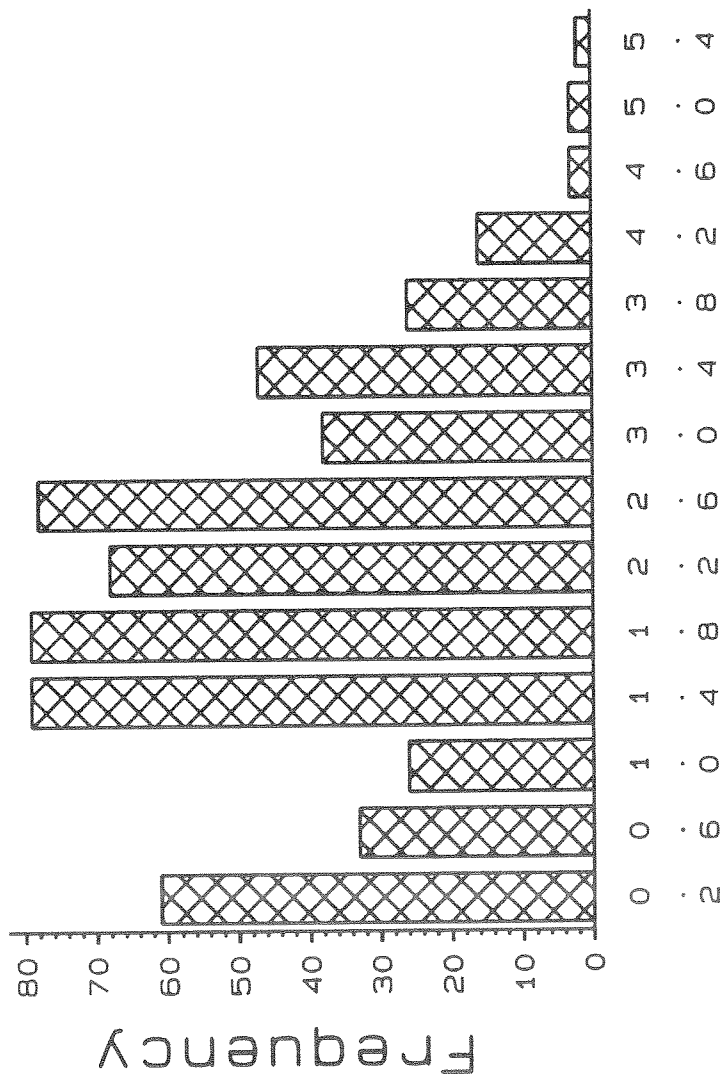


Figure 6.2.7. Frequency distribution of log scaled mean total stomach weight in the 40-50cm length class bulked within hauls for USA East Coast.

Ecosystem effect on scaled stomach weight

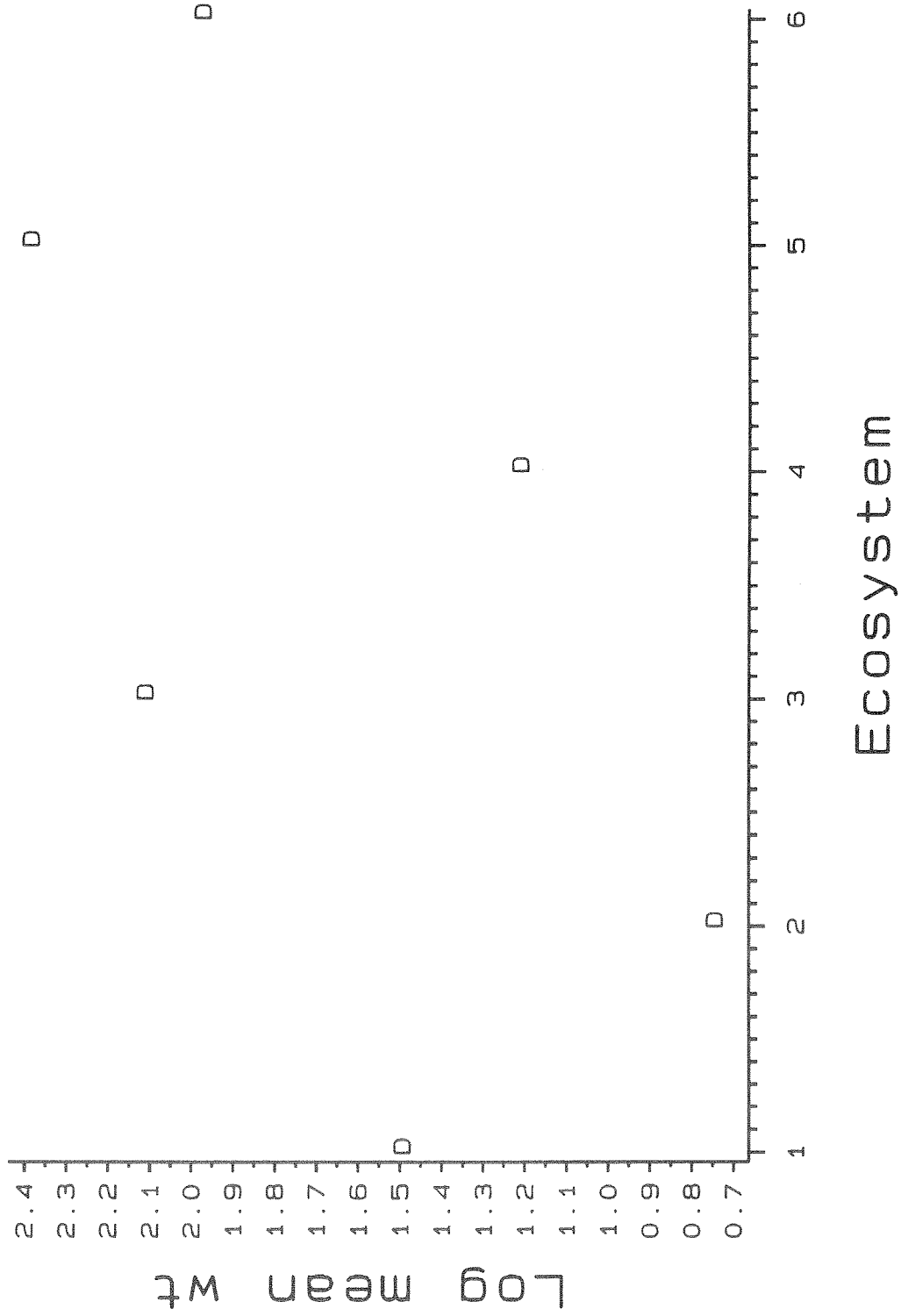


Figure 6.2.8. Ecosystem effect on log scaled mean total prey weight bulked within 10cm length classes (by stratum or haul).

Ecosystem effect on logits of prop empty

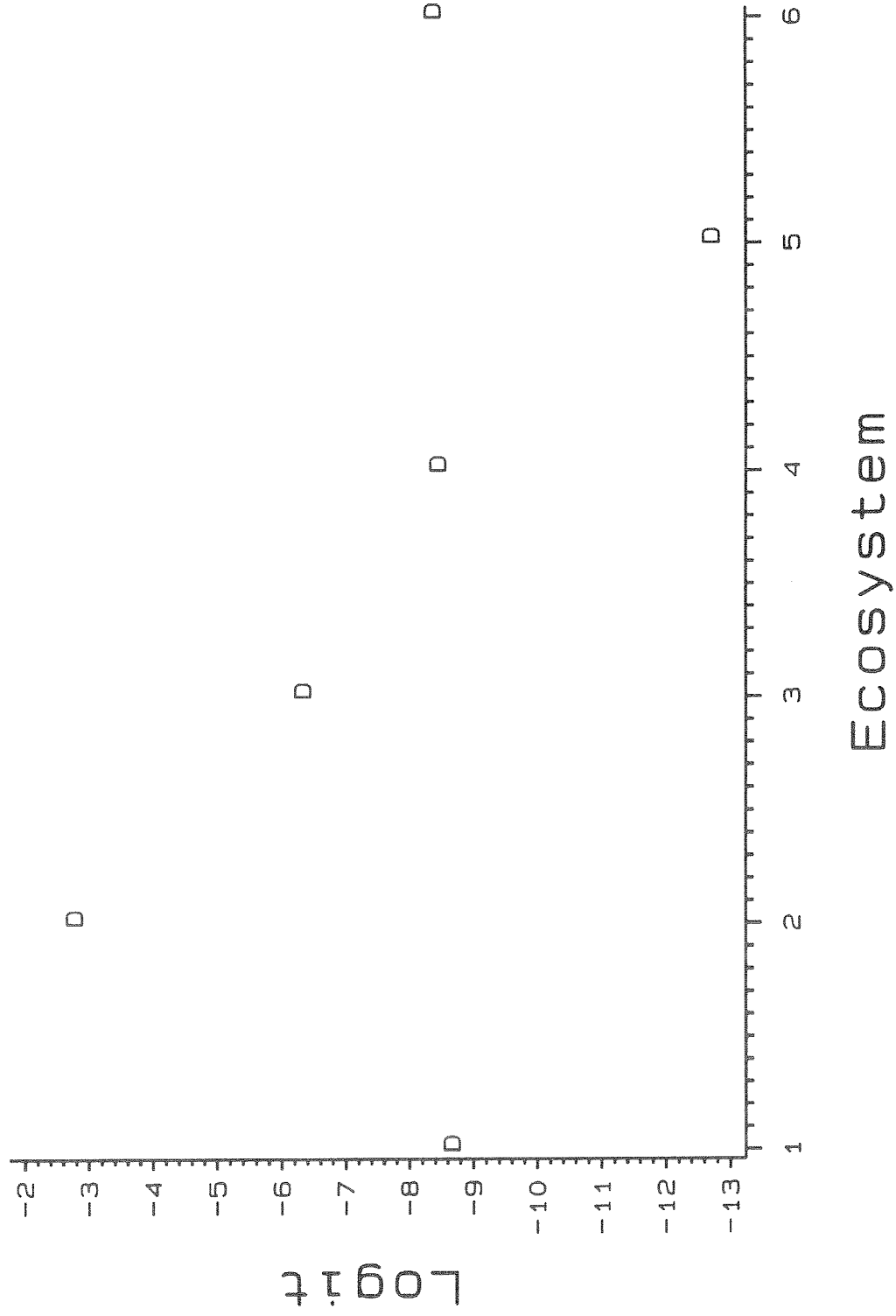


Figure 6.2.9. Ecosystem effect on the logit of proportion of empty stomachs in the bulked samples per 10cm length classes (by stratum or haul).

Length effect on scaled stomach weight

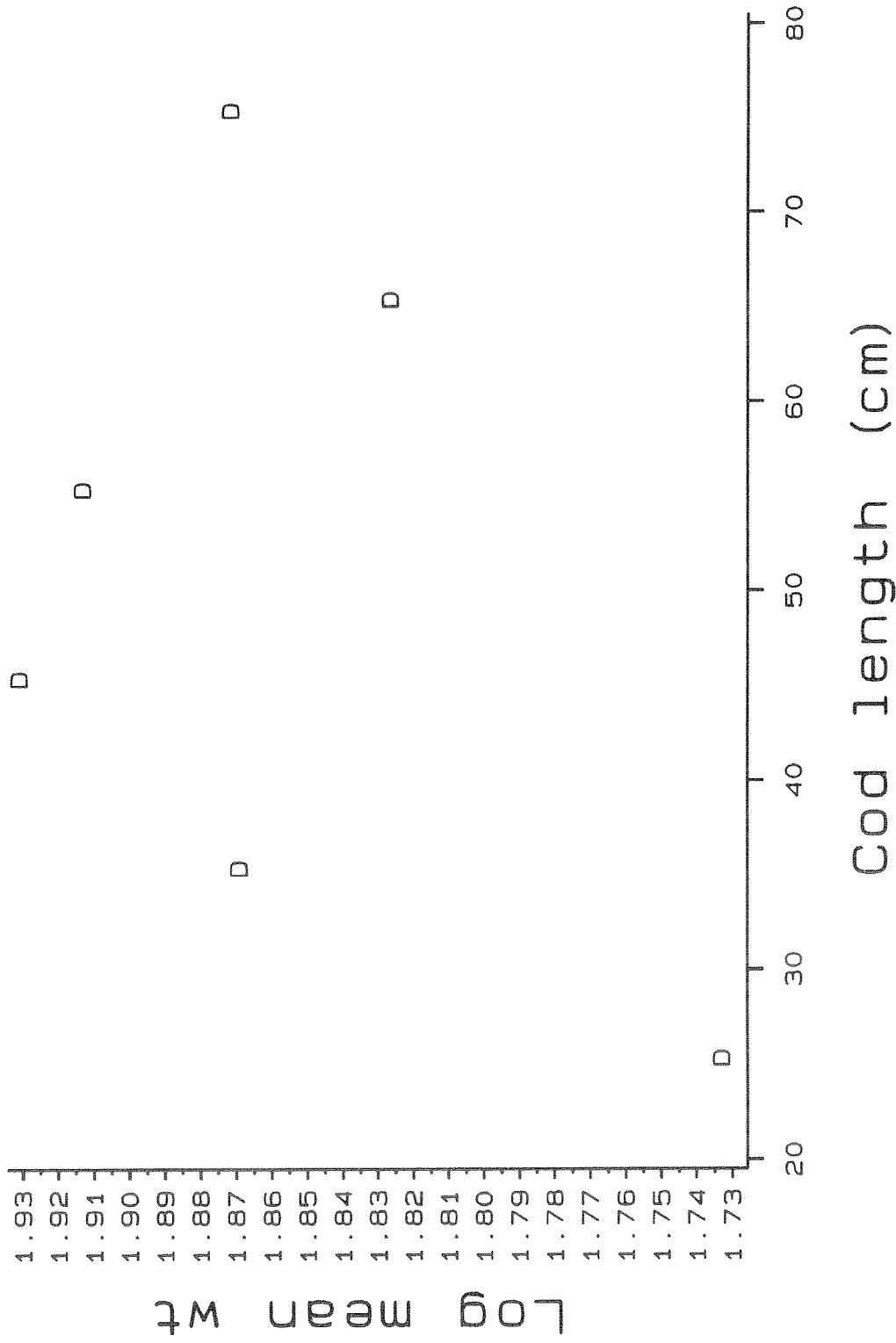


Figure 6.2.10. Length effect on the log scaled mean total prey weight bulked within 10cm length classes (by stratum or haul).

Growth effect on scaled stomach weight

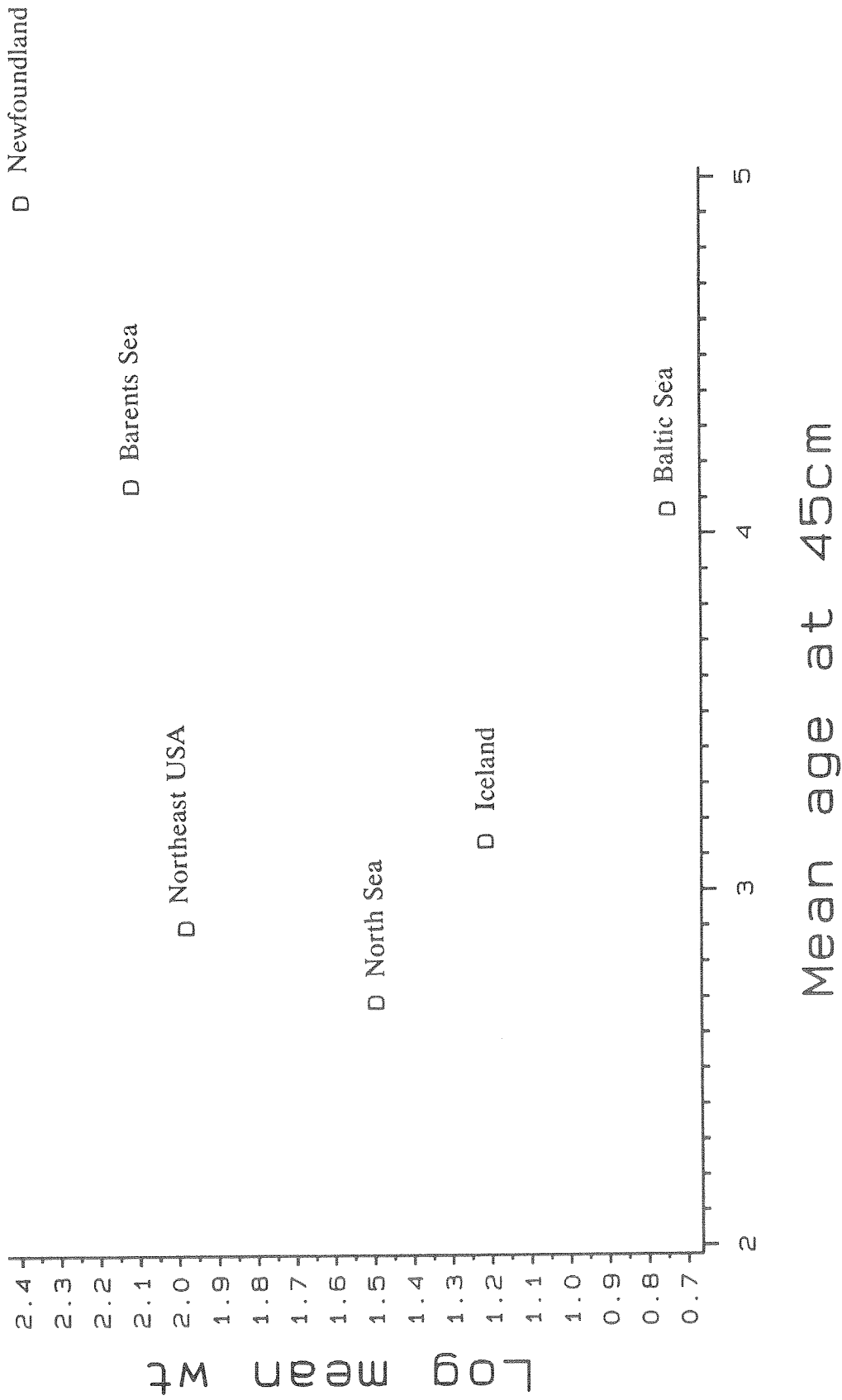


Figure 6.2.11. Growth effect on log scaled mean total prey weight bulked within 10cm length classes (by stratum or haul). Growth is measured as mean age at 45cm.

Temperature effect on scaled stomach weight

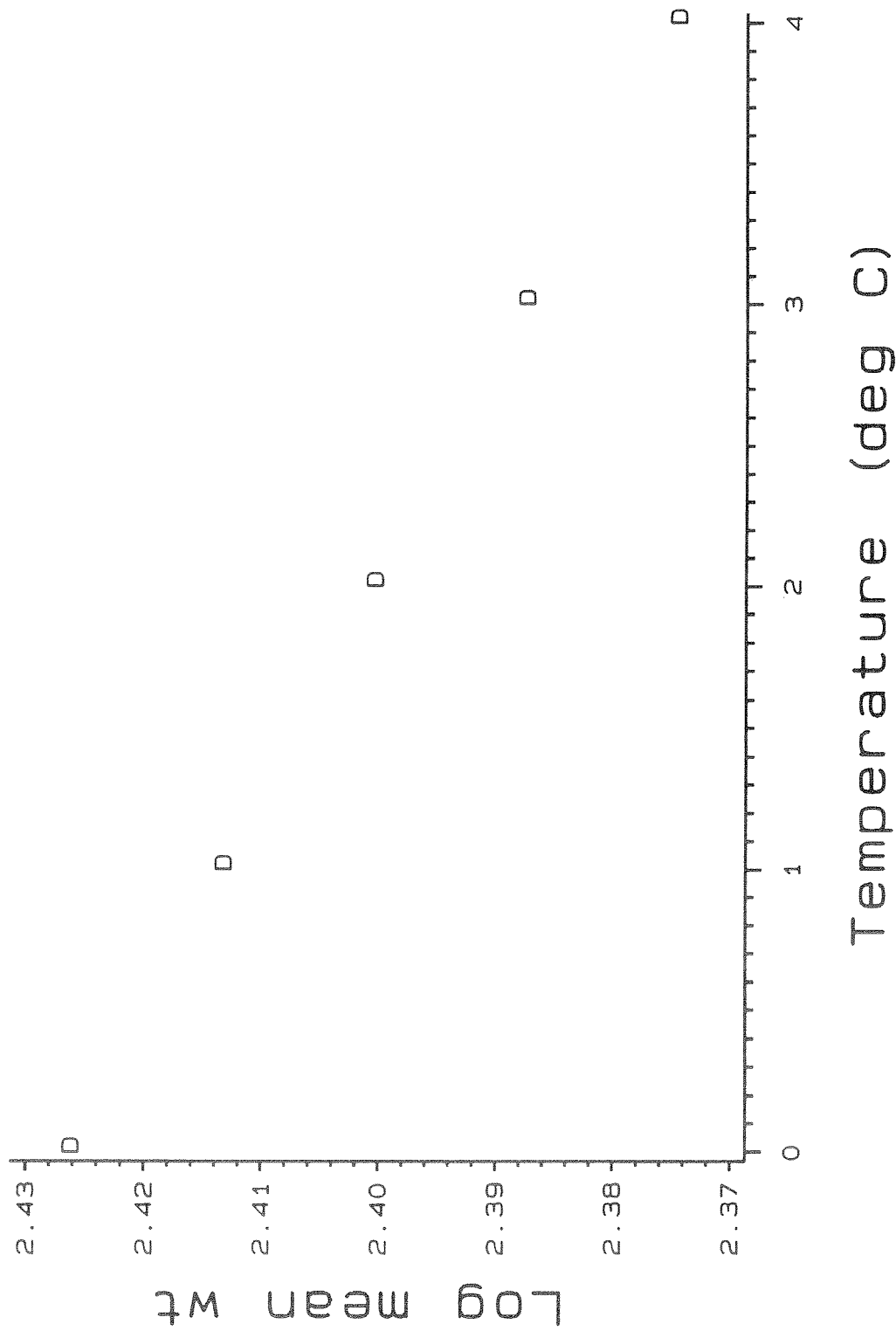


Figure 6.2.12. Temperature effect on log scaled mean total prey weight bulked within 10cm length classes (by stratum or haul). No data for the North Sea or Baltic Sea are included.

Temperature effect on logits of prop empty

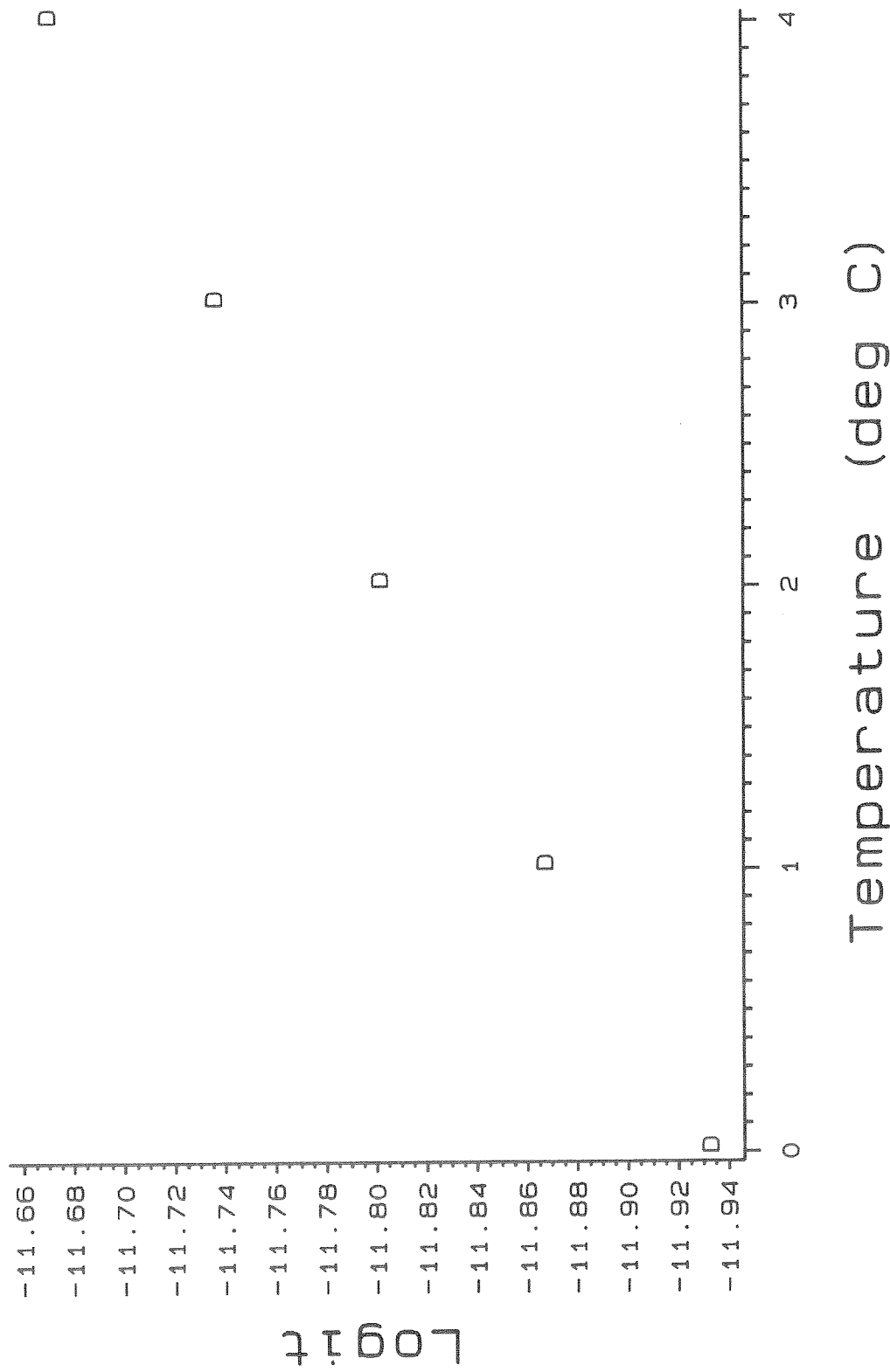


Figure 6.2.13. Temperature effect on logit of proportion empty stomachs in bulked samples per 10cm length classes (by stratum or haul).

Growth effect on scaled stomach weight

Temperature effect removed

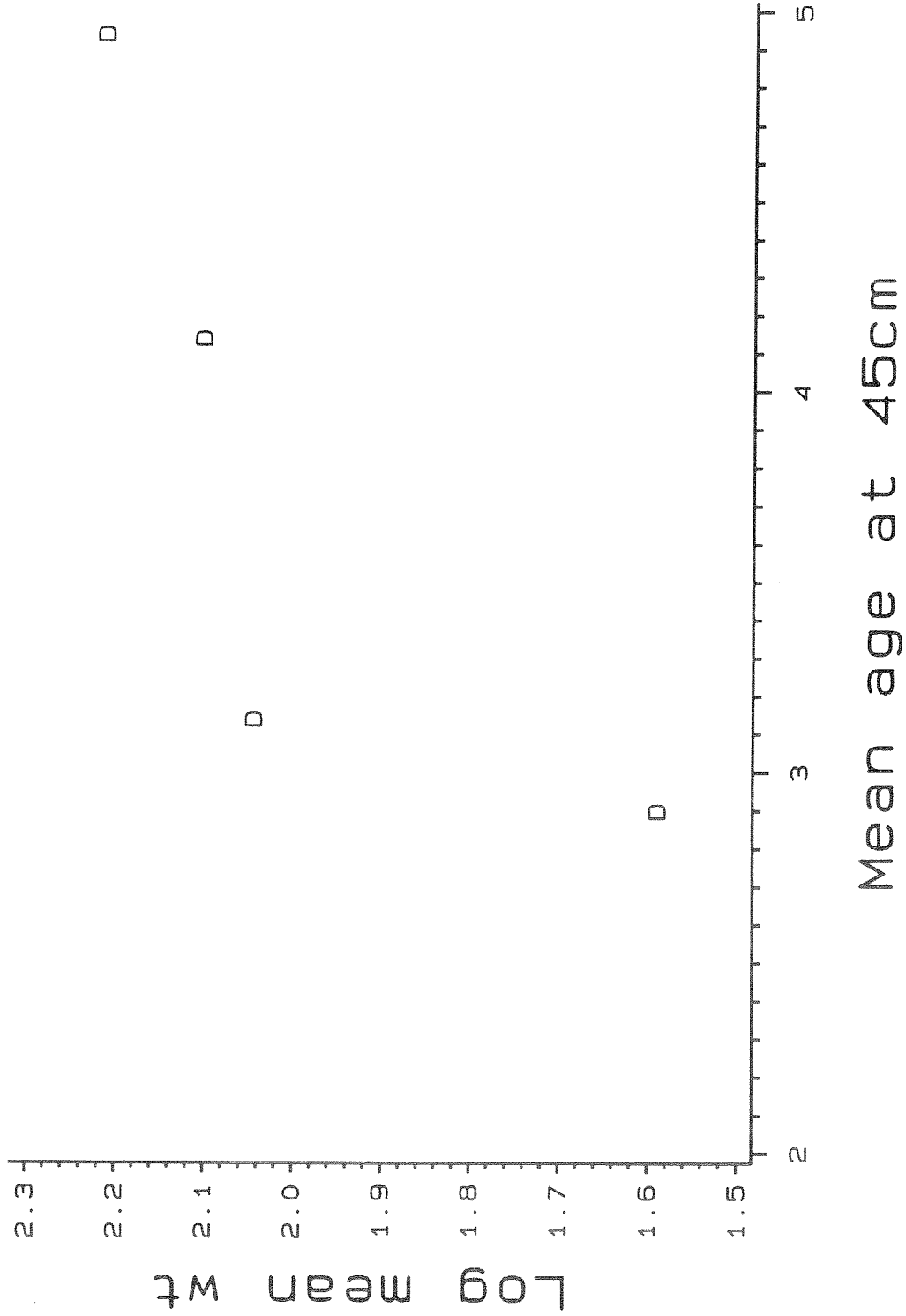


Figure 6.2.14. Growth effect after removing temperature effect on log scaled mean total prey weight bulked within 10cm length classes (by stratum or haul).

Ecosystem effect on scaled stomach weight

Length effect removed

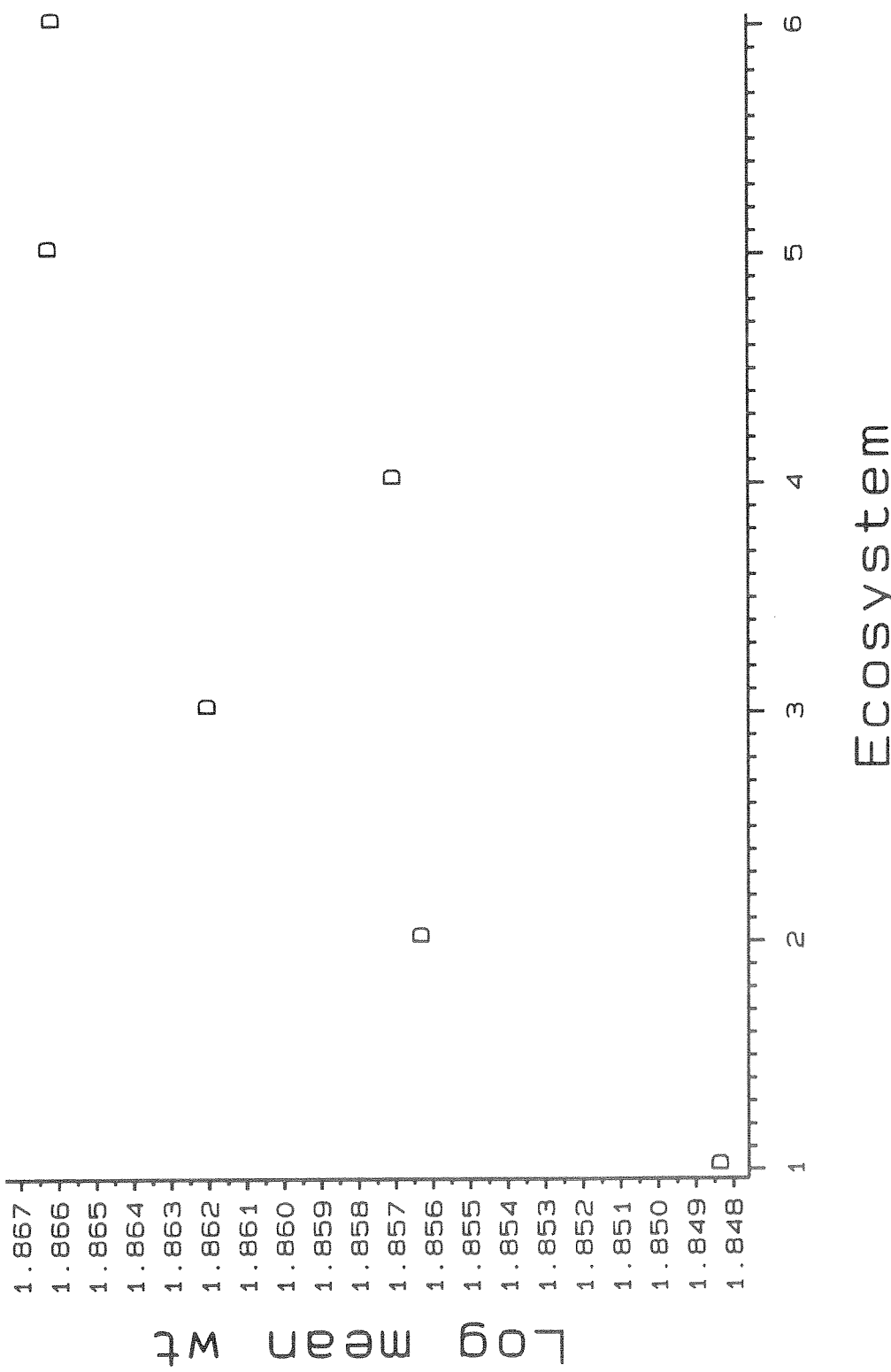


Figure 6.2.15. Ecosystem effect after removing length effect on log scaled mean total prey weight bulked within 10cm length classes (by stratum or haul).

TOTAL STOMACH CONTENT WEIGHT

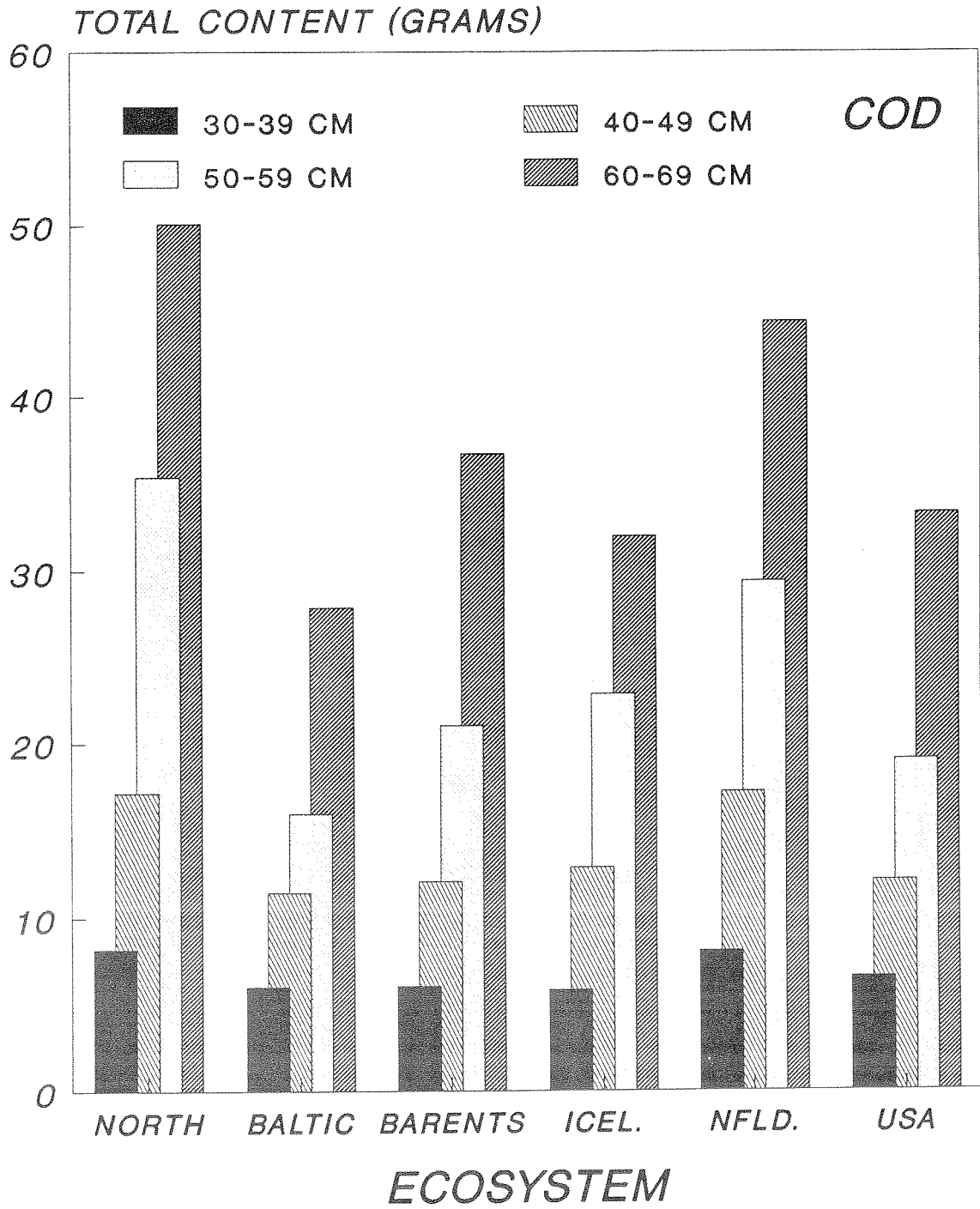


Figure 6.2.16. Mean total prey weight by 10cm cod length class and ecosystem.

COD 20-29 CM LENGTH

- | | | |
|---|--|--|
| <div style="display: flex; justify-content: space-around;"> <div style="width: 40%;"> FISH</div> <div style="width: 40%;"> MOLLUSK</div> </div> | <div style="display: flex; justify-content: space-around;"> <div style="width: 40%;"> CRUST</div> <div style="width: 40%;"> MOLLUSK</div> </div> | <div style="display: flex; justify-content: space-around;"> <div style="width: 40%;"> MOLLUSK</div> <div style="width: 40%;"> MOLLUSK</div> </div> |
| <div style="display: flex; justify-content: space-around;"> <div style="width: 40%;"> POLYCH</div> <div style="width: 40%;"> MOLLUSK</div> </div> | <div style="display: flex; justify-content: space-around;"> <div style="width: 40%;"> ECHINO</div> <div style="width: 40%;"> MOLLUSK</div> </div> | <div style="display: flex; justify-content: space-around;"> <div style="width: 40%;"> MOLLUSK</div> <div style="width: 40%;"> MOLLUSK</div> </div> |

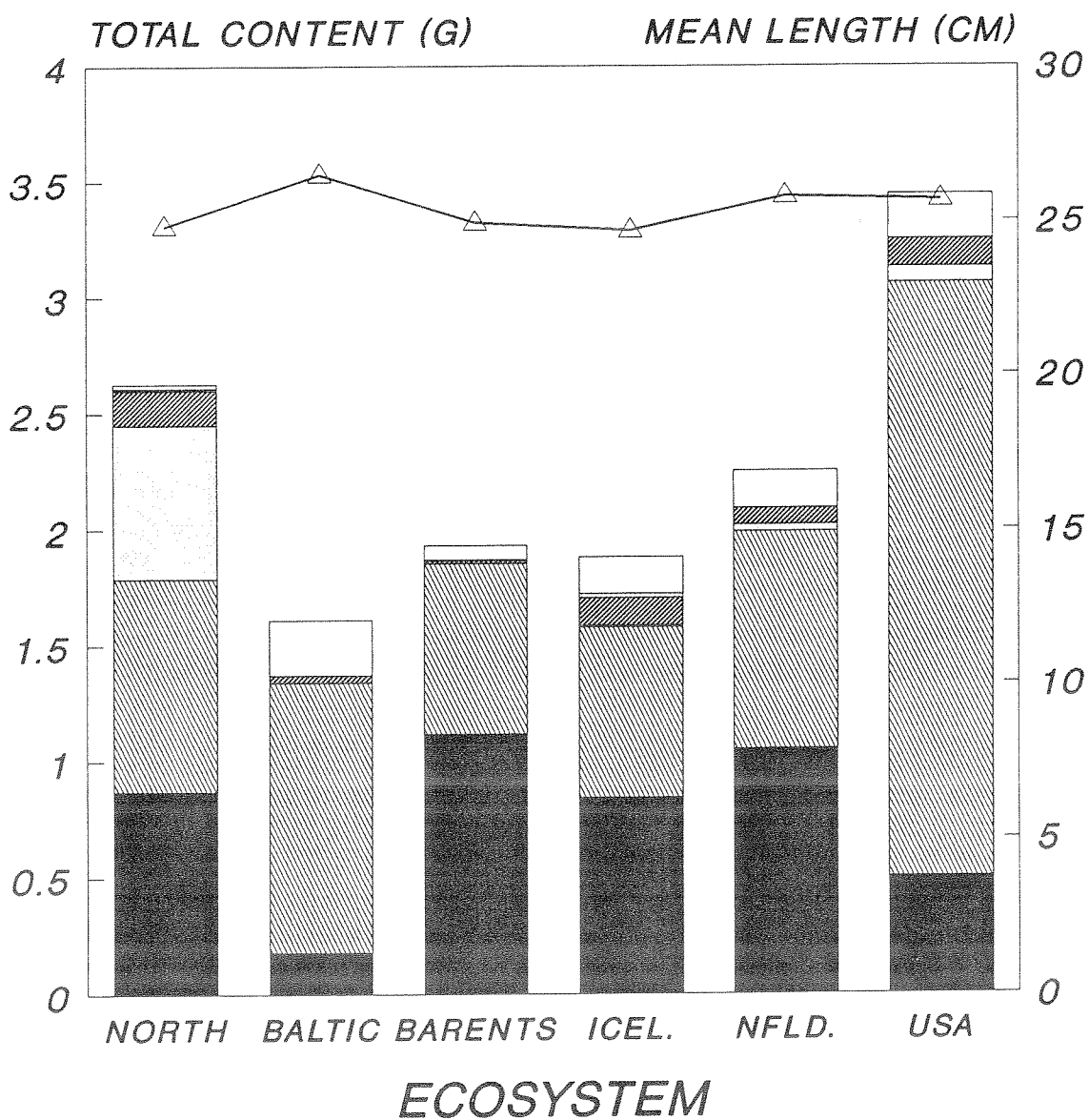


Figure 6.2.17. Mean prey weight by species category for cod in the 20-29cm length class by ecosystem.

COD 30-39 CM LENGTH

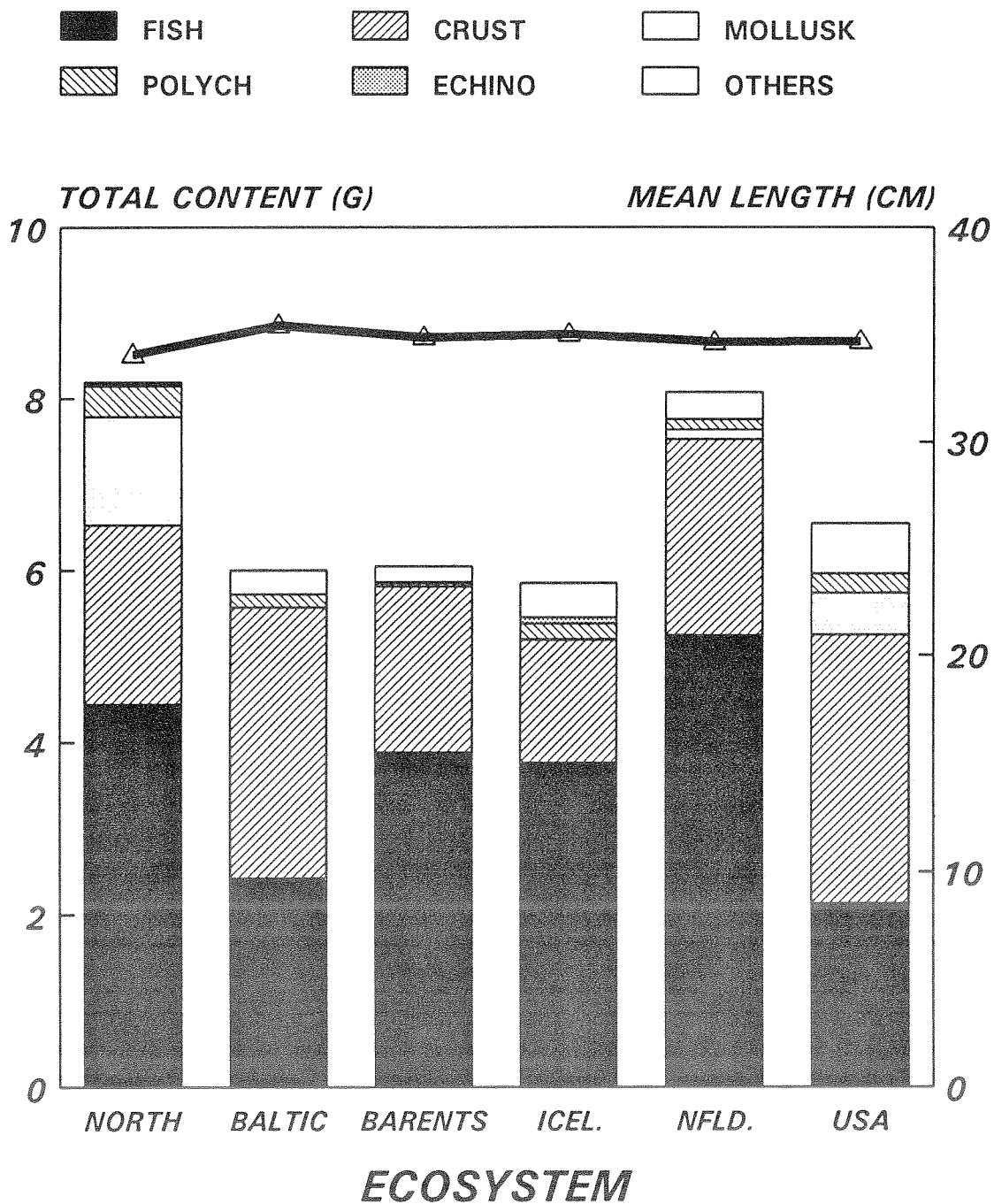


Figure 6.2.18. Mean prey weight by species category for cod in the 30-39cm length class by ecosystem.

COD 40-49 CM LENGTH

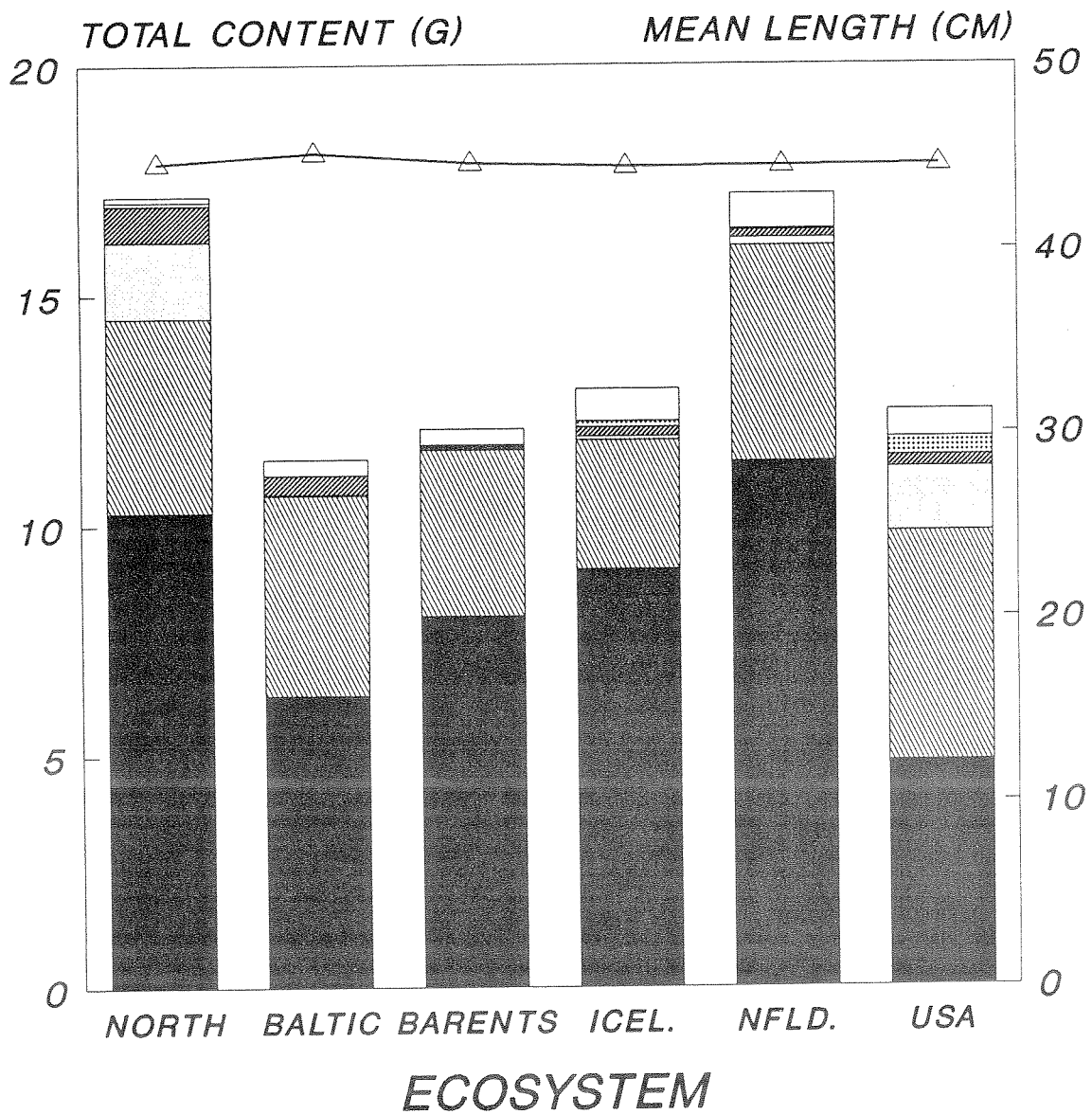
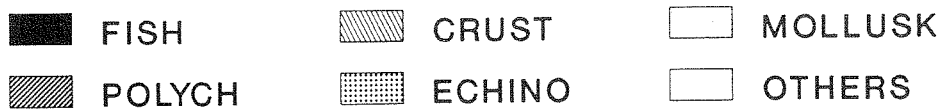


Figure 6.2.19. Mean prey weight by species category for cod in the 40-49cm length class by ecosystem.

COD 50-59 CM LENGTH

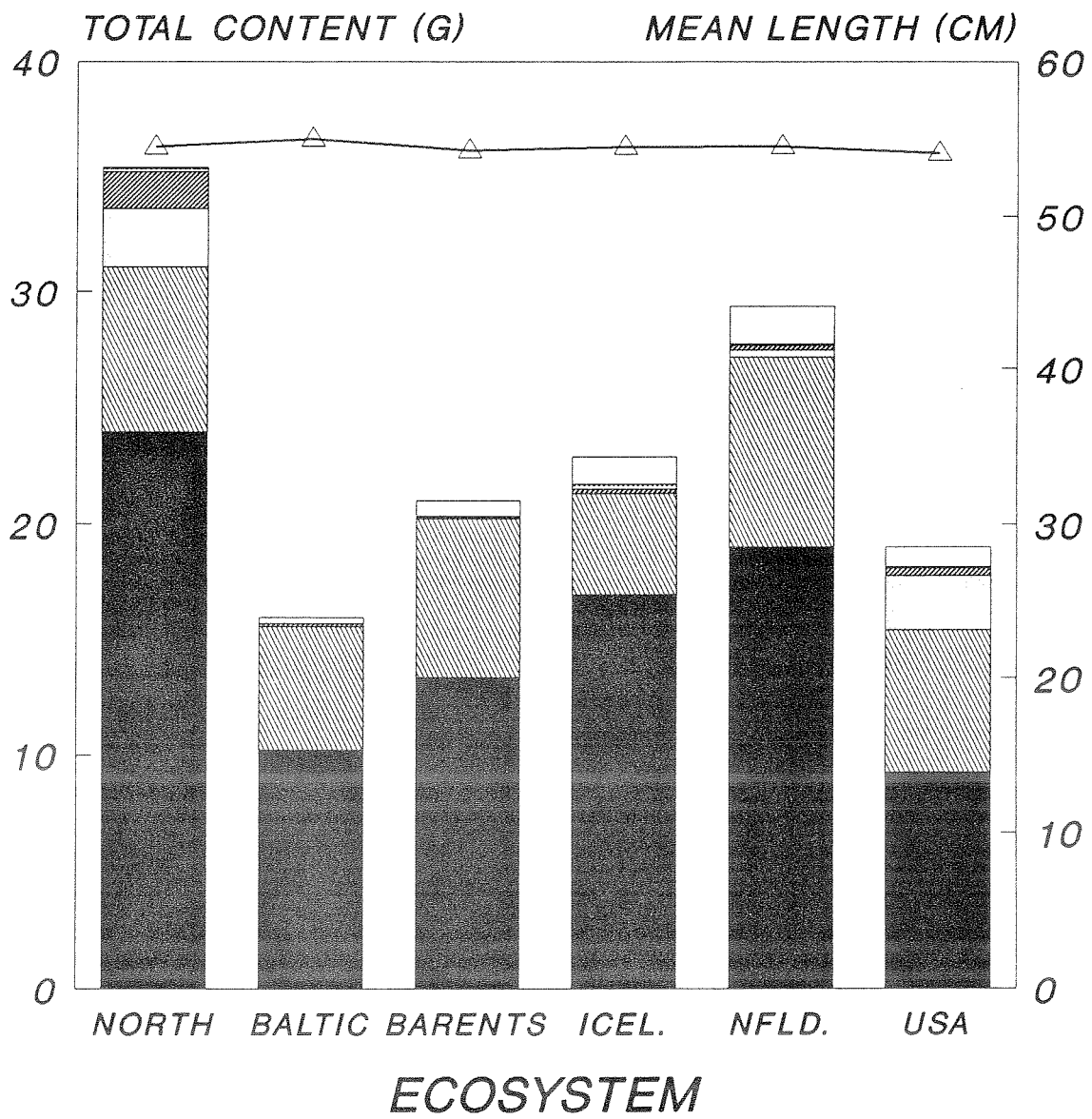
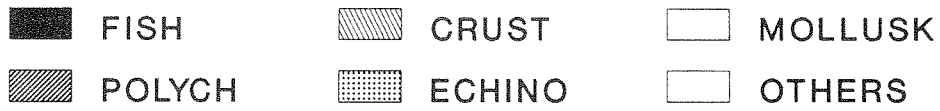


Figure 6.2.20. Mean prey weight by species category for cod in the 50-59cm length class by ecosystem.

COD 60-69 CM LENGTH

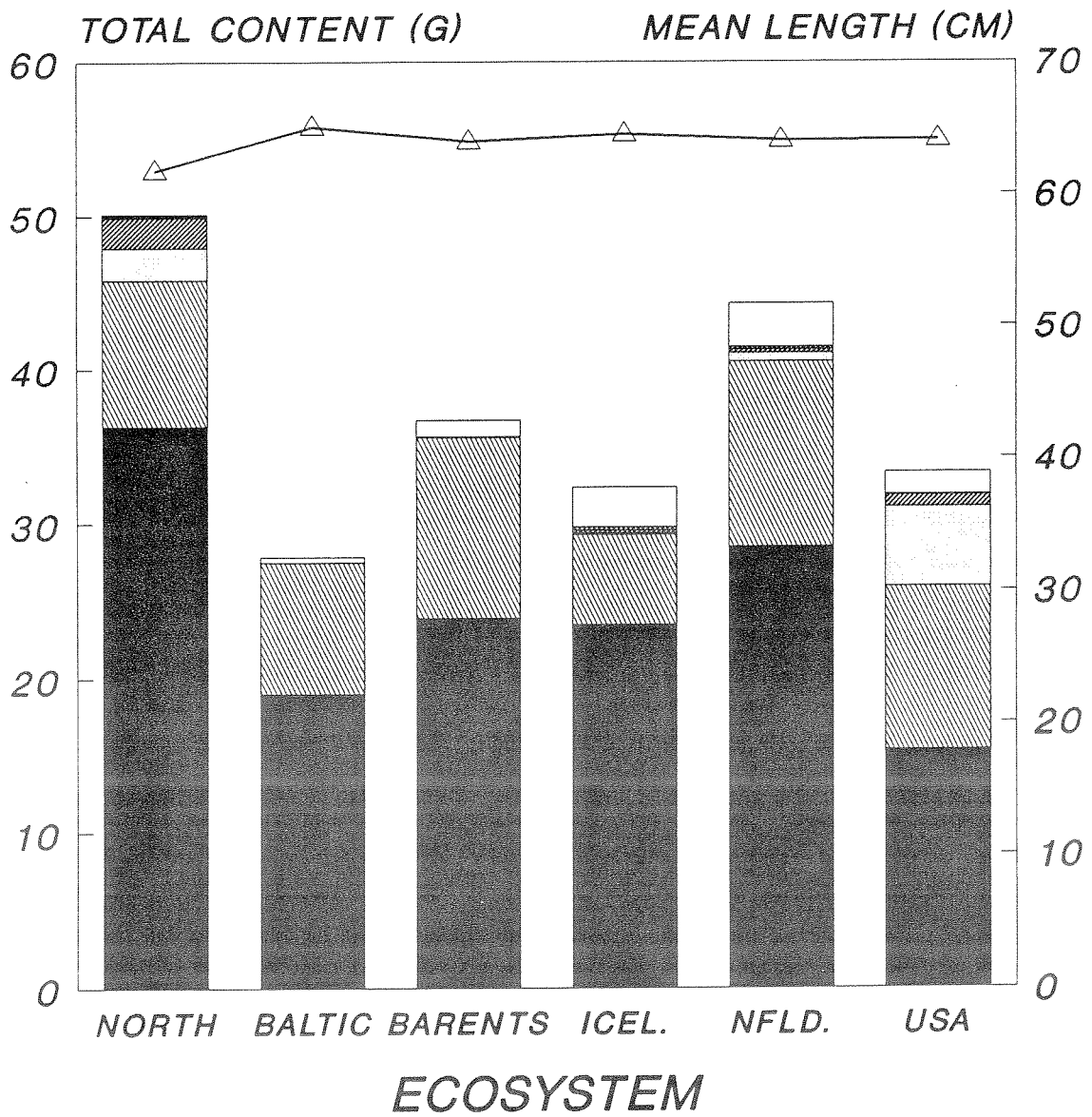
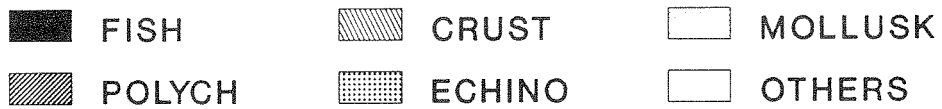


Figure 6.2.22. Mean prey weight by species category for cod in the 60-69cm length class by ecosystem.

COD \geq 70 CM LENGTH

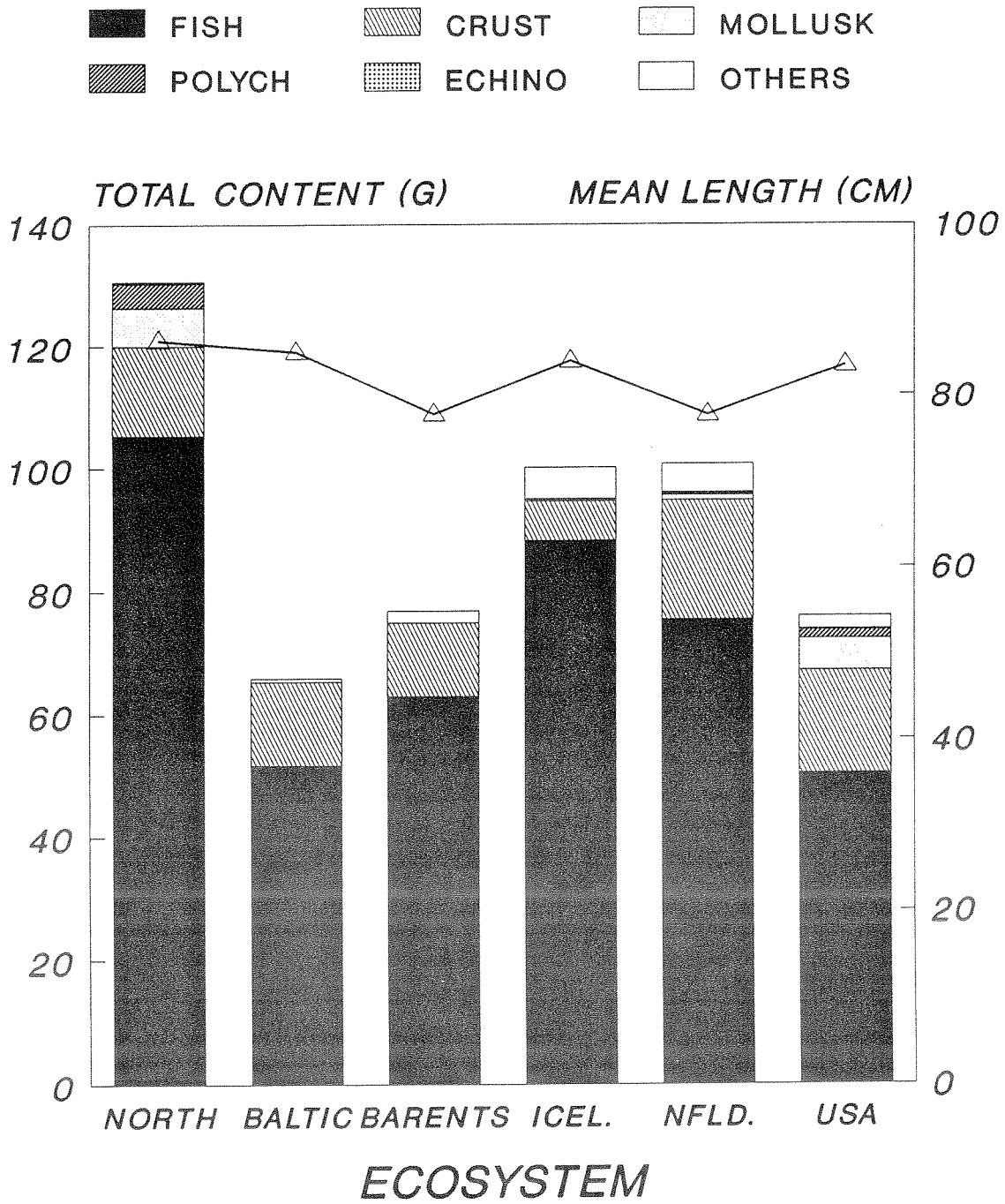


Figure 6.2.22. Mean prey weight by species category for cod in the \geq 70cm length class by ecosystem.

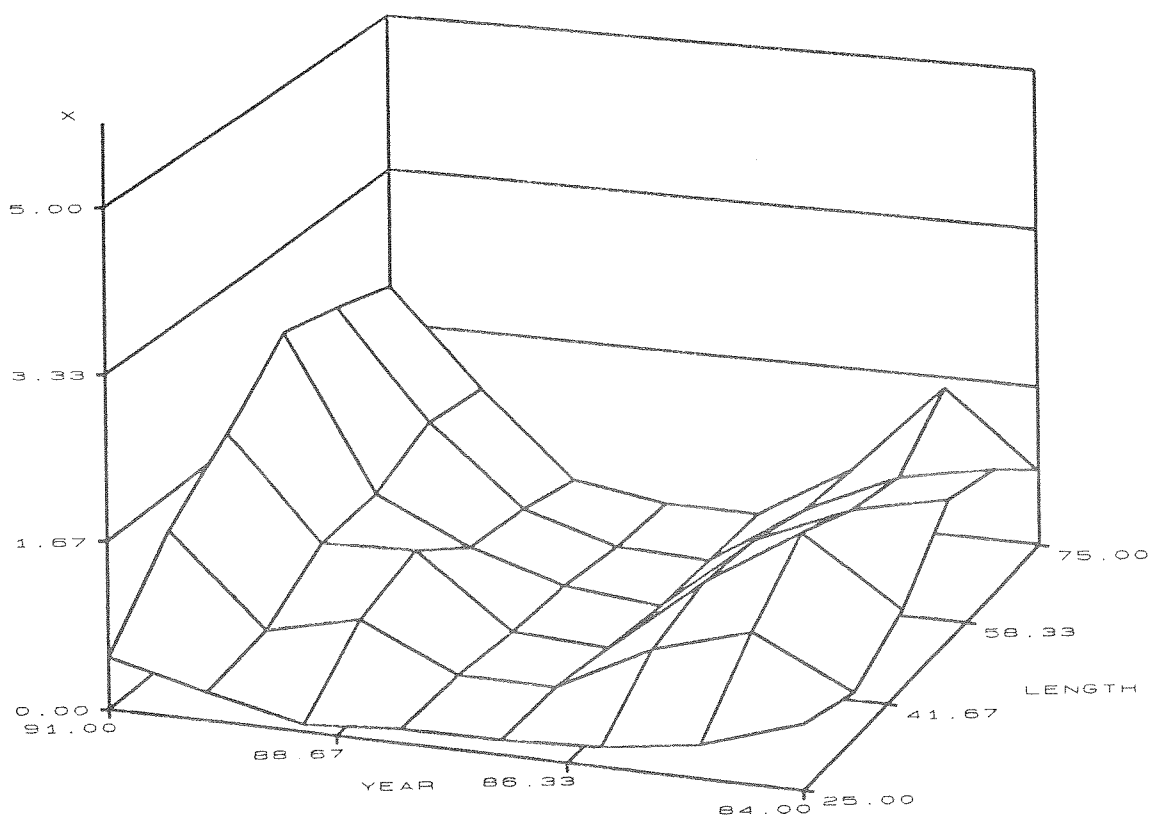
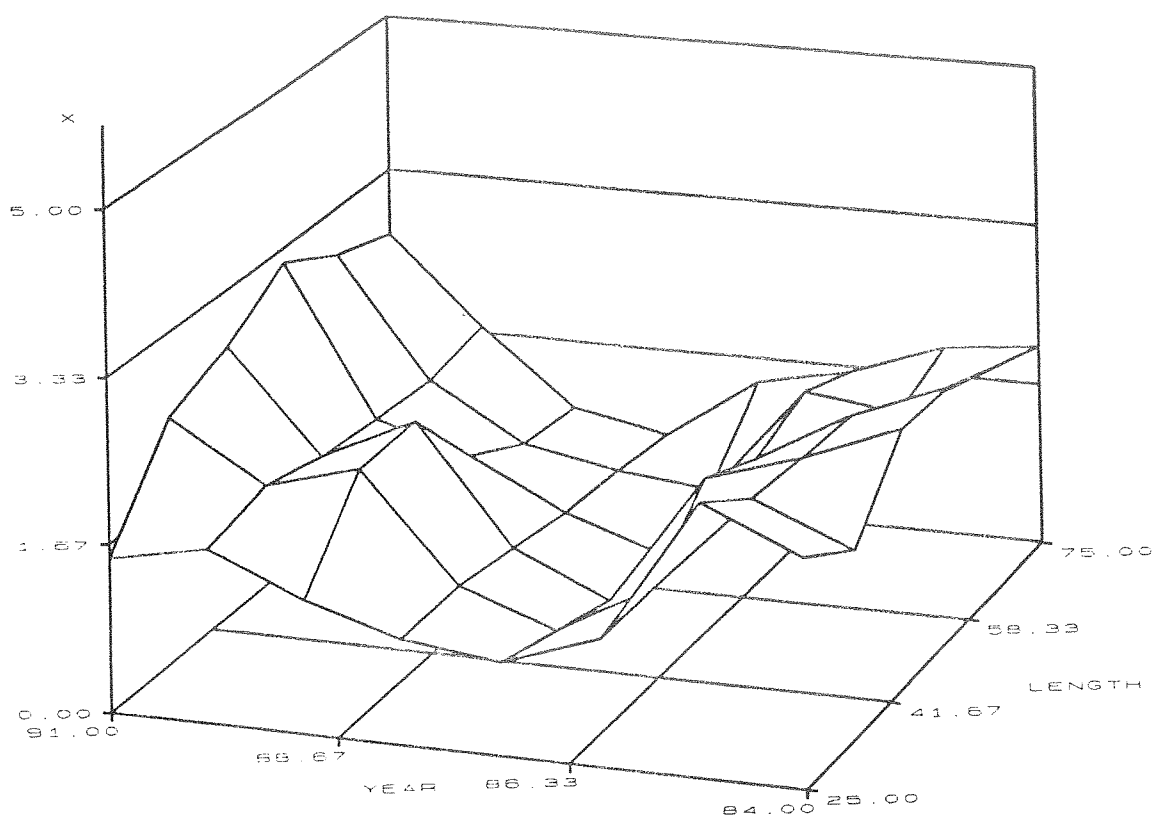


Figure 7.1.1a-b. Scaled and logged total stomach content (a) and content of capelin (b) vs. year and predator length for cod sampled in the Barents Sea in 1984-1991.

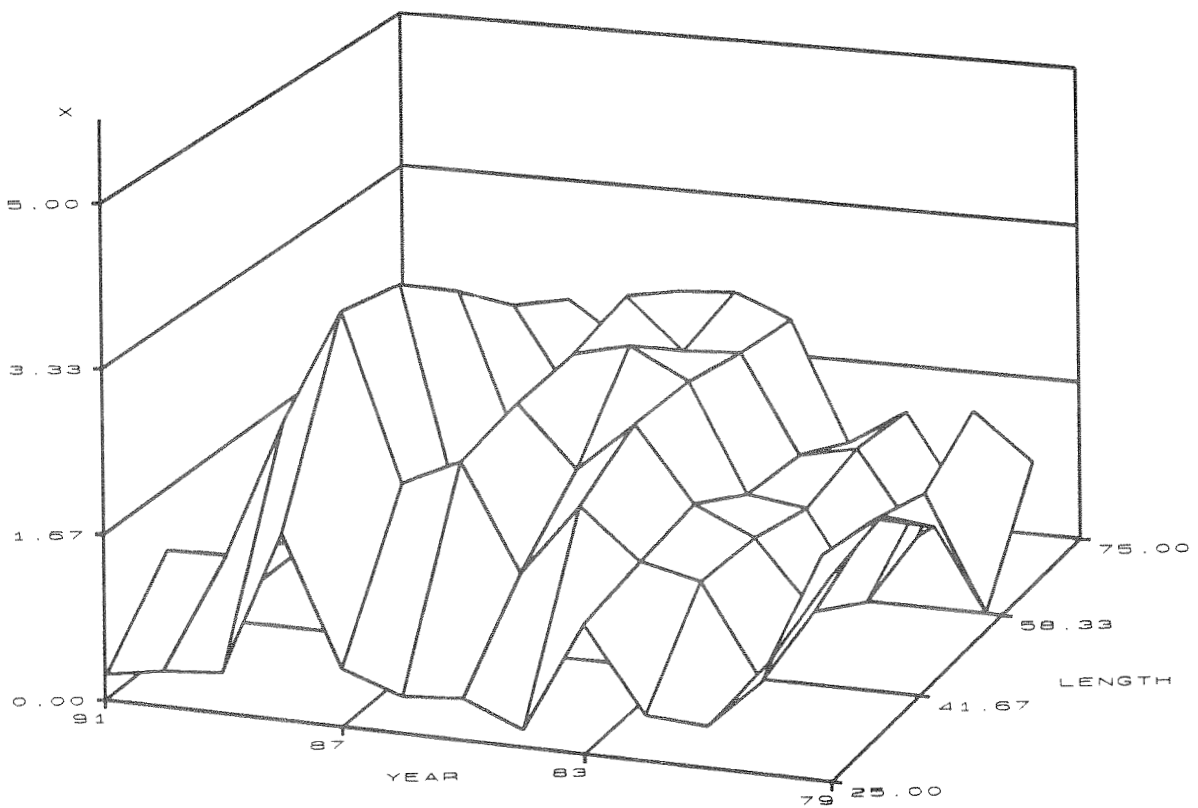
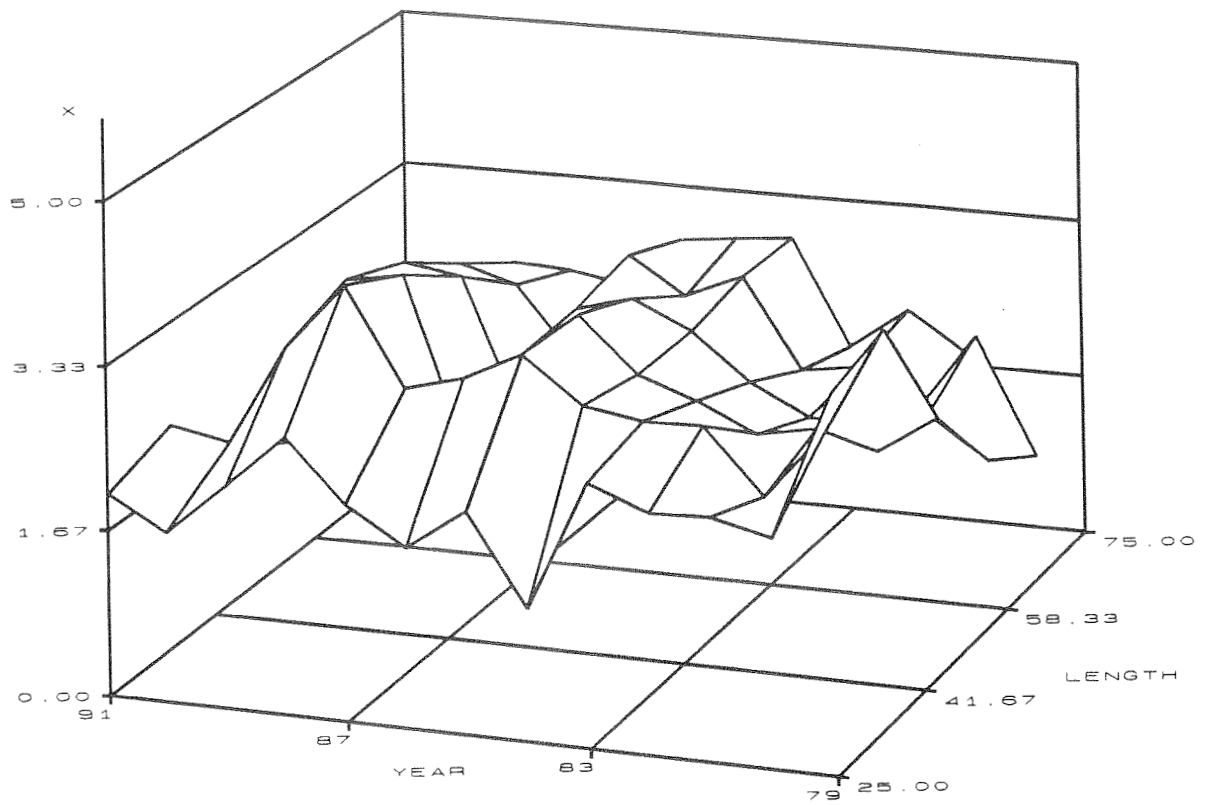


Figure 7.1.2a-b. Scaled and logged total stomach content (a) and content of capelin (b) vs. year and predator length for cod sampled in Icelandic waters in 1979-1991.

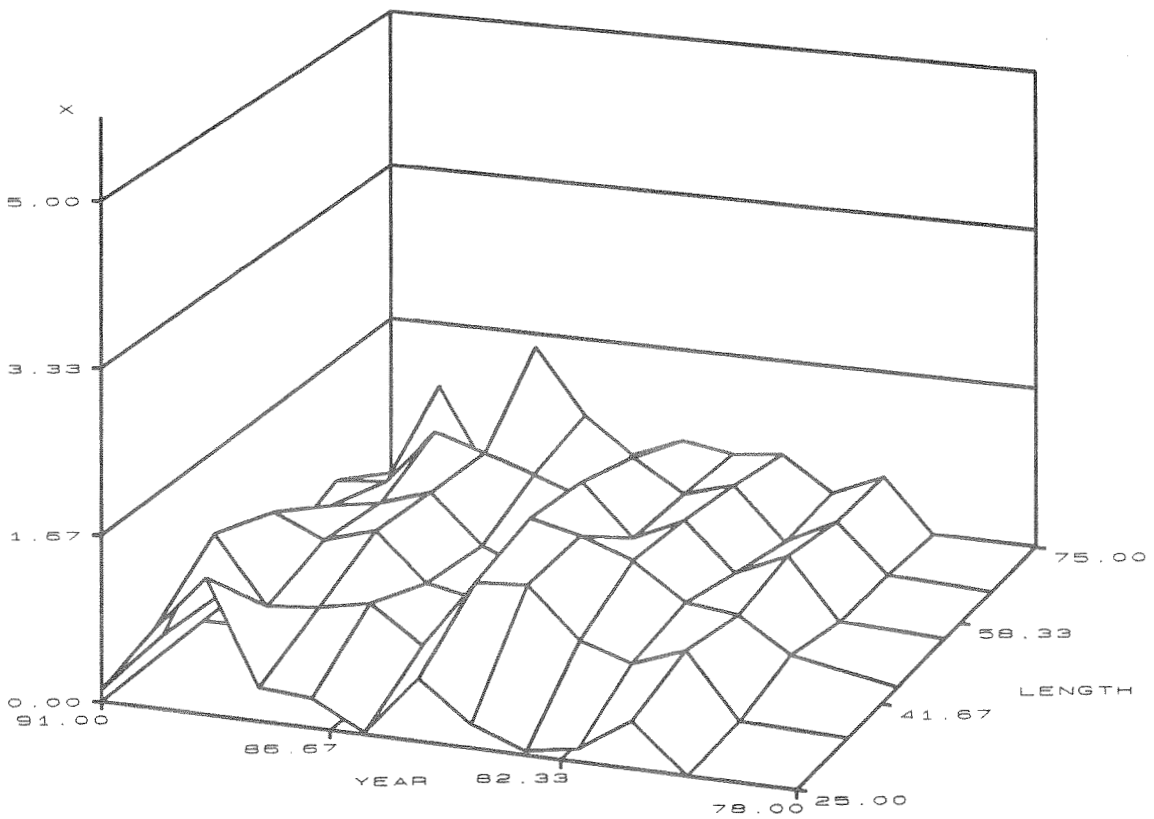
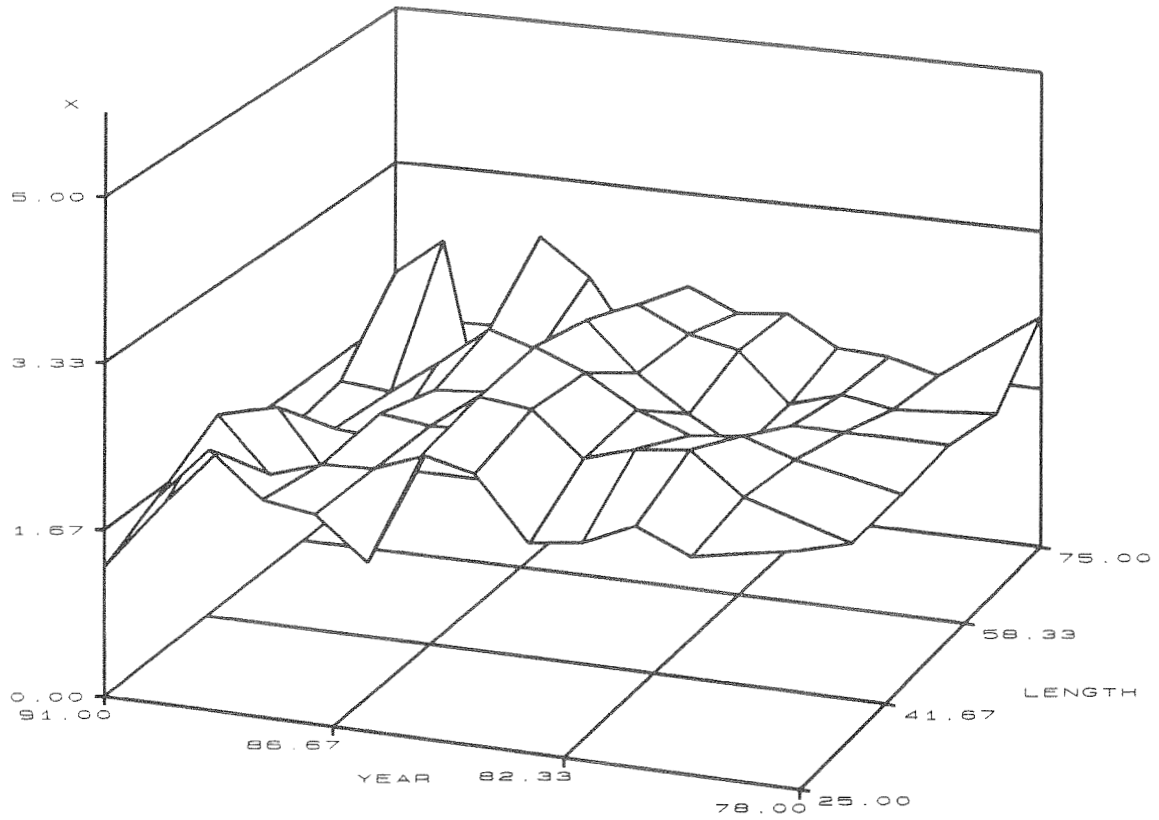


Figure 7.1.3a-b. Scaled and logged total stomach content (a) and content of capelin (b) vs. year and predator length for cod sampled off Newfoundland in 1979-1991.

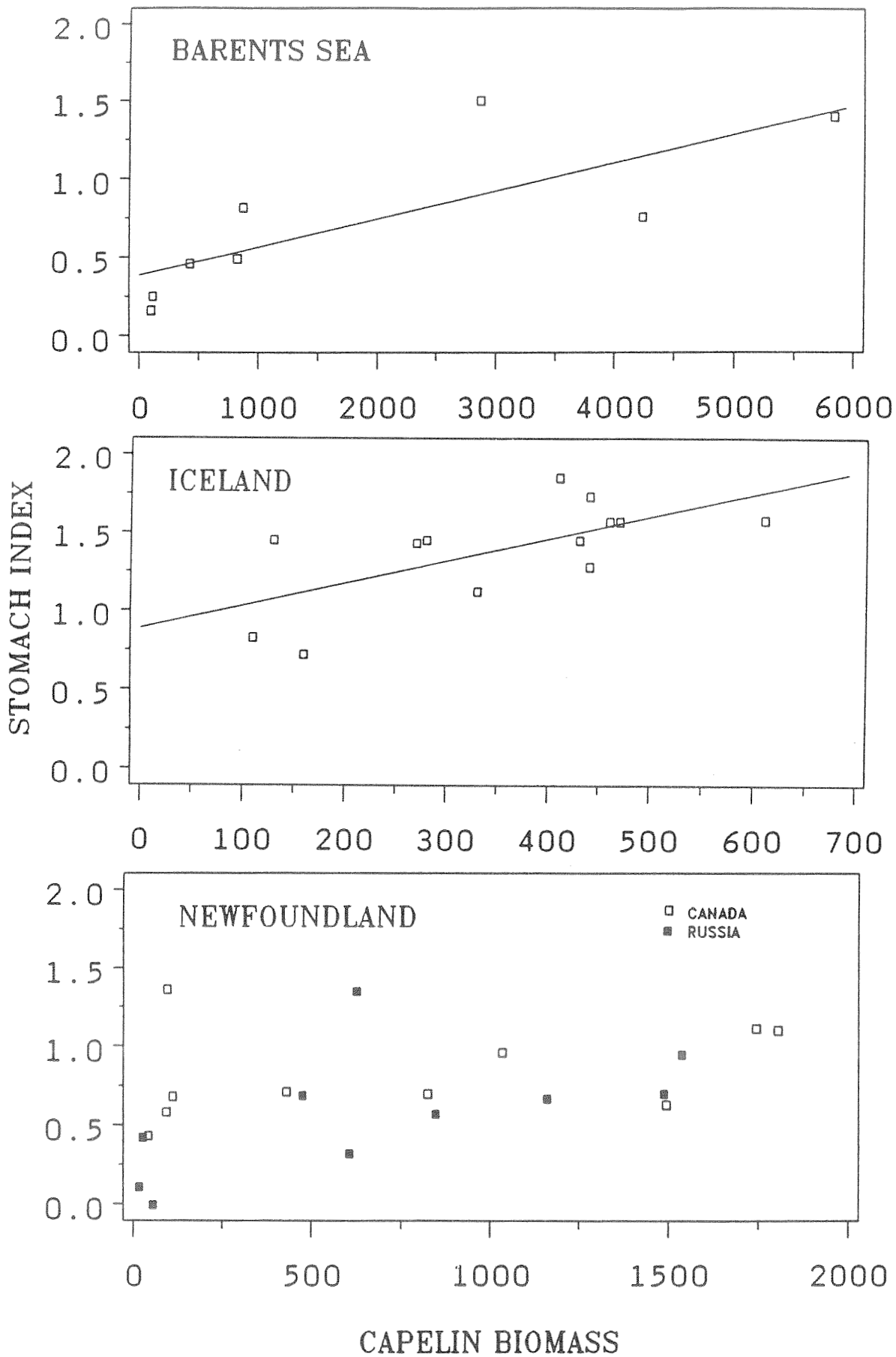


Figure 7.2. Capelin biomass vs. indices of capelin in cod stomachs (stomach fullness indices) for the Barents Sea, Iceland and Newfoundland.

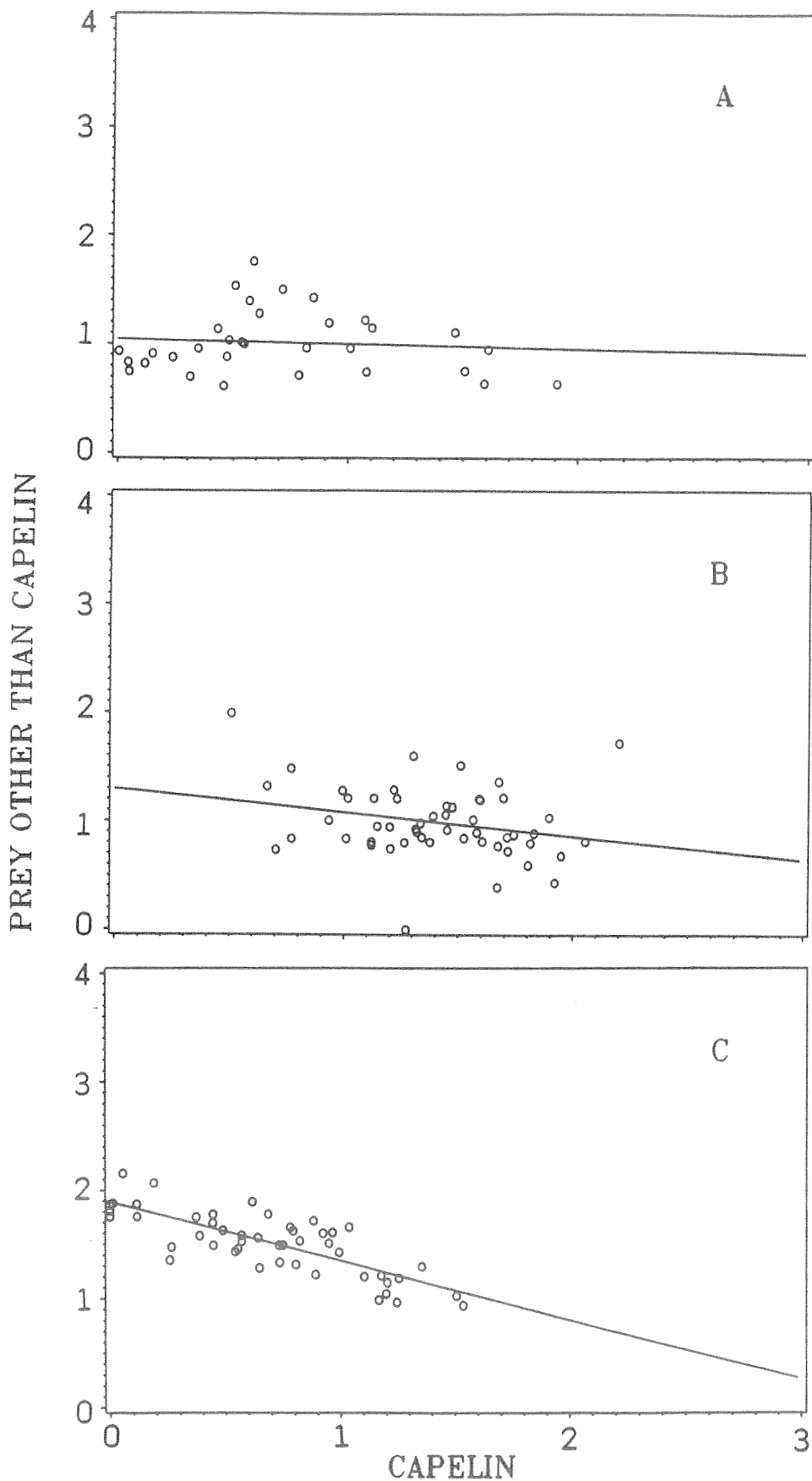


Figure 7.3. Mean scaled and logged weight of prey other than capelin vs. capelin alone, for cod in (A) the Barents Sea, (B) at Iceland, and (C) off Newfoundland. A mean was calculated for each year and 10-cm length group, for length groups from 30-69 cm. Capelin includes prorated portion of the unidentified fish.

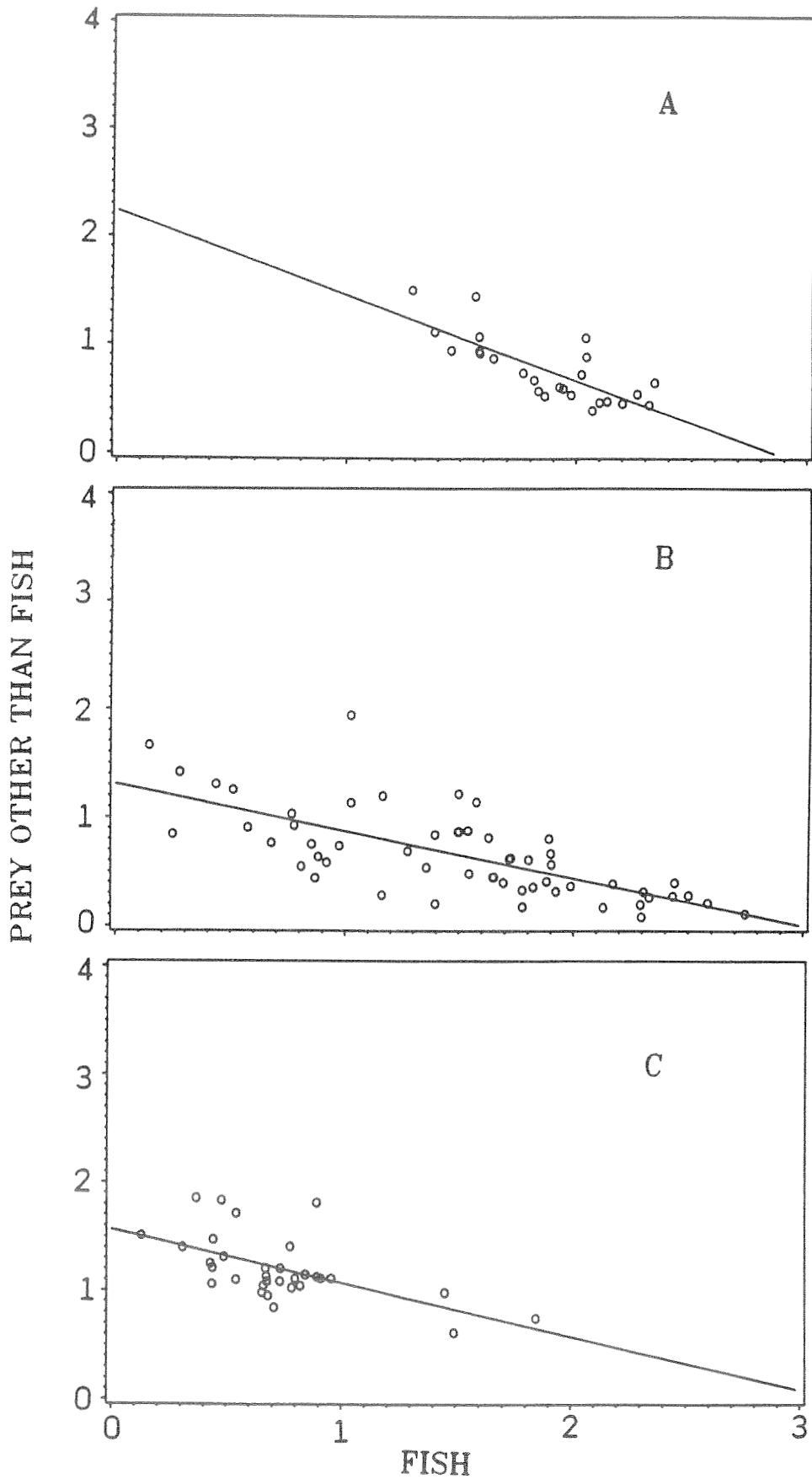


Figure 7.4. Mean scaled and logged weight of prey other than fish vs. fish alone, for cod in (A) the North Sea, (B) the Baltic Sea, and (C) off the Northeast USA. A mean was calculated for each year and 10-cm length group, for length groups from 30-69 cm. unidentified fish.

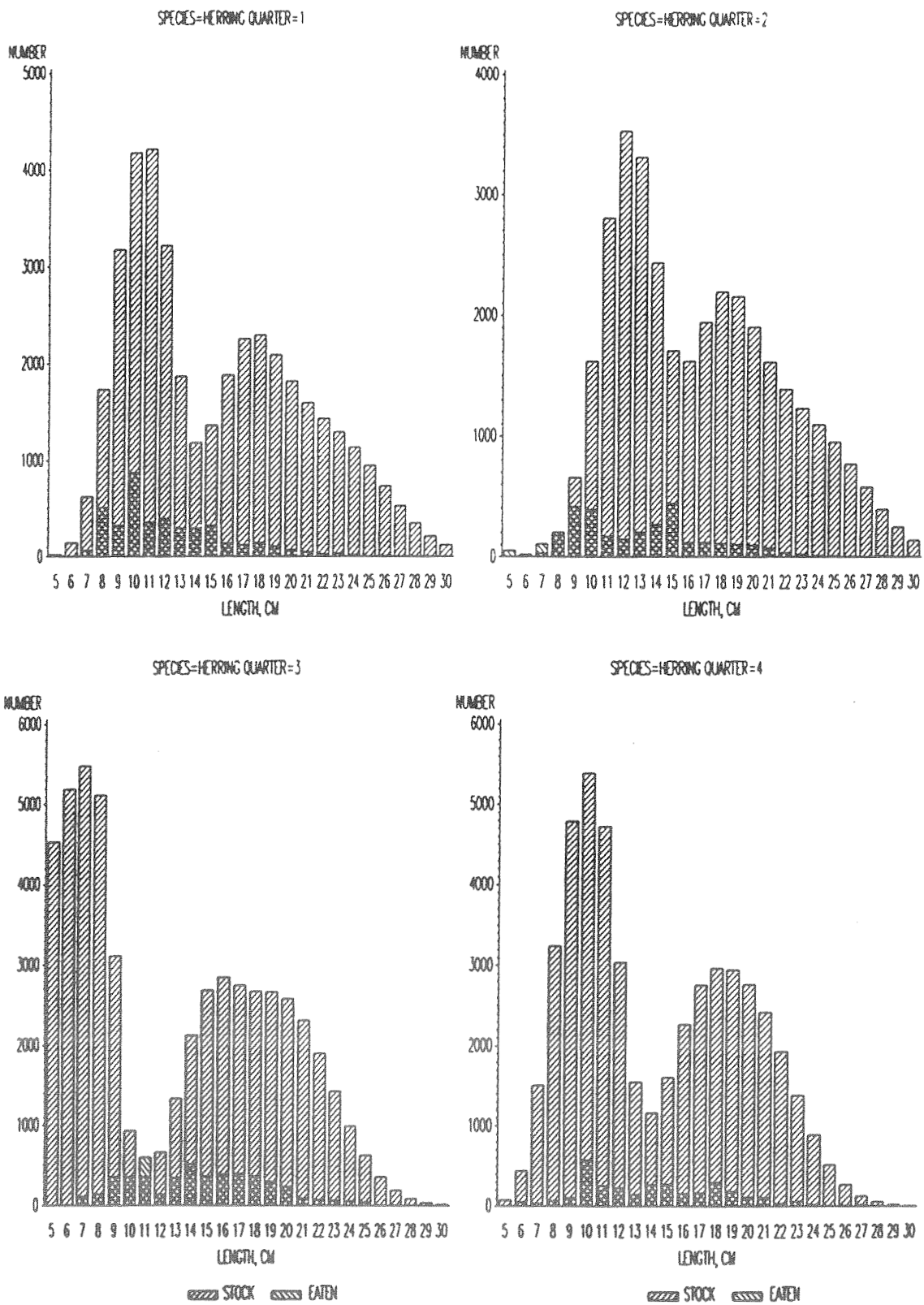


Figure 8.4.1. Baltic Sea herring in Sub-divisions 25, 26 and 28. Length distributions of the stock and those eaten by cod, by quarter. Data are a mean over 1977-1989.

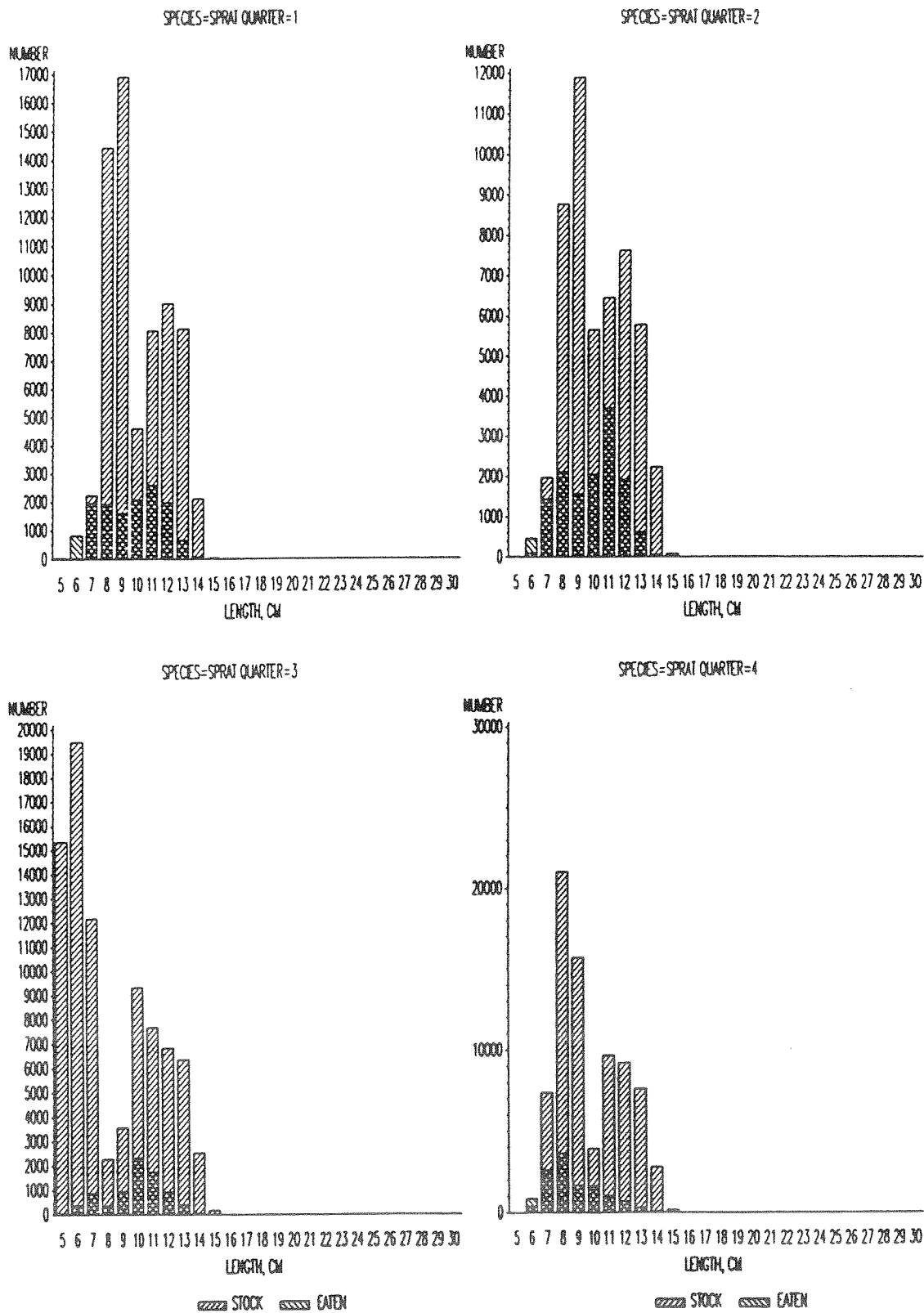


Figure 8.4.2. Baltic Sea sprat in Sub-divisions 25, 26 and 28. Length distributions of the stock and of those eaten by cod, by quarter. Data are a mean taken over 1977-1989.

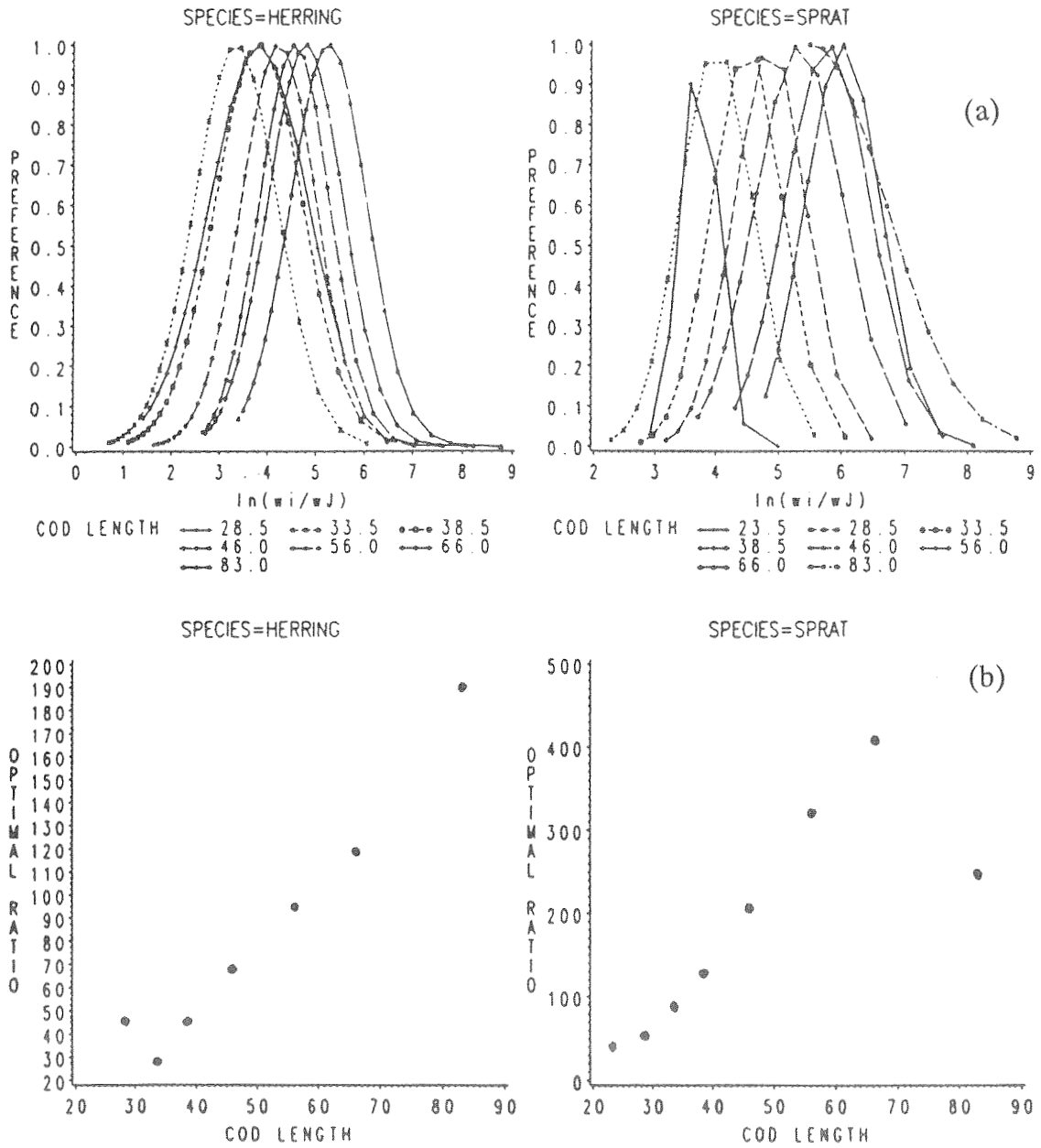


Figure 8.5. Prey size preference of Baltic Sea cod: (a) normal distributions of partial M2 for each cod length group for prey species = herring and sprat.(b) optimal size ratio plotted against cod size.

NORTH SEA 1981

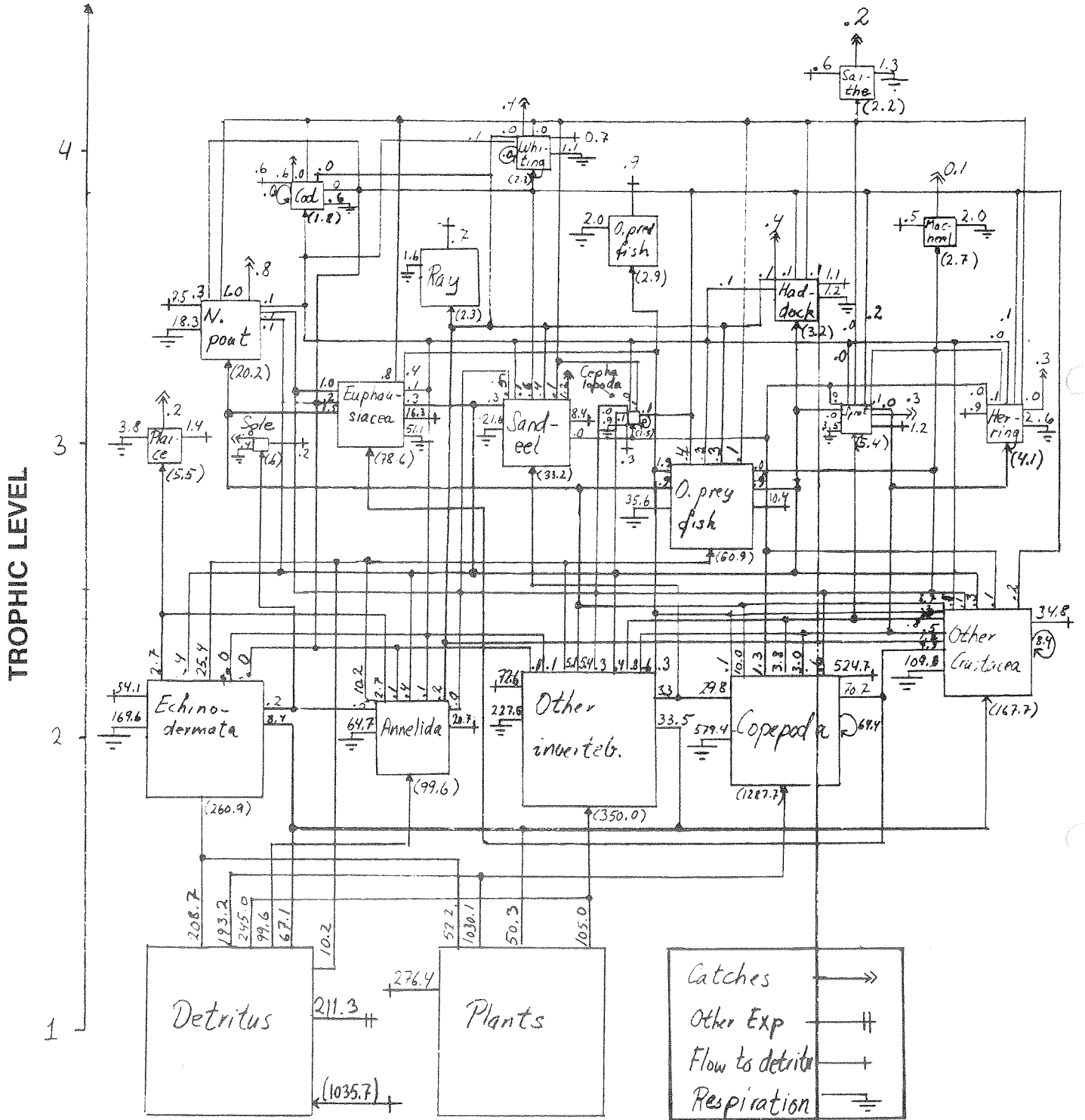


Figure 8.7.1. A quantified network of trophic interactions in the North Sea in 1981. The surface areas of the boxes are proportional to the biomasses of the groups. The boxes are arranged on the y-axis after trophic levels as estimated by ECOPATH II. All groups are balanced so that input equals output. Flows exiting a group do so from the upper half, while flows enter the lower half of the groups. Flows exiting a box cannot branch, but can unite with flows exiting other groups. Flows are expressed in $t\ wet\ weight\ km^{-2}\ year^{-1}$.

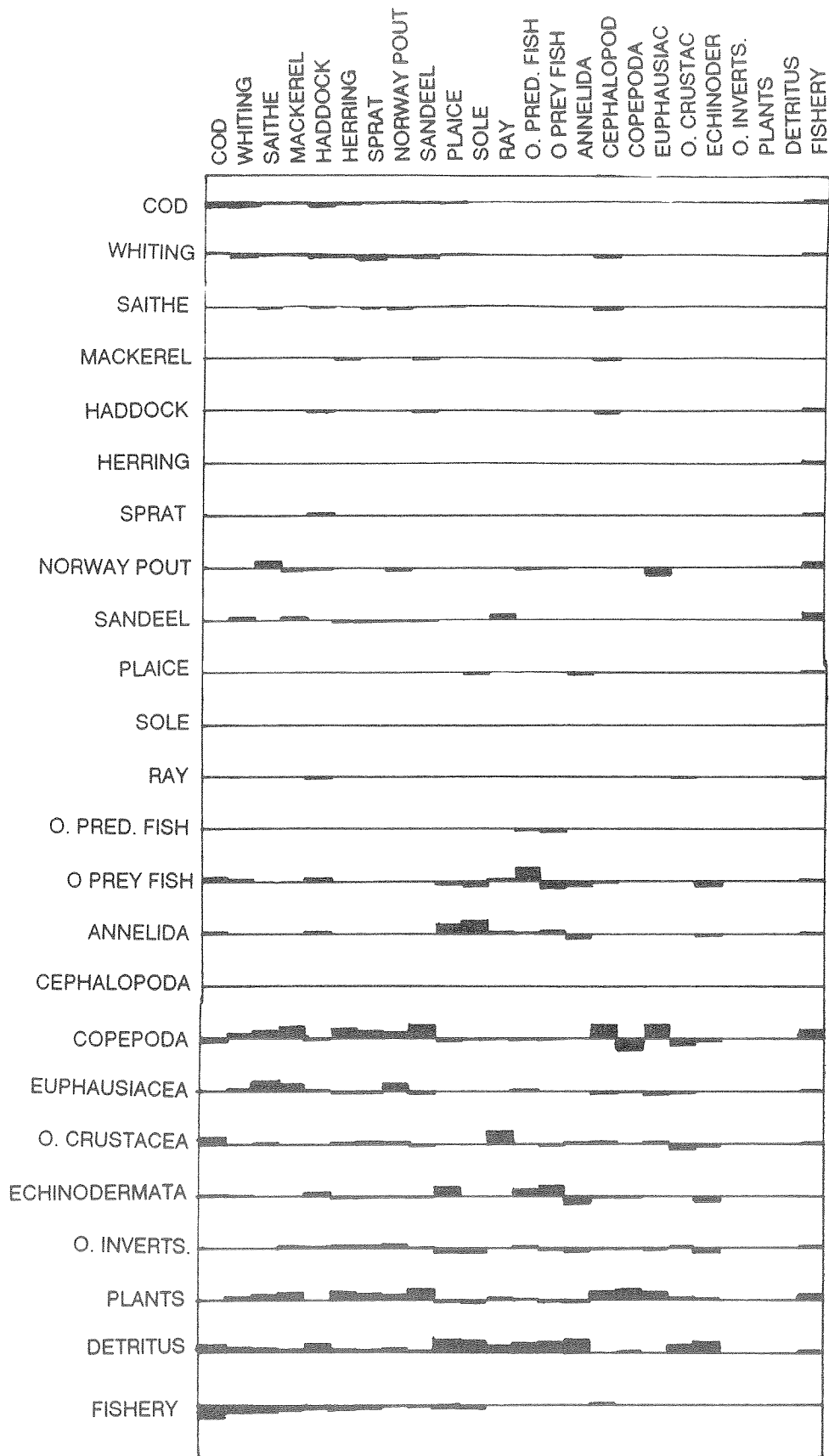


Figure 8.7.2. Mixed trophic impacts in the 1981 North Sea ecosystem. The bars quantify the direct and indirect trophic impacts that the groups on the left of the histograms have on the groups mentioned at the top. The impacts are relative but comparable between groups. Positive impacts protrude above the baseline while negative are below.

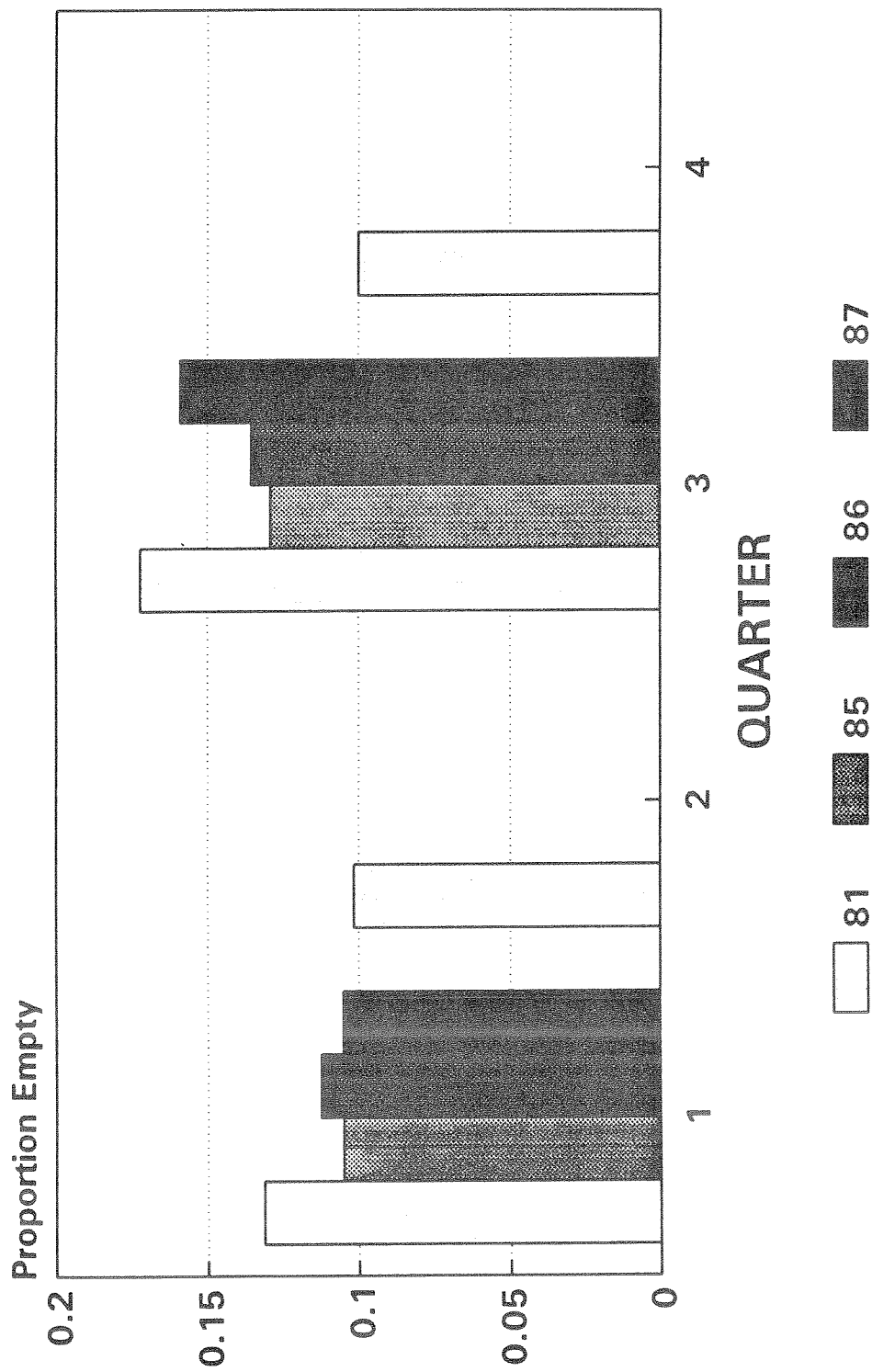


Figure 9.1.1. Weighted mean proportion of empty stomachs of North Sea cod, by quarter, in 1981, 1985, 1986 and 1987. Data are for the entire North Sea sampling area.

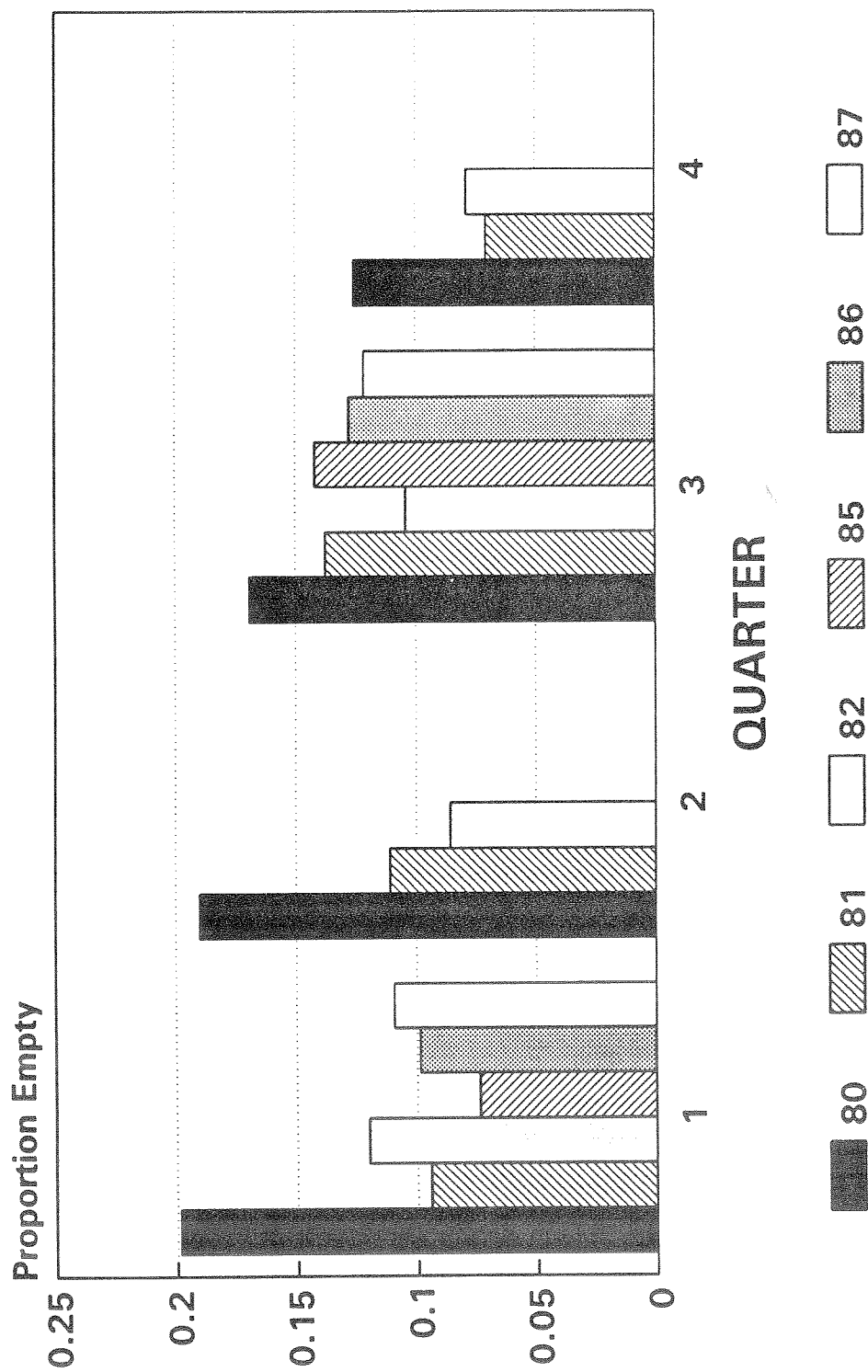


Figure 9.1.2. Weighted mean proportion of empty stomachs of North Sea cod, by quarter, in 1981, 1982, 1985, 1986 and 1987. Data are for the North Sea region south of 55.5° n. latitude.

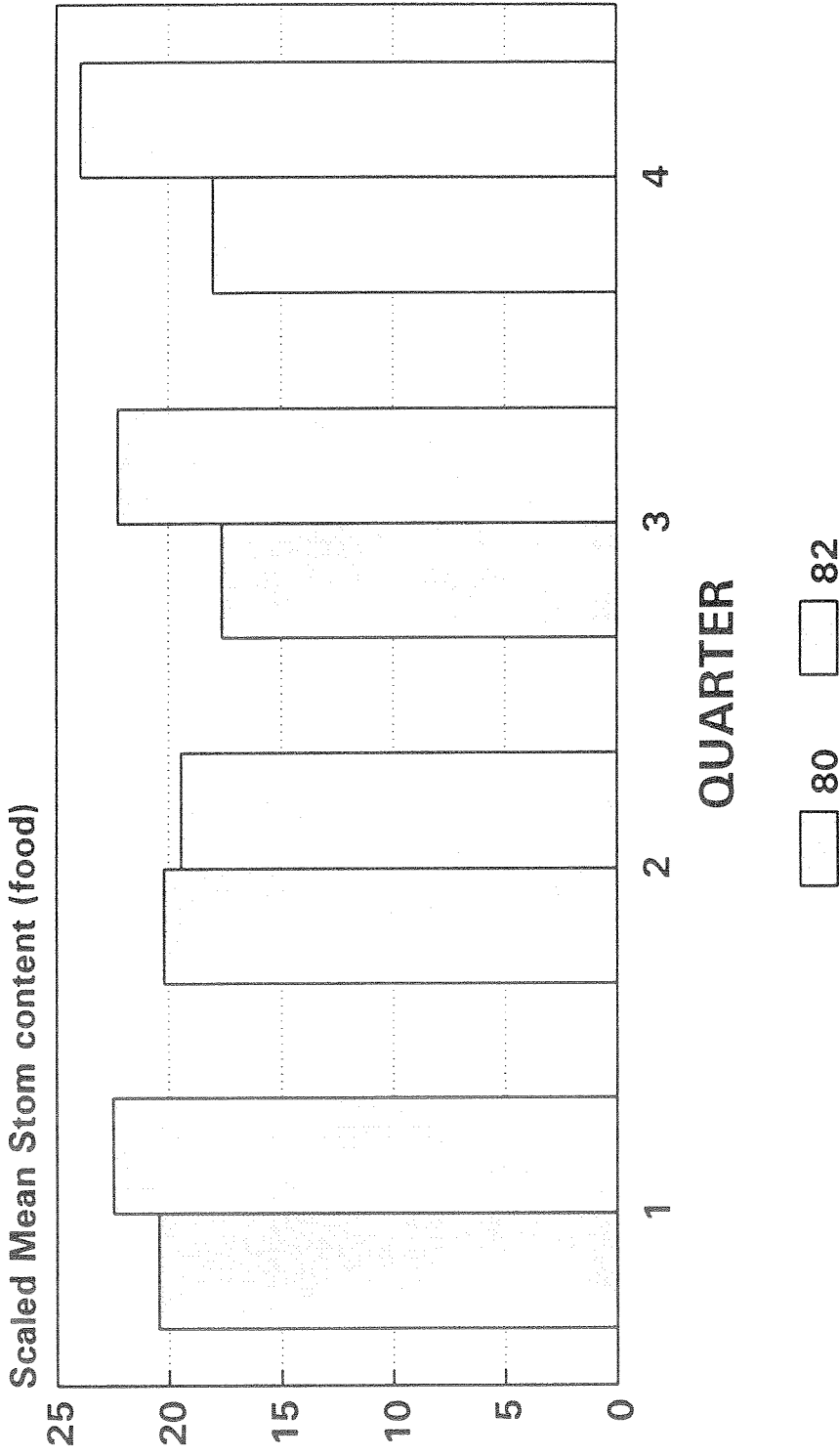


Figure 9.1.3. Scaled mean stomach content weight of North Sea cod, by quarter, in 1980 and 1982.

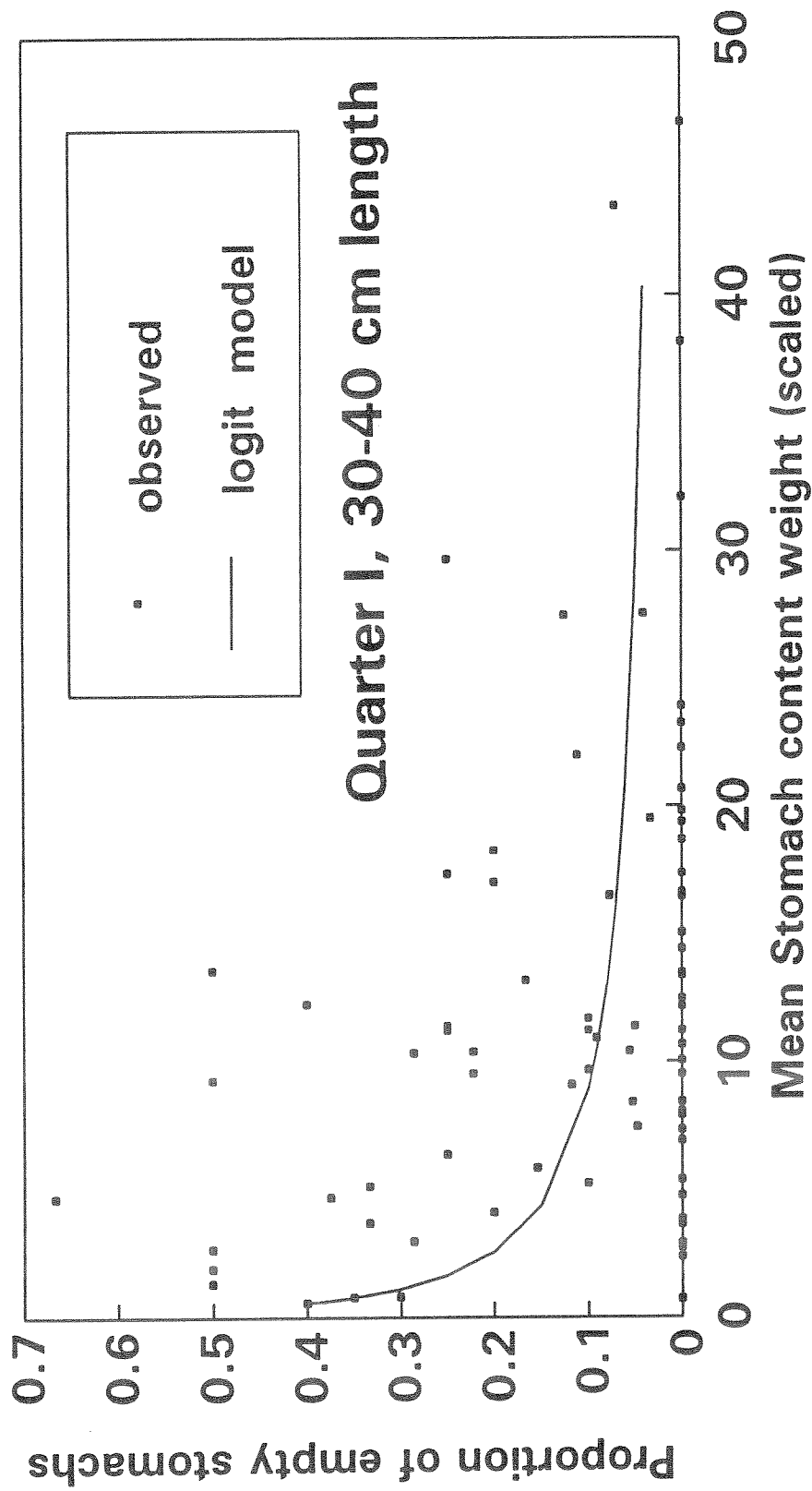


Figure 9.1.5. Proportion of empty North Sea cod stomachs as a function of mean scaled stomach content weight

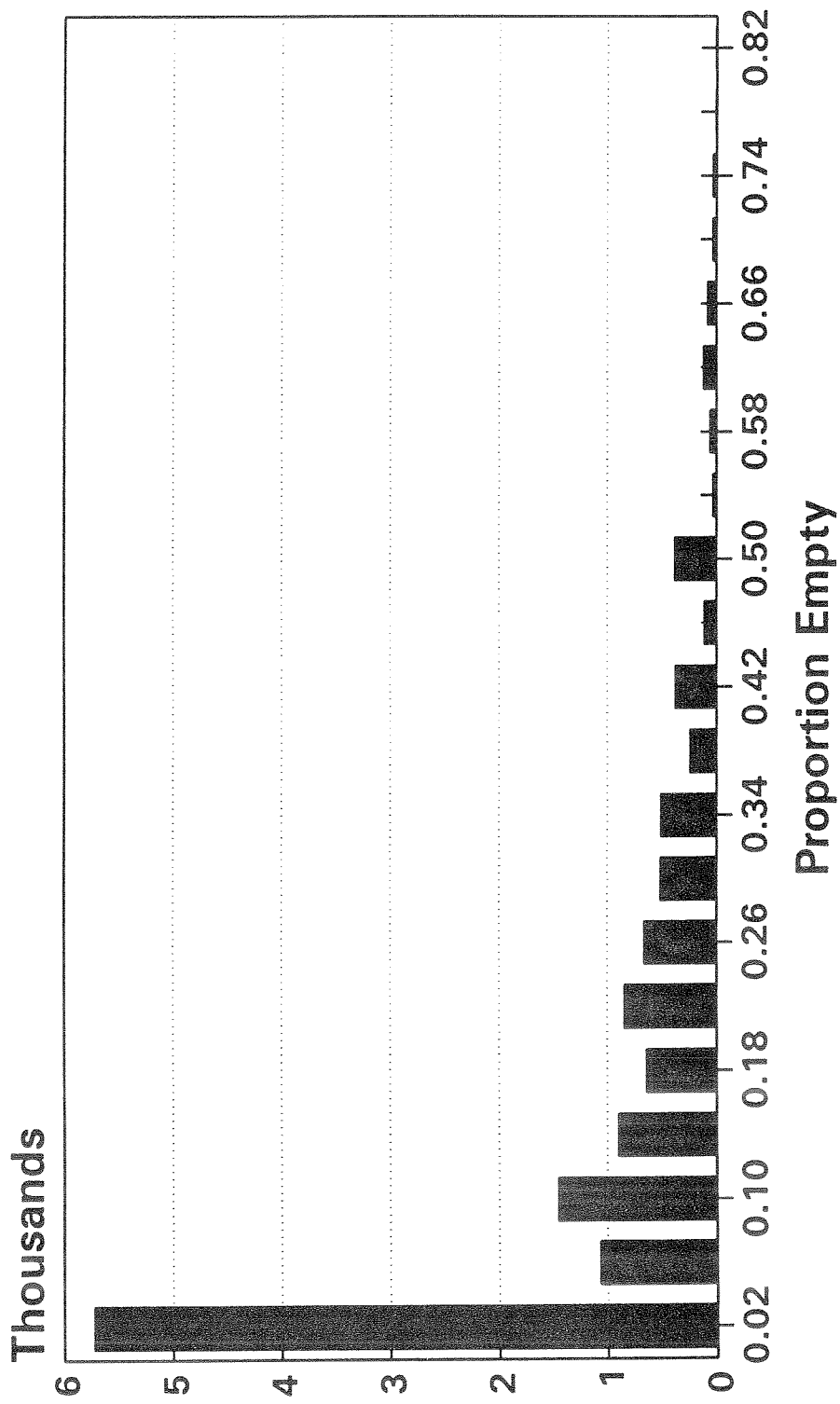


Figure 9.1.4. Frequency distribution of the proportion of empty stomachs per bulked sample for North Sea cod.

CV OF TOTAL STOMACH CONTENT

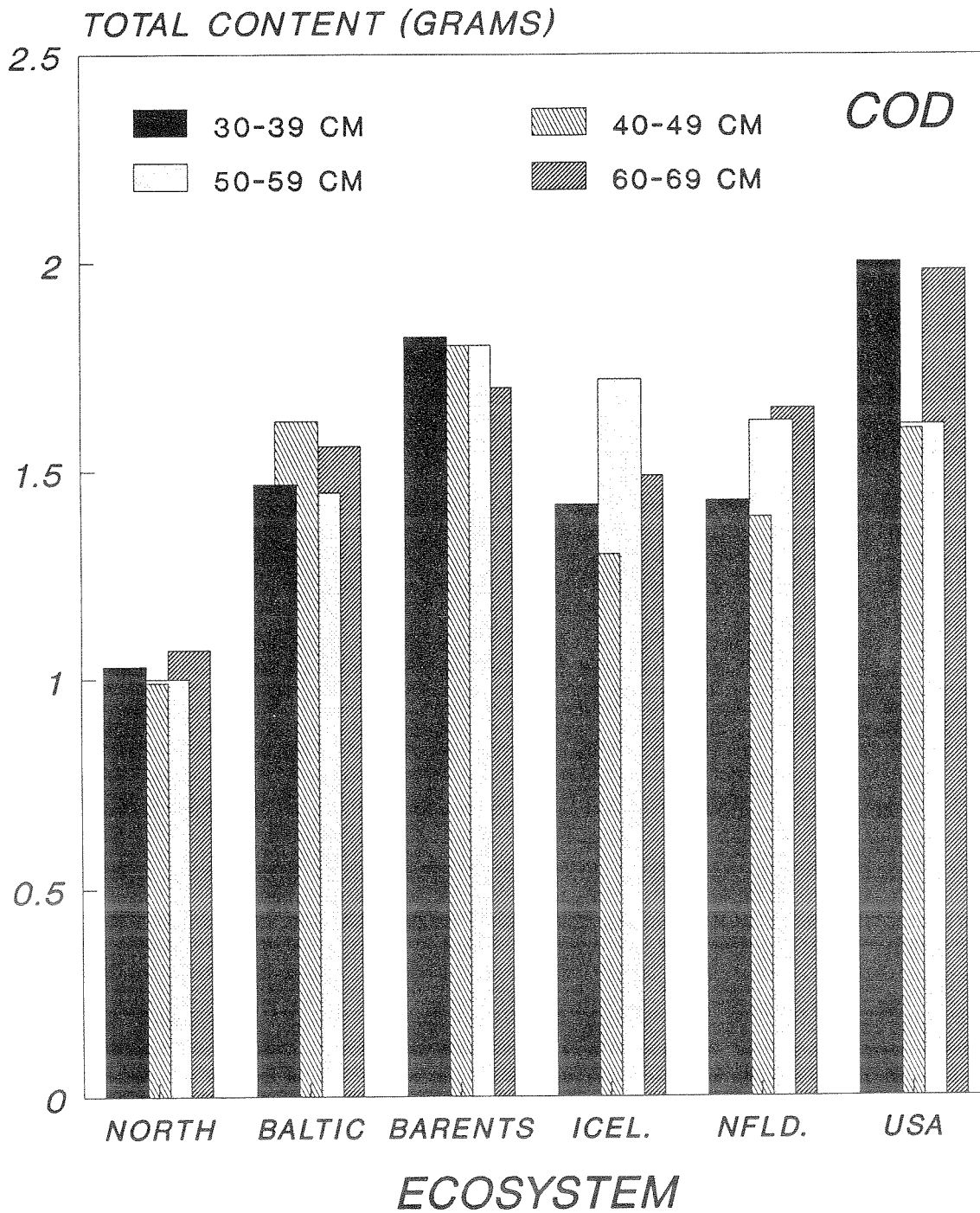


Figure 9.2. Coefficients of variation (sd/mean) for total stomach content weight of four size classes of cod sampled in six ecosystems.

Appendix A. Pseudo-computer code for inclusion of the extended survivors method into multispecies virtual population analysis.

Read MSVPA files including an initial estimate of terminal F for all species and carry out the initialisation procedures

Perform one MSVPA VPA to initialise the population arrays and M2 arrays

Do while SUIT current <> SUIT previous

Perform 5 iterations of XSA to generate fleet data tuned terminal F's and read to MSVPA array (for species with tuning data).

MSVPA VPA

Calculate new suitabilities

Enddo

The pseudocode for the XSA section is :

For each species with catch at age tuning data
Read MSVPA populations, M1, M2 and catches
Use (M1+M2) and the catches to generate Pc
Use the populations generated by MSVPA to
calculate F, ECF, Z, ECZ

Do 5 iterations or less if convergence is achieved

For each fleet

Calculate weighted reciprocal catchability and its variance

Enddo fleet

For each fleet, age, year

Calculate Pest

Enddo fleet, age, year

For each cohort

Calculate weighted mean survivors (Pt)

Calculate new Pypa values from the Pt values

Enddo cohort

End of iteration loop.

Copy terminal populations to MSVPA array

Next species

Appendix B. SAS code for core GLM runs of categorical and discrete effects influencing total fish and total food in cod diets in six ecosystems.

```

* Sas code for the Agreed Core Run
* Monday 22 June. It includes:
*   Scaled data only (inverse wt cubed) * 100000
*   Logged data only
*   No completely empty stomachs/samples
*   Weighted by sample size
*   YEAR QUARTER AND TIME OF DAY EFFECTS
*   A categorical analysis with 6 categories
* Jake Rice 22 June 1992 ;
options ls=80 ps=66;

libname save '/usr/lib/multi92/sasdata';
data d1;
* set save.nsea;
* set save.baltic;
set save.norway;
* set save.iceland;
* set save.nfld;
* set save.usacod;
scale = ( 1. / (predlen **3)) * 100000 ;
NSAMPLE = NFOOD + NREGURG + NEMPTY ;
IF NSAMPLE EQ NEMPTY THEN DELETE ;
TOTFISH = WCAPELIN+WUNIFISH+WOTHFISH ;
TOTFOOD = TOTFISH + WCRUST+WMOLLUSC+WPOLYCH+WECHINOD+WOTHFOOD ;
totfood = totfood * scale ;
totfish = totfish * scale ;
IF TOTFISH NE 0 THEN TOTFISH= LOG (TOTFISH) ;
IF TOTFOOD NE 0 THEN TOTFOOD= LOG (TOTFOOD) ;
TOFDAY = INT ( TIME / 600. );
IF TOFDAY EQ 4 THEN DELETE ;
PLENCAT = INT ( PREDLEN / 100. ) ;
IF PLENCAT LT 2 THEN DELETE ;
IF PLENCAT GT 7 THEN DELETE ;

PROC GLM ;
  CLASS QUARTER YEAR TOFDAY ;
  MODEL TOTFISH= YEAR QUARTER TOFDAY PREDLEN(YEAR)
    / SOLUTION SS1 SS3 SS4 ;
  WEIGHT NSAMPLE; LSMEANS YEAR QUARTER TOFDAY / PDIFF STDERR ;
  TITLE 'LOGTOTFISH X BY SCALED LEN NESTED BY YEAR - BARENTS SEA ' ;
PROC GLM ;
  CLASS QUARTER YEAR TOFDAY ;
  MODEL TOTFOOD = YEAR QUARTER TOFDAY PREDLEN(YEAR)
    / SOLUTION SS1 SS2 SS3 SS4 ;
  WEIGHT NSAMPLE; LSMEANS YEAR QUARTER TOFDAY / PDIFF STDERR ;
  TITLE 'LOGTOTFOOD X SCALED LEN NESTED BY YEAR - BARENTS SEA ' ;
PROC GLM ;
  CLASS YEAR QUARTER TOFDAY PLENCAT ;
  MODEL TOTFISH = YEAR QUARTER TOFDAY PLENCAT YEAR*PLENCAT
    / SOLUTION SS1 SS2 SS3 SS4 ;
  WEIGHT NSAMPLE; LSMEANS YEAR QUARTER TOFDAY PLENCAT / PDIFF ST
  TITLE 'CATEGORICAL TOTFISH BY Y Q T PLENCAT - BARENTS SEAS ' ;
PROC GLM ;
  CLASS YEAR QUARTER TOFDAY PLENCAT ;
  MODEL TOTFOOD = YEAR QUARTER TOFDAY PLENCAT YEAR*PLENCAT
    / SOLUTION SS1 SS2 SS3 SS4 ;
  WEIGHT NSAMPLE; LSMEANS YEAR QUARTER TOFDAY PLENCAT / PDIFF ST
  TITLE 'CATEGORICAL TOTFOOD BY Y Q T PLENCAT - BARENTS SEA ' ;

RUN;

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