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# REPORT OF THE WORKSHOP ON STOMACH EVACUATION RATES IN FISH

Lowestoft, 3-5 April 1989

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## 1. *TERMS OF REFERENCE*

1. At the Council Meeting in Bergen during 1988, the Demersal and Pelagic Fish Committees recommended that:

A Workshop on Stomach Evacuation Rates in Fish will be established under the chairmanship of Dr P.J. Bromley and wil meet in Lowestoft for 3 days in March/April 1989 at national expense to:

a) evaluate the results of digestion experiments with a view to estimating the rates of food intake in natural fish populations on the basis of stomach content data;

b) report to the Symposium on Multispecies Models Relevant to Management of Living Resources in October 1989.

## 2. PARTICIPANTS

| | |
|---|---|
| P J Bromley | (UK, England, Chairman) |
| S Singh | (" " ) |
| T K Stokes | (" " ) |
| J Pope | (" " ) |
| A D Graham | (" " ) |
| J M Last | (" " ) |
| H Sparholt | (Denmark) |
| J Reinert | (Faroes) |
| I Olaso | (Spain) |
| F Köster | (Germany) |
| J R G Hislop | (UK, Scotland) |
| A P Robb | (" " ) |
| G Lilly | (Canada) |
| J Santos | (Norway) |
| P Grotnes | (" ) |
| B Bogstad | (" ) |
| S Mehl | (" ) |
| N Daan | (Netherlands) |
| H G L Heessen | (" ) |

## 3. BACKGROUND AND OBJECTIVES

During the last decade there has been a shift in abundance of North Sea fish from gadoids to pelagic species, particularly herring. The feeding data used in Multispecies Virtual Population Analysis (MSVPA) relies heavily on results from the 1981 year of the stomach programme, which may no longer be applicable and a new, comprehensive stomach sampling programme for North Sea is being considered.

In the run up to such a programme, it is appropriate that there should be an appraisal of recent stomach evacuation experiments. The way in which the results of such experiments can be used to develop feeding models to convert data on the stomach contents of fish in the wild into estimates of predation also needs consideration.

The purpose of this meeting was to evaluate the role of stomach evacuation experiments in the development of models for predicting the feeding rates of natural fish populations and to develop a generalised model for predicting feeding rates. The aim was to come up with a model which was applicable to a wide range of species and feeding situations. Further objectives were to recommend the optimum design and method of analysis of evacuation experiments and to give a clearer indication of what information needs to be collected in future stomach sampling programmes. For example, whether to analyse stomachs individually rather than collectively, as was the case in the 1981 ICES Year of the Stomach.

The agenda started with stomach evacuation studies and covered the stages in the process of deriving a feeding model. It concluded with a session on the application of such models to MSVPA. There was a Wash up session at the end to review progress, make recommendations and point the way to future research. Each session started with a brief introduction, followed by short presentations of individual topics with plenty of discussion in between. It was agreed that the following participants would be responsible for the various sections of the report and that the deadline for the report would be June in order to present it at the multispecies meetings in June and October 1989.

| | |
|---|---|
| J Santos | Gastric evacuation - the state of the art |
| P J Bromley | Modelling gastric evacuation |
| J R G Hislop | Field sampling |
| B Bogstad | Modelling feeding of natural fish populations |
| H Sparholt | Applications in MSVPA |

## 4. GASTRIC EVACUATION EXPERIMENTS: THE STATE-OF-THE-ART

Multispecies stock assessment models require information on predator feeding rates as a means of determining predation mortalities of the prey population(s). As a result of the need for accurate estimates of feeding rates a number of laboratory and field investigations have been implemented.

### 4.1 LABORATORY WORK

The usual assumption in food consumption modelling is that, for a given fish in a steady state, feeding rate equals gastric evacuation rate. The traditional approach in the estimation of evacuation rates has been based upon experimental work where predators are fed discrete meals and sampled at given intervals in order to determine gastric emptying over time. The time-dependent evacuation function fitted to the observations depends on the decay pattern. The introduction of gastric lavage techniques has reduced the needs for large experimental resources and has allowed an increased number of observations on small numbers of fish.

A number of experimental design variations have been used, and to a certain degree the shape of the evacuation curve is dependent upon the experimental design. Hence, contradictory data were presented at this meeting. Experimental observations on whiting and turbot led Peter Bromley to propose a linear model of gastric evacuation. Independent of any assumption of clearance pattern, Susan Singh presented evidence for i) prey type dependent evacuation rates in cod and whiting and ii) the presence of a possible interaction effect on evacuation rate when other prey are consumed together with lugworm. Preliminary results of Sandy Robb's work on whiting also point towards a constant gastric evacuation rate independent of ration size but dependent on predator size and temperature. Jorge Santos' research on individually fed cod contrasts with the works above since: i) curvilinear models seemed to give a better overall fit to the observations than the linear model and ii) ration size effects are relevant, the gastric evacuation curve decreasing non-linearly with ration size.

Two main reasons may contribute to the apparent disparity of results obtained: differences in experimental design and artifacts in the fitting of the models. In order to achieve reliable information from gastric evacuation experiments the main factors should be adequately monitored. At this stage, factors like predator species and size, temperature, and prey species and size are all potentially significant and should, therefore, be precisely controlled. While there seems to be agreement on the importance of these factors on evacuation rates, the effects of another factor - meal size - are still controversial, but care should be taken not to underestimate its importance. Communal feeding, for instance, may lead to a great deal of variation in meal size. Unless the individual starting meal sizes are known (by feeding individual fish or tagging the prey) errors may easily be introduced to both the interpretation of the evacuation pattern and the estimation of evacuation rate. In addition, preliminary experiments are recommended in order to determine the required sample size and when to sample in order to obtain reliable estimates.

Incorrect evacuation patterns may also be inferred from inappropriate treatment of the data. Some of the most common faults found in literature include: i) neglecting the censoring effect of the observations at low levels of stomach content ii) use of the mean values of stomach content at a given time to fit the evacuation model instead of using individual observations; iii) use of inappropriate or inadequate statistics (e.g. the coefficient of determination) to compare fits of different models to sets of observations transformed in distinct ways; iv) omitting a final check of the assumptions and fitting of the selected model by means of analysis of residuals. Most statistical packages offer a means of non-linear fit of the different models to untransformed data and this technique should therefore be preferred. Analysis of residuals (probability plots, plots of residuals vs. estimators, tests of normality, etc) is also becoming easier to perform.

Criticisms of the "classical" experimental approach have arisen and include such pertinent questions as the extent to which data obtained from confined fish may be extrapolated to populations in the wild. Laboratory experiments fail to mimic natural conditions in various ways, some of which (e.g. behavioural) can hardly be corrected for. For instance, for the range of predators considered in the current MSVPA for the North Sea, empty stomachs seldom occur. Nevertheless, experimental work has usually been carried out using starved fish or has been based on 'single meal' studies. In this context, 'sequential meal' experiments are a necessity in order to validate models derived from single meal experiments. George Lilly presented a few sets of observations for cod fed sequential meals consisting of tagged capelin. In this way, the amount of prey eaten by individual cod could be tracked successfully. This experimental design does not permit derivation of a gastric evacuation model, but could provide useful independent data by which to validate an evacuation model.

## 4.2 FIELD WORK

The traditional field approach to determine food consumption and derive patterns has been the "24 hour fishery" experiments. This technique functions best for predators which eat large and discrete meals once a day - a "feed and wait" strategy. Frederik Köster for instance, found reasonable evidence of diurnal cycles of food intake in Baltic herring preying intensively on copepods. Predators like cod, however, seem to rely on a more continuous-feeding strategy which, when associated with a large stomach capacity and low digestion rates, usually precludes the determination of food consumption from field data. Even so, Henrik Sparholt reported findings by Poul Degnbol and Hanna Stokkholm of feeding rhythms in wild cod measured from the occurrence of fresh items in the stomachs. This approach deserves further attention as a means of determining food consumption for this kind of predator. In addition, these types of observations may also be used to validate gastric evacuation data from lab experiments.

## 5. MODELLING GASTRIC EVACUATION

It would appear that the shape of the gastric evacuation curve can vary dependent on factors such as species and prey type. A power exponential model (Jorges Santos) could be fitted to most evacuation curves, including the sigmoidal. The latter occurs when there is an initial delay in digestion, a situation which is likely to be more prevalent in the wild where fresh prey is almost certain to be initially more resistant to digestion than in the preserved prey used in most gastric evacuation experiments.

Not surprisingly perhaps, participants could not agree on a simple, unambiguous gastric evacuation model which they felt could be applied with confidence to a wide range of species and feeding situations. As a result it was decided that any future stomach sampling programme needs to collect information which enables a variety of evacuation/feeding models to be tested.

For example, exponential and allied models of gastric evacuation require information on the level of stomach fullness since in such models evacuation rate varies with the amount of food in the stomach. In a linear model evacuation is constant in g $h^{-1}$ and is independent of stomach fullness. What is important in this model is the proportion of time food is present in the stomach, which in the case of most large predatory fish, is equal to the percentage of fish with food in their stomachs. Empty stomachs indicate a zero evacuation rate. In practice, fish with stomachs containing only skeletal remains are also classed as empty. Skeletal remains tend to be evacuated more slowly than the rest of the prey and may persist in the stomach for several days, during which time evacuation can be regarded as effectively zero.

The prey spectrum gives the proportion of the various prey in the stomach, but since various prey types can be evacuated at different rates (Susan Singh), multipliers are required to correct for different residual times of prey in the stomach. A simulation model (John Pope and Kevin Stokes) was developed which applied the linear evacuation model to the situation where fish were feeding at random on prey of different digestibilities. This proved to be a useful way of visualising how stomach contents fluctuate on a daily basis, and the model might be developed to investigate feeding strategy.

The contribution by Jorges Santos stimulated an analysis of half life estimates derived from evacuation experiments conducted by working group members.

The half life of food in fish stomachs is the time it takes a fish to reduce its stomach content to 50% of the ingested weight and is an easily observed and easily available statistic from most of the evacuation experiments reported to the working party. Moreover, half life (H) has a central place in many of the models for example in a linear model

$$P = 1 - \left(\frac{.5}{H}\right) t$$

and the double exponential model

$$P = 2^{-\left(\frac{t}{H}\right)^{s}}$$

where P is the proportion of food remaining, t is time and s is a parameter of the model. Through these formulae H relates directly to the time to evacuate 50% of food, which corresponds approximately to the time that a prey item is recognisable at species level and sizeable. Clearly a description of the factors which influence H needs to be made and as a start, a simple linear modelling approach was adopted. The information available were (factors) predators (cod, whiting and mackerel) prey (Clupeods, sandeel, capelin, crustacea lugworm) and (covariates) meal size, temperature, prey size, and predator size.

When all the half life data (64 items) were analysed (with log of half life the dependent variable) most variance was explained by predator species followed by prey then temperature and log meal size. Log predator size failed to reduce variance significantly. Table 1 shows the ANOVA table associated with this order of fitting. An interaction between predators and the other model terms can also be fitted. This is equivalent to fitting the model to the experiments for each predator separately. The interaction of predator with the above model accounts for an additional sum of squares of 1.9 on 6 degrees of freedom. Parameter estimates for the three predator species are shown in Table 2. The parameter estimate for log meal size is consistent for both cod and whiting and temperature has the same sign but different size of effect. Results for mackerel seem somewhat different, but are based on only a few data points and one prey item (Crustacea).

Table 1. ANOVA of log half life

| Cause | DF | S. Sq | MSq | F |
|---|---|---|---|---|
| Predator species | 2 | 13.1 | 6.55 | 59.5 |
| Prey species | 4 | 4.0 | 1.00 | 9.1 |
| Temperature | 1 | 3.3 | 3.30 | 30.0 |
| log meal size | 1 | 1.2 | 1.2 | 10.9 |
| Residual | 55 | 6.0 | 0.11 | |

Table 2 Parameter Estimates of the fit of Ln (Half life)

| | | All Expt. | Expt. on cod | Expt. on whiting | Expt. on mackerel |
|---|---|---|---|---|---|
| Cod | Pred (1) | 3.65 | 3.38 | - | - |
| Whiting | Pred (2) | 4.34 | - | 4.58 | - |
| Mackerel | Pred (3) | 3.13 | - | - | 5.09 |
| Clupeoids | Prey (1) | 0.00 | 0.00 | 0.00 | - |
| Sandeel | Prey (2) | -.44 | -1.81 | -0.32 | - |
| Capelin | Prey (3) | -.94 | -.88 | - | - |
| Crustacea | Prey (4) | -.19 | -.26 | -.24 | 0.00 |
| Lugworm | Prey (5) | -1.02 | -1.08 | - | |
| | Temp | -.09 | -.04 | -.12 | -.19 |
| | Ln (meal size) | .20 | .18 | .19 | -.03 |

It was decided to expand the concept of comparative analysis of the results of gastric evacuation experiments. Under the organisation of Peter Bromley and Andy Graham a data base of results is to be set up in a common format to facilitate this objective. The results of the comparative analysis are to be presented in poster form at the multispecies meeting at the Hague in 1989.

## 6. FIELD SAMPLING OF STOMACHS

It was decided that the fine details of a stomach sampling scheme intended to determine a) the species composition of the diet and b) the consumption rates of North Sea fish should be discussed during the forthcoming meeting to plan a second 'year of the stomach'. However, there was a lengthy discussion about whether stomachs should be collected, analysed and processed on a pooled basis, as in 1981 and 1985-87, or treated individually.

The most obvious gain from adopting the single stomach approach would be the possibility to estimate the errors associated with mean stomach weights etc from different areas, seasons and years. No such estimates can be made for the pooled data. Also, although it appeared that some methods for calculating species composition of the diet and consumption rates could be applied to either individual stomachs or pooled data, others could not.

On the other hand, the single-stomach approach would undoubtedly cause many practical difficulties. It would take much longer to collect samples at sea and more containers would have to be stored and/or exchanged. Stomach analysis and data processing would take longer. Estimates of the increased workload that would result from adopting this system ranged from 2x to 4x the present level of effort. In addition, the data base would become much larger.

Suggestions were made as to how some of these problems might be overcome, such as storing individually wrapped stomachs in bulked containers and reducing the numbers of stomachs in a sample. Alternatively, subsampling say 1 in 20 stomachs individually and bulking the remainder might be feasible. Nevertheless, it was recognised that changing to a single-stomach strategy is not a trivial matter and should only be considered if it could be demonstrated that the gains would outweigh the disadvantages and it was up to the proponents of the single-stomach strategy to present a convincing case. It was agreed that J Last and J Hislop would analyse data sets held in Lowestoft and Aberdeen to evaluate the two approaches and prepare poster papers for the ICES Multispecies Symposium to be held in the Hague in October 1989.

The workshop briefly discussed the levels to which stomach contents should be identified. It was agreed that whereas fish prey should be identified to species and size class, other prey could be treated more superficially. However, in view of the fact that different taxa may be digested at different rates (e.g. Susan Singh's finding that Polychaeta were digested more rapidly than Crustacea in fish), the weights of different types of prey (worms, molluscs, crustacea etc) should be recorded. This is, of course, a minimum requirement. It was pointed out that fish are probably very efficient sampling instruments and ecologists might learn much about the distribution of the fauna of the North Sea by examining in detail the contents of fish stomachs. It was a recommendation of the workshop that such workers should be actively encouraged to participate in stomach analysis. A valuable opportunity to study the broader aspects of feeding ecology will otherwise be lost.

## 7. MODELLING FEEDING OF NATURAL FISH POPULATIONS

A working document on estimates of the North-East Arctic cod stock's food consumption based on stomach content data and gastric evacuation rates was presented. The average conversion efficiency was calculated to be about 10%, with the highest efficiency for the youngest fish. The data show that there is an inconsistency between the cod stock estimates, the capelin stock estimates and the consumption calculations. When modelling growth of fish as a function of food consumption, it would be interesting to have upper limits on conversion efficiency from laboratory experiments.

Regarding modelling of species interactions, there was some discussion on how to estimate suitability from trawl catches. There seem to be a need for discussing various ways of improving the modelling of species interactions.

A working document on the use of measured stomach evacuation rates (Santos' data) in the multispecies model for the Barents Sea (MULTISPEC) was presented. In MULTISPEC, the evacuation rates are only used when estimating interaction parameters. Both an exponential and a linear evacuation rate model can be used. The estimation procedure requires that the stomachs are collected individually. No estimation results are available so far. The model should prove useful in testing the effects of the differing evacuation rate models on the estimates of predation mortality.

While MSVPA has commercial catch data as its main data source, MULTISPEC is based on direct stock measurements. The participants working with the North Sea were interested in investigating how a model for the North Sea based on acoustic measurements could be constructed.

## 8. APPLICATIONS IN MSVPA

John Last presented a review of the literature on the stomach contents of a large number of fish species in the North Sea. This showed how feeding strategy changed during development from the larval to the adult stage and gave insight to the mechanisms which operate to avoid feeding competition. The vast complexity of feeding interactions of fish was summarised in a food web which proved to be useful in appraising which species should be included in MSVPA for improving estimates of predation rates attributable to non commercial fish species. Scad and spurdog might be important predators but presently there is no experimental work on the evacuation rate of these species, which necessitates the extrapolation of results from other species. Evacuation in haddock, whiting and saithe is fairly similiar and it can be expected that the same is probably true of North Sea and Baltic cod for example.

Information on the feeding in 0-group fish was particularly sparce. Since this is a critical stage in development during a period which plays a role in determining recruitment, it was felt that more effort on research into feeding of 0-groups would be beneficial.

The MSVPA needs data of total amount of food in grams consumed by a particular predator by age and quarter. The precision of the estimate of food consumption should be rather high because the errors in the data will create an almost equal error in the MSVPA estimate of predation mortality. A precision of about 20% was considered acceptable.

## 9. SUMMARY

A recommendation was made that John Hislop and John Last appraise existing stomach content data collected on an individual basis to test the potential disadvantages of bulking samples. The results are to be presented in poster form at the Multispecies Symposium at the Hague in October 1989.

It was also recommended that a common database of gastric evacuation experiments be set up. The common format would be water temperature, predator species, predator size, prey species, prey size, number of prey ingested, meal size, time after ingestion, and weight of stomach contents observed. It was agreed that Peter Bromley would centralise data and arrange the logistics of the operation. Supercalc 4 was the agreed format. The results of comparative analysis are also to be presented in poster form at the Hague meeting.

It was also agreed that benthic ecologists should be actively involved in the stomach sampling programme as the large quantity of stomach samples collected would make this study of wider ecological interest. Peter Bromley is to inform the Chairman of the Biological Oceanography Committee, ICES.