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Does the diet of cod and whiting reflect the species composition estimated from trawl surveys?

by

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Abstract

The diet of predatory fish can effect the abundance of their prey considerably. In multispecies models such as the MSVPA, the relative abundance of a prey species age group in the diet of a predator is often assumed to be directly proportional to its relative abundance in the surroundings. To investigate the validity of this assumption, this paper compares the stomach content of cod and whiting obtained during the ICES stomach sampling project in the North Sea with the species and size composition of the prey in trawl catches. The models describing the dependence of the composition of the stomach content on the IBTS catches explained about 40% of the total variation in stomach content composition and revealed significant negative switching by the predators. These results may be caused by prey switching or indicate that the suitability model is not an appropriate model for describing prey choice by the predators.

Key words: Diet composition, suitability, prey switching, MSVPA.

Introduction

When trying to understand ecosystem dynamics, describing the dependence of the diet of predators on the abundance of prey is an essential problem. Not only will the nature of this relationship provide information on energy flow in the system it may also have profound effects on ecosystem behavior and stability. Predators may act to stabilize or destabilize the population of their prey, depending on the way the number eaten is affected by prey abundance. Murdoch and Oaten (1975) suggested, that predators exhibiting more than proportionally increased preference for the most abundant prey (positive switching or simply switching) will act to dampen extreme variation in prey abundance and improve ecosystem stability. Alternatively, a predator seeking to maintain its diet composition irrespective of prey density (negative switching or counter-switching (Kean-Howie et al., 1988)), will increase the variation in the system by further diminishing the stock of a prey with low abundance. Switching has been examined by numerous authors (Manly et al., 1972, Murdoch & Marks, 1973, Murdoch et al., 1975, Murdoch & Oaten, 1975, Chesson, 1984, Kean-Howie et al., 1988, Chesson, 1989).

It is difficult to compare investigations of switching carried out in the laboratory or in smaller confined areas of natural ecosystems with a larger context. As an attempt to analyze switching in the North Sea, Larsen & Gislason (1992) tested this factor as part of the MSVPA (Gislason & Helgason, 1985). The model used was a slightly altered version of the suitability model (Larsen & Gislason, 1992):

$$\frac{I_i}{I_j} = s_{ij} * \left(\frac{N_i}{N_j}\right)^b$$

for a given predator species and age, where i,j=prey species and age, I_i=number of i ingested, s_{ij}=suitability of i relative to j, N_i=number of i present in the North Sea and b=switching coefficient. A b<1 indicates negative switching, b=1 no switching and b>1 positive switching. Examples of the three responses are shown in fig. 1.

Larsen & Gislason (1992) found a tendency to negative switching, though this did not improve model fit significantly.

In the general application of the MSVPA, predators are assumed not to exhibit switching (Gislason & Helgason, 1985). However, if the predators do exhibit switching behavior, this will have important effects on the predictions of the MSVPA. Thus, recruitment is likely to be underestimated for small year-classes and over estimated for large year-classes.

This paper compares the stomach content of cod and whiting with the species and size composition of the catch in the International Bottom Trawl Survey (IBTS). The stomachs analyzed were gathered in the North Sea during the stomach sampling projects carried out under the coordination of ICES in the years 1981, 1985, 1986, 1987 and 1991.

To obtain unbiased estimates of trawl catch, a model was build to describe the average number of fish caught in the IBTS in a given area and time. Using the predictions from this model, the ratio between the number caught of different species and lengths of fish were calculated. This ratio was then compared to the ratio of the same species and lengths observed in the stomach content of the predators.

A number of models were build to determine, which factors have an effect on the relationship. The different models investigated the significance of relative prey density, pooling of stomachs into larger samples, year, quarter and area, predator- and prey species and lengths and spatial scale on switching and suitability as defined in the suitability model presented by Larsen & Gislason (1992).

Materials and methods

Survey data

The survey data used to estimate the abundance of the prey species is the data collected during the International Bottom Trawl Survey (IBTS) (former the International Young Fish Survey) conducted in the North Sea under the coordination of ICES (ICES, 1981, ICES, 1996a).

Stomach data

The stomach data used in this project were collected in 1981, 1985, 1986, 1987 and 1991 during the ICES stomach sampling projects (ICES, 1988, ICES, 1991, ICES, 1992, Hislop et al., 1991, Kikkert, 1993). Samples were collected during all quarters in 1981 and 1991, and during 1st and 3rd quarter in 1985, 1986 and 1987. For details on sampling procedure, see ICES (1991) and ICES (1992). As the IBTS has only been carried out in the 1st quarter of 1981, 1985, 1986 and 1987, the remaining quarters of these years could not be used in analyses.

Only the prey species cod, haddock, herring, norway pout, sprat and whiting are considered in the analyses, as these species all have been caught and measured regularly in the IBTS. Prey, that was too digested to be measured, counted or classified to species were ignored.

The predators were divided into the lengthgroups seen in table 1. Cod smaller than 300 mm or larger than 1000 mm and whiting smaller than 200 mm or larger than 400 mm were excluded from analyses, as they either contained few fish prey or were caught infrequently. To minimize the number of parameters in the models, prey was divided into 50 mm length groups as seen in table 1.

Methods

The suitability in the MSVPA is a North Sea average. This may introduce additional variation in the calculation of the suitability and switching coefficient. It was therefore decided to compare the relative abundance of the prey in the stomach with the relative abundance of the species caught in the IBTS in that area. Furthermore, the model was build grouping prey and predator by species and length instead of species and age as in the MSVPA, as the predators are more likely to distinguish prey by length than age. As described by Daan, (1986), the suitability model applies equally well to number and weight eaten. For convenience, all models therefore examined the relative frequencies by number.

The relative number of one species caught in the trawl as compared to another species is not necessarily equal to the relative abundance actually present in the water volume trawled (Engås & Godø, 1989, Ona & Chruickshank, 1986, Walsh, 1989). Trawl selection thus acts differently upon different species and lengths. The trawl is assumed to catch a constant percentage, q, of the actual abundance of a species in that area (Cook, 1997):

$$T_{i,l} = q_{i,l} * N_{i,l}$$

where i= species, l=length of fish, $T_{i,l}$=number caught of i at length l and $q_{i,l}$=catchability of i at length l.

The ratio observed in the stomach content is not necessarily the ratio in which the prey was ingested, as some prey may be digested faster than other (Jones, 1974). The number present in the stomach content, F, is assumed to depend on the number ingested pr. time unit, I:

$$F_{i,l} = d_{i,l} * I_{i,l}$$

where d=number of time units a prey of species i and length l can be identified to this group for a given predator species and length.

Combining these two models with the original suitability model, and assuming *s*, *d* and *q* to be constant within prey species and length and predator species and length, the expression is simplified to

$$\frac{F_i}{F_j} = c_{ij} * \left(\frac{T_i}{T_j}\right)^b$$

where

$$c_{ij} = s_{ij} * \frac{d_i}{d_j} * \left(\frac{q_i}{q_j}\right)^b = s_{ij} * d_{ij} * q_{ij}^b$$

Indices of length of i and j omitted for simplicity.

It cannot be determined from the present analyses how large the influence of d and q on c is, and suitability cannot directly be calculated from c.

Catch estimates

As the number of fish caught in a haul is very variable, it decided to estimate the average number of fish caught and the calculate the relative frequency from this. To obtain an estimate for the number of fish caught of a certain species and length that has the least possible error, it was decided to build a model for the IBTS-data.

To obtain a sufficient number of observations (hauls) in each area, the squares were gathered in 4-square areas (fig. 2). Two models were formulated: One describing the probability of catching something and another describing the number caught given something is caught. The model describing whether or not something was caught was analyzed as a generalized linear model with binomial distributed observations. A haul was noted as an observation with the outcome 0 if nothing was caught of the particular species and length and 1 otherwise. The number caught given something was caught was assumed to be log-normal distributed and modeled as a general linear model for each species and length. The factors tested in both models were area, year, quarter, ship and the crossed effects between area and year, area and quarter and between year and ship. This model was used to predict the catch in a given area at a given time. As most models showed significant and large ship-effects on catches, predictions were standardized to one ship. This reduced variation in the following models slightly, but did not alter parameter estimates significantly.

The models describing the catch in the IBTS explained on average 50% of the variation in trawl catches. Further results from the model can be obtained from the authors. This model is thus not mentioned in the results section.

Comparison of ratios

Examining the ratio within a square led to very few observations. It was therefore decided to examine all stomachs within predator species, sizegroup, 4-square area, year and quarter together, assuming that all predators in a 4-square area had been exposed to the same prey-abundance and had equal preferences. As stomachs were already pooled in larger samples, analyzing the predators individually was not an option. All samples were thus pooled within area, year, quarter, ship, predator species and –sizegroup. The total number of stomachs in the pooled samples was calculated. As only stomachs containing food provide information on the relative abundance, only these were included in analyses.

The prey species and length-groups that most often occurred together with other species were chosen as reference species and lengths. The ratios of the number of all other prey species- and size-groups to the number in these reference groups were calculated. The reference groups chosen are seen in table 1. Using different reference groups should, according to the suitability model, only affect the suitability factor.

The IBTS predictions and the stomach data were combined on 3 different spatial scales: 4-square areas, roundfish areas and the whole North Sea. Preliminary analyses indicated, that the variance increased with the ratio in the stomach. To make the observations variance-homogenic was therefore decided to log-transform all ratios, and the analyses were done on ln(stomach ratio) and ln(IBTS-ratio). For each of the three spatial aggregations 4-square area, roundfish area and the North Sea, the model analyzed was:

$$\ln\left(\frac{F_{i,l(i)}}{F_{ref}}\right)_{area} = k_{i,ref,pr,l(pr),l(i)} + b_{i,ref,pr,l(pr)l(i)} * \ln\left(\left(\frac{T_i}{T_{ref}}\right)_{area}\right) \qquad (1)$$

where ref=reference species and length, pr= predator species, k= ln(c).

One analysis of ratios was done for each reference group apart, to avoid correlation between observations. A general linear model was built, examining both linear and categorical effects of a line of independent variables on $\ln(F_i/F_j)$. Due to the unbalanced sampling design, the type IV sum of squares was used to test for significance of effects. This type of analyses measures the significance of each parameter, provided all other parameters have an effect while taking the unbalance of the data into account. Because of the limited overlap between predator length groups of the two predator species, crossed effects between predator species and size group could not be tested when length of predator was tested as a categorical variable.

Unfortunately, stomachs sampled from predators collected from the same haul cannot be considered to be independent sub-samples, as shown by Warren et al. (1994) and Bogstad et al. (1995). As stomachs have not been examined individually, it was not possible to estimate the intra-haul correlation, and thus the weight, that should be assigned to each sample when performing the analyses. Furthermore, pooling stomachs from variable predators may result in population prey switching, though individual predators do not exhibit this behavior (Chesson, 1984). All other analyses apart from the analysis of the effect of number of stomachs were weighted by the number of stomachs in a sample. This was considered as good an approximation as any. The weighting had little effect on parameter estimates. It rather increased than decreased the switching coefficient.

Basic analyses

The basic analyses, with which all other analyses were compared, was an analyses of the ratios compared at 4-square areas. The factors prey, prey length, predator and predator length and the 1st and 2nd order effects of these on the parameters defined in (1) were tested for significance. The same model was built comparing data at roundfish areas and at North Sea scale, to estimate the effect of scale on the switching coefficient.

Effect of number of stomachs in the sample

To examine if pooling of the stomachs had an effect on the switching coefficient found in the analyses, a set of models were built including the number of stomachs in the sample as a linear variable in the model of ratios.

Test for effect of year, quarter and area

To test if the low switching coefficient observed was caused by a difference in suitability between areas, years and quarters, analyses were made on 4-square area only testing the effect of prey species and length, predator species and length, year, quarter and 4-square area on the parameters defined in (1).

Dependence on length as polynomial

The parameter values of prey and predator length estimated in the basic analyses were examined, but no trend was evident. This was presumably due to the large amount of variation in the data. It has been suggested by several authors (Andersen & Ursin, 1977, Hahm & Langton, 1984, Bannon & Ringler, 1986), that predators prefer a certain size of prey, but is more or less willing to eat prey in other sizes. Building on a line of assumptions, it is possible to use Andersen and Ursin's formula along with other assumptions to build a model of the ratios where dependencies of ln(prey length) and ln(predator length) are described as 2nd degree polynomial. This model has the advantage of smoothing the differences between suitabilities for adjacent length groups. The assumptions and the resulting model is described in the appendix.

A summary of the scale the models are built on and the effects tested are seen in table 2.

Significance level and software

A significance level of $\alpha=0.05$ has been used throughout the project. All analyses were carried out using SAS®-software version 6.12 on a UNIX platform.

Results

Plots of residuals as a function of predicted values and independent linear variables were examined for all analyses. Where no trends were found, plots are not commented.

Basic analyses

A summary of the analyses is given in table 3 and 4. Selected predicted and observed values of ln(stomach ratio) as a function of ln(IBTS ratio) are shown in fig. 3.

Residuals tend to decrease as number of stomachs in the sample is increased, as should be the case, when analyses are weighted with this factor (fig. 4). However, the residuals should be distributed with a variation of $\sigma_i^2=\sigma^2$/(number of stomachs in sample i) (the curve plotted on fig. 4)(Tjur, 1979). This is far from being the case. Rather, residuals are too large for large samples and/or too low for small sample sizes. This is most likely due to intra-haul correlation (Bogstad et al., 1995). Even though a very high number of fish is sampled in each haul, the variation between hauls will still be large. As the increased number of stomachs in a sample does not correspond to an increased number of hauls, the variation is reduced by less than the number of stomachs.

There is a significantly different slope in the different prey or prey length groups for all reference groups at 75 mm and norway pout at 125 mm. This is in conflict with the suitability model, as the switching coefficient should only vary with predator and predator length. It may be due to a dependence of visibility on abundance as suggested by Kean-Howie et al. (1988) and Abrams & Matsuda (1993). Another cause for these effects could be the highly unbalanced data-set.

The model for the reference whiting at 75 mm is very complicated, only reducing the dimension of the model to 32% of the dimension of the full model, whereas the other models reduce the dimension to 2% to 11%. It is furthermore based on the smallest number of observations for any of the models, which means, that there must be quite a lot of cells having only a few observations. This increases the risk of building a model, that describes the present data set well, but has little general application value. The models build for this reference are thus considered less reliable than the models for the other references.

The slope is significantly different from 0 and 1 in all models ($p<0.0001$). The upper limit for the 95% confidence limit for the switching coefficient (where no crossed effects are found) has a maximum value of 0.29. The lowest 95% lower confidence limit is 0.077. Even the upper limit denotes powerful negative switching.

Investigations on the effect of number of stomachs in a sample

The effects found to be significant differ from one model to the next as was the case for the basic model (table 5 and 6). The number of stomachs in the sample have an effect on all models but one, explaining from virtually 0% to 3.7%. When included, number of stomachs has at least one significant 1st order crossed effect, leaving the total explanation of number of stomachs and crossed effects with this factor at 2.4% to 9.1%.

There is a significant effect of the number of stomachs on the switching coefficient in 7 of the 10 models. In all models but for the reference norway pout at 125 mm, this is a positive effect, increasing the slope with the number of stomachs in the sample. For norway pout at 125 mm, one predator length-group shows a negative effect of number of stomachs on slope, but the remaining length-groups all show positive effects. The low switching coefficient does thus not appear to be due to artificial lowering by pooling of stomachs as suggested by Chesson (1984). It may even be the other way around, that is, the individual predator exhibits even more powerful negative switching, but this levels out when examining the population as a whole.

The effect of number of stomachs on the switching coefficient could also be caused by random (individual) variation being larger at smaller sample size, thus lowering the dependence on IBTS ratio by increasing variation from other sources. Furthermore, the limited stomach size of the predator may affect the slope. A saturated predator will thus attain a maximum ratio, which cannot be exceeded. This effect will tend to lower the slope. As and increasing the number of stomachs in the sample will increase the number of prey, that can be eaten, sample size will have a positive effect on slope by increasing the maximum ratios observed.

If the predator reaches a maximum ratio, one would expect the effect of the number of stomachs in the sample on the slope to be largest for small predators and large prey and reference group as these would reach saturation at the lowest number of prey ingested. If there is such an effect on these data, it is not strong enough to be visible at this scale. For one reference group, there is a significantly different effect of number of stomachs in the sample on the slope for the different predator lengthgroups. There is, however, no clear tendency for the effect to rise or fall with predator length.

Effects of year, quarter and area.

Area, year or quarter have a significant effect on all models. Explanation is increased to 73% to 88% when including these factors (tables 7 and 8). Model dimension is however also increased, making the model dimension 28-50% of the full model. The residuals, though still one-topped, are no longer normal distributed in 8 of the 10 models.

Crossed effects between slope and area are found only for sprat. Here, the slope becomes negative in several cases. It does seem highly unlikely, that predators will increase the relative frequency of a prey in the diet, when the relative abundance of the prey in the surroundings is increased. In two models, slopes differ significantly between years, but in all cases the slope is significantly different from 1.

Dependence on length as polynomial.

The models show a decrease from the r^2 of the basic model of 4.7% on average. However, as model dimension is simultaneously decreased, the standard deviation is decreased by less than 2% on average (table 9).

The models once again gave different significant factors (table 10). It should be remembered, that the parameters are a combination of several factors, and can thus not easily be interpreted.

Switching and the dependence of switching on predator length

As in the basic model, switching coefficient shows no consistent pattern with predator length when comparing the models for different references (fig. 5). The significance of the factor may thus be due to model estimation techniques and the unbalance of the data-set. Another way to visualize, if the switching parameter is dependent on predator length is to examine the dependency of the switching parameter on length of reference. As the largest reference is eaten only by the largest predators, a trend in switching as a function of reference length should be apparent, if switching depends on predator length. Such a trend is however not present, and if switching does depend on predator length, the tendency is lost in the variation of the data.

The switching coefficient is significantly different from zero and 1 in all models. The lowest and highest 95% lower and upper confidence limit is 0.09 and 0.38, respectively. The predators thus exhibit powerful negative switching.

To summarize, the length dependencies of the models are generally well described by a 2^{nd} degree polynomial of ln(predator length) and ln(prey length). The slope or switching coefficient does not appear to vary consistently with predator length.

Analyses at different spatial scales

Roundfish areas

A summary of the fit of the models is given in tables 11 and 12. Building the models on roundfish area as opposed to 4-square area increases the number of observations for all models except norway pout at 75 mm and 125 mm. It does however also increase the dimension of the model by as much as 10% of the full model dimension (sprat at 125 mm). The proportion of the total variation explained by the model is increased in all models.

There is a weak tendency for residuals to fall with the predicted value of the ln(stomach ratio), indicating that modeling ln(stomach ratio) as a linear function of ln(IBTS ratio) may not be reasonable at this scale (fig. 6). This is probably part of the reason for the many crossed effects with slope in these models. The residuals plotted as a function of ln(IBTS ratio) shows no trends, indicating that the error is in the formulation of the model rather than in the transformation of the independent variable.

Note that the residual variation cannot be compared directly due to the problem of weighting the samples by number of stomachs in the sample mentioned above. This should however not impair the comparison of r^2 and parameter estimates.

The crossed effects with slope make it difficult to compare the parameter estimates for this factor with estimates from the basic model. However, the models for norway pout at 125 mm and 175 mm does not have a great number of crossed effects with slope in either model. Slope has increased in the model of roundfish areas for norway pout at 125 mm. For the 175 mm size group, if any change is seen at all, it is a decrease in slope in the roundfish area model.

North Sea

Model explanation is further improved when increasing the spatial scale to the whole North Sea as compared to roundfish areas (tables 13 and 14). However, with a maximum of 8 observations for each combination of prey species and length, predator species and length and reference, the explanation of the model should be high. In half the models, the number of observations is increased, generally for the references, that have a limited geografical distribution. The increase is partly from new ratios now appearing between species, that do not occur to in the same roundfish areas, such as norway pout and sprat. The biological relevance of these ratios is questionable. The increased number of observations decreases the dimension of the model in percent of the full model, as model dimension is generally not simultaneously increased. In all but one model, explanation is higher in the North Sea model than in the basic model.

The plots of residuals as a function of predicted ln(stomach ratio) shows a decreasing tendency for sprat and whiting at 75 mm. The comments in the section on roundfish areas refer to these plots as well. The residual variances cannot be compared to the variances of the basic and roundfish area-models due to reasons given above. The slope is generally increased at this scale as compared to the basic model where no crossed effects with slope are found to be significant (0.33 and 0.19, respectively). However, as only two model do not show crossed effects with slope, caution should be taken when comparing parameter values.

The crossed effects found significant in the model on roundfish areas are generally not the same as the significant factors when examining the whole North Sea. In fact, not one model ends up with the exact same significant effects as when built on another spatial scale.

The improvement in total model description when increasing the spatial scale seems to come largely from a greater number of significant effects. The model on roundfish areas does not describe the data set well, as residuals are not without trends. The model on North Sea scale have limited biological meaning, as ratios are also calculated between species not overlapping in distribution.

Discussion

The problem of unequal sample sizes

The pooling of the stomachs represent a serious problem, as this impairs modeling of stomach content (Stefánson & Pálsson, 1997) and prevents the intra-haul correlation from being estimated (Bogstad et al., 1995). This again makes it difficult to determine the weights that should be assigned to each sample when performing the analyses.

The effect of number of stomachs is difficult to interpret. It is likely, that the increase in slope as a function of number of stomachs is merely due to the reduced variation in a larger sample. However, it may also be, that the predators are more abundant where one prey is very abundant (at the scale observed here (Rose & Leggett, 1990)). This would also give an effect of number of stomachs on slope, but this would just indicate, that the ratio and number of stomachs rose simultaneously. Which of the factors affect the other is not determined in statistical analyses. Building a model including a factor describing predator abundance in that area could clarify this problem. This factor should then also take mutual interference by the predators into account, as this may be an important factor affecting diet composition (Arditi & Akçakaya, 1990, Gotceitas, 1990).

The effect of time and space on suitability and switching

Even in the models where a significant crossed effect between year and switching is found, the switching parameter never exceeds 0.6. Thus, negative switching is always the result of the analyses, and is not caused by excluding year-to-year effects from the analyses.

It is a general problem when modeling biological parameters with statistical models, that the high variation in the data tend to make all crossed effects significant (Rice et al., 1991). As the model dimension is increased, the ability of the model to describe an identical experiment is decreased. Furthermore, many of the effects tend to be difficult to interpret. Year, quarter and area could have an effect on predator diet, but it is more likely, that the effect is caused by associated factors such as depth, temperature, light intensity, bottom texture, mutual interference of predators and abundance of other food.

Year to year differences in suitability did not improve model significantly when analyzing the data as part of the MSVPA (Rice et al., 1991). This result may not be comparable to the result in this analysis, as the model used there did not include switching and was based on ages rather than lengths. The result was thus subject to strong smoothing by the broad range of lengths in each agegroup. It nevertheless indicates, that the year effect found here may be caused by a change in other factors than suitability.

Suitability as a function of predator and prey length

The model of suitability as a function of prey and predator length describes the data almost as well as the basic model. Unfortunately, the parameter values cannot be compared to those of Sparre (1984) and Horbowy (1989) as these authors do not include switching in the model, and as the suitabilities calculated in this paper furthermore are on length basis rather than age basis.

Spatial scale

The models tend to get very complicated when spatial scale is increased. The model on North Sea scale does describe the data better as measured by r^2, but it is difficult to separate this from the fact, that the models are built on very few observations in each cell. Even if the models do describe the present data more accurately than the basic model, a model on this scale is likely to be very sensitive to differences in distribution and thereby changes in overlap between predators and prey species. As this distribution changes from year to year as inferred from trawl catches, this may be the reason for the many significant crossed effects. The dependence of the relationship between predator diet and abundance of prey on the scale at which data are compared is in accordance with the observations of Rose & Leggett (1990).

The model build on North Sea scale may thus be of value when building a large model as the MSVPA. However, the biological interpretation of the parameters is difficult, as the calculated ratio between prey on a North Sea scale is likely to be very different from the relative densities experienced by the predators.

Switching

All analyses reveal powerful negative switching. This is in accordance with Larsen and Gislasons (1992) results, which indicated that cod and whiting in the North Sea may exhibit negative switching. The switching coefficient found to minimize the deviation of the MSVPA estimates of the stomach content of cod from the observed values was around 0.5. For whiting, a minimum did not seem to be reached as deviation continued to fall as the switching coefficient was decreased down to a value of 0.4, which was the lowest value tested. The low coefficients were mainly due to herring and sandeel. The deviation for these species continued to fall as the switching coefficient was decreased down to the lowest value tested (0.4). This is consistent with the two basic analyses, in which a significant difference in slope between different prey is found. Here, herring also has a low switching-coefficient.

It is interesting, that the switching coefficient tested by Larsen & Gislason (1992) in no cases become significantly different from one (zero in their parameterization). The difference between this result and the result found in this project is probably due to the transformation of suitability to length rather than age. This increases the number of observations, and suitabilities may be fitted to each length. As this decreases the variation, effects of other variables are more easily detected.

Negative switching appears to be more common in nature, than one would suppose from the rather complicated theories, that seeks to describe the biological reasons for it. Kean-Howie et al. (1988) found negative switching in sticklebacks feeding on fish larvae. The switching coefficient found was 0.66, which is higher than the result in the present analysis. Reed (1969 in Murdoch & Oaten, 1975) found a tendency to negative switching in bluegill sunfish feeding on insect larvae, but this tendency was quite weak. Both authors examined average values of several predators, and it can thus not be rejected, that negative switching in these cases was caused by individual variation among predators as suggested by Chesson (1984). Abrams & Matsuda (1993) suggest, that negative switching will be prevalent at high prey densities, whereas no switching is likely at low prey densities. Negative switching may thus indicate a plentiful food supply.

The negative switching found here may be caused by a number of factors. First, the predators may exhibit negative switching at encounter of the prey. This means, that though one prey becomes very abundant, the predator does not eat only this prey. This may not imply, that the predator has to search for food for a longer period, as high numbers of one prey does not necessarily mean low numbers of the alternative prey. Thus, when the predator have eaten a certain amount of a prey species, it starts looking for something different, and begin to ignore the abundant prey at encounter. This could be due to confusion of the predators search image at high prey densities as suggested by Kean-Howie et al. (1988). This behavior may also be expected, if prey species contain different amounts of important nutrients. The predator then must have a bit of everything to grow optimally. However, such a predator will be very vulnerable to decrease in abundance of prey, and is likely to show high mortality if one of the prey types needed is absent.

Predators may become more picky in their prey choice as they get less hungry (Mangel, 1992, Hart & Gill, 1993). Thus, a predator showing a very large or very low ratio must necessarily have eaten large numbers of one species, and may not be very hungry. This could cause the predator to ignore all prey, but the preferred, if the predators forage according to optimal foraging theory (Hart & Gill, 1993). This leads to the question of which prey is the preferred. The ratio between the two most preferred prey should show a higher slope than the other ratios, as the most preferred prey should always be eaten, provided the predator is not too full (Hart & Gill, 1993). The highest slope found for whiting at 75 mm is for herring and cod for the predators cod and whiting, respectively. For norway pout, the maximum slope found is 0.55, which is found for the combination of pout and sprat. This is lower than for whiting and herring (0.74) and whiting and cod (0.65). Other investigations will have to be carried out to examine, if the low switching coefficient could be due to the predators foraging according to the state dependent foraging theory suggested by Mangel (1992) rather than the suitability model.

A second factor that may cause switching is the dependence of visibility on relative prey density. Prey may become less visible to the predator as prey density is increased, if this causes schools to increase in size. This would also explain the differences in slope for different prey found in the basic analyses of the reference norway pout and whiting at 75 mm. However, if this was the case, herring and sprat should show similar slopes, as these two species behave similarly and often school together. This is not the case, as the difference between switching coefficients is around 0.2 in both the basic models revealing a significant crossed effect between slope and prey. Thus, if differences in visibility is the cause of the low switching coefficient, these visibilities do not depend on prey behavior in any obvious way. As suggested by Abrams and Matsuda (1993), prey visibility may depend on the predation rate on the prey. If a high predation rate causes the prey to evade predators to a greater extent, the visibility of this prey is reduced as predationrate is increased. If food is plentiful, this will lead to the predators exhibiting negative switching. However, this effect would still be expected to be similar for species with similar behavior and does not explain the large difference between herring and sprat.

As suggested by Murdoch and Oaten (1975) and later Chesson (1984), negative switching could be caused by the pooling of several individually variable predators. However, this does not appear to be the case here, as the number of stomachs tend to increase the switching coefficient rather than decrease it. Nevertheless, this theory cannot be completely rejected, as the number of stomachs in a sample may have an effect due to several reasons, and a negative effect may be obscured by other effects.

Yet another possible reason for the negative switching observed is, that it is a product of the model in some way. This again can come about in several ways, but basically, this means that the way the model is built here is wrong, either because it eliminates important factors that should be considered or because prey choice can not be described in this way. If the ratio in the stomach to a large extent is regulated by something other than the ratio in the surroundings of the predator, this could dampen all high and low stomach ratios. Thus, even though the number of cod eaten is regulated to some extent by how many cod are encountered, it may be influenced to an even larger degree by the availability of some other (more interesting) prey.

Another problem could be, that the suitability is held constant over the years: If the intercept changes from year to year, this could affect the slope. However, in none of the models including year effect was the slope above 0.6. Thus, the year effect cannot be the reason for the low slope.

Whether the trawl catches give an accurate picture of the abundance of a fish species can be questioned. Even if the model of catches predicts demersal abundance quite well, predators are known to migrate vertically to feed, and may thus be exposed to pelagic prey densities different from the density at the bottom (Daan et al., 1990). However, these densities are not likely to vary completely independently of the density at the bottom at the depths encountered in the North Sea (apart perhaps from the Norwegian deep), so the difference in depth-distribution should be included in the visibility-factor in the suitability model used here. For this effect to cause the negative switching observed, catchability would have to be an increasing function of abundance, rather than a constant. The explanations for such a relationship are not obvious. The variability of the trawl catches could act to lower the slope of the dependency of relative stomach content on trawl catch. However, including this variability in the analyses does not change slope to any extent.

The observations in the model are the ratios between the number of two prey given both are present. This may eliminate extreme values, as the predator at very low or high ratios should exclude the less abundant prey almost completely from the diet. Furthermore, the trawl may not catch a species that has a very low abundance at all. This may be a problem, and perhaps is the reason why the slope tends to increase slightly, when examining the model build on the North Sea scale. However, even in this model, the slope is nowhere near 1, and so negative switching is still found, though no observations are excluded due to lack of one of the species. Predators approaching saturation, and thus being unable to ingest more prey may similarly dampen the very low and very high ratios. Saturation should thus be included in a future model.

Negative switching has been found in other investigations of fish, and may thus be exhibited by the predators, perhaps due to changes in visibility with the abundance of prey (Kean-Howie et al., 1988). It is consistent with the model developed by Abrams and Matsuda (1993), provided the total abundance of prey is high. Varying negative switching at high prey densities is also consistent with state dependent models (Hart & Gill, 1993, Mangel, 1992), provided less switching (stronger dependence on abundance) is found for the more profitable prey. It cannot be determined from the present results, which of these explanations is the cause of the observed negative switching.

Positive switching has been suggested as a factor acting to stabilize variable populations in nature (Murdoch & Oaten, 1975). However, predators exhibiting negative switching to the degree found in this paper, may act in the exact opposite way. Thus, the number of prey eaten by the predators will vary little with the abundance of the prey, and a small yearclass will loose a larger proportion of its individuals to predation than will a large yearclass. This will aggravate the effect of reduced recruitment, further diminishing a small yearclass. The destabilizing effect of predation may be part of the reason of the great variance in yearclass strength observed in fish populations (ICES, 1996b). Thus, variance from other sources is amplified by the selective predation pattern.

Conclusion

The pooling of several stomachs into larger samples presents a serious problem when examining stomach data. It would facilitate analyses, if future stomach sampling projects would examine the stomachs individually.

It cannot be rejected from the present models, that switching and suitability may vary with time and place. This must be investigated either by including additional variables in the analyses, or by approaching the problem differently. Due to the relatively few data and the already high number of variables, caution should be taken if including additional parameters.

Significant negative switching by the predators cod and whiting is found. This could be caused by changes in prey visibility, either due to confusion of the predators search image (Kean-Howie et al., 1988) or due to changes in prey behavior in response to changes in predation pressure (Abrams and Matsuda, 1993).

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Appendix

It has been suggested by several authors (Andersen & Ursin, 1977, Bannon & Ringler, 1986, Hahm & Langton, 1984), that predators prefer a certain size of prey, but is more or less willing to eat prey in other sizes. Andersen & Ursin suggests a symmetric preference pattern of the sizeratio $\ln(w_{predator}/w_{prey})$. The model describing the size preference of a predator is

$$g_{pr,l(pr),i,l(i)} = \exp\left(-\frac{\left(\ln\left(\frac{w_{pr,l(pr)}}{w_{i,l(i)}} \right) - \eta_{pr} \right)^2}{2\sigma_{pr}^2} \right)$$

$0 < g_{pr,i} \leq 1$

Where pr,i= predator and prey, respectively, l(i)=length of i, w_i=weight of i, η_{pr}=preferred size ratio of predator pr, σ_{pr}=particularity of pr.

Building on a line of assumptions, it is possible to use Andersen and Ursin's formula to build a model of the ratios where dependencies of ln(prey length) and ln(predator length) are described as 2nd degree polynomial. Detailed calculations are available from the authors. Only the assumptions of the model are described here.

Weight-length relationship

The weight of a fish (both prey and predator) is supposed to be a potency function of length of the fish:

$w_i(l) = c_i * l^{f_i}$

where c, f = Constants within prey species

Suitability in relation to predator preferences and prey visibility

The suitability is a combination of predator preferences at encounter, α, and visibility, v, which is a combination of predator-prey overlap and the vulnerability of the prey, given the two species overlap (Gislason & Helgason, 1985):

$s_{ij,l(i),l(j)} = \alpha_{ij,l(i),l(j)} * v_{ij,l(i),l(j)}$

for a given predator species and length, where i,j=prey species, $s_{ij,l(i),l(j)}$ =suitability of i at l(i) relative to j at l(j), $\alpha_{ij,l(i),l(j)}$ preference for i at l(i) relative to j at l(j), $v_{ij,l(i),l(j)}$ =visibility of i at l(i) relative to j at l(j).

Note that switching in the suitability model could be due to visibility, preference or any combination of the two being a function of prey abundance:

$$s_{ij} = \alpha_{0,ij} * \left(v_{0,ij} * \left(\frac{N_i^{\gamma_i}}{N_j^{\gamma_j}} \right) \right)^{\beta}$$

$$\text{if } \gamma_i = \gamma_j = \frac{b-1}{\beta} \text{ then}$$

$$s_{ij} = \alpha_{0,ij} * v_{0,ij}^{\beta} * \left(\frac{N_i}{N_j} \right)^{b-1}$$

where β = switching at encounter - coefficient, γ = visibility - potency, $\alpha_{0,ij}$ = preference at equal densities, $v_{0,ij}$ = relative visibility at equal densities

Indices of prey lengths, predator species and length omitted for simplicity.

If the fish are evenly distributed, the encounter-rate is proportional to the abundance (Gerritsen & Strickler, 1977). Visibility is thus constant for a given combination of predator and prey. However, as fish are not randomly distributed, this is not necessarily true. Visibility could be a potency function of relative abundance, if the prey had a limited number of refugees. As these fill up, the visibility of the prey to the predator increases (that is, $\gamma>1$). On the other hand, a schooling species could become less visible, as the number of fish in the school increased, and the individual fish thus became less available to the predator. This would lead to $\gamma<1$. Both these factors would be expected to vary from species to species such that γ_i is not equal to γ_j. As suggested by Kean-Howie et al. (1988), visibility may decrease with the abundance of a species as the predators search image is confused ($\gamma<1$). Prey behavior may also change with predation rate, such that a lower relative number of a species would make this species more visible to the predator (Abrams & Matsuda, 1993)(again, $\gamma<1$). Thus, if the visibility was the cause of switching, one would expect a different switching coefficient for different combinations of prey.

Prey preference

Prey preference can be split into two contributions: a size-preference, g, and a species preference, φ.

$$\alpha_{i,l(i)} = g_{l(i)} * \varphi_i$$

For a given predator species and length, where l(i)=length of i.

It is assumed, that size preference does not depend on prey species (Andersen & Ursin, 1977).

The relative preference of one prey species to another is likely to show a consistent pattern with predator length. The prey may be increasingly preferred with length, or may show a maximum preference at a certain predator length. Note, that only the prey species and not the prey size is considered here. As a simple approach, it was decided to model prey species preference as a 2nd degree polynomial of ln(predator length). This formula can fairly well describe the case, where preference for a species peaks at a particular predator length.

The dependence of species preference on predator length is thus modeled as

$$\ln\left(\frac{\varphi_{i,pr,l(pr)}}{\varphi_{j,pr,l(pr)}}\right) = \ln\left(\frac{\varphi_{0,i,pr}}{\varphi_{0,j,pr}}\right) + \lambda_{ij,pr} * \ln(l_{pr}) + \Gamma_{ij,pr} * (\ln(l_{pr}))^2$$

where $\frac{\varphi_{i,pr,l(pr)}}{\varphi_{j,pr,l(pr)}}$ = preference of the predator pr at length l_{pr} for prey of species i as compared to j, $\varphi_{0,i,pr}$ = the theoretical preference for i at predator length 0, $\lambda_{ij,pr}, \Gamma_{ij,pr}$ = factors describing the dependence of preference on length

Dependence of catchability on length of fish

Catchability appears to be a sigmoid function of fish length (Engås & Godø, 1989, Walsh, 1989), but as the lengths examined here are unlikely to be fully available to the trawl (at least not cod and haddock (Engås & Godø, 1989)), a potency function is thought to be a reasonable approximation for the range of lengths examined. Thus, catchability (*q*) of a fish of species i at length l to the trawl is modeled as

$$q_i = q_{0,i} * l_i^{r_i}$$

where q_{0i}, r_i = constants.

Effect of difference in digestion rates

It is assumed, that it is possible to identify a prey to length and species as long as the weight remaining of the prey is higher than some percentage, *p*, of weight of prey at ingestion, $w_{0,i}$. Thus, the weight of i after d time units, w(d), is

$$w_i(d_i) = p_i * w_{0,i}$$

The time elapsed before this percentage has been reached is described by Jones (1974) as

$$(w_i(d_i))^B = w_{0,i}^B - \frac{Q_i * \Lambda * d_i}{175 * l_{pr}^{-1.4}}$$

where B, Λ = constants, Q_i = rate of elimination of species i in the stomach of the predator, l_{pr} = length of predator (in cm), d_i = number of days prey i can be allocated to species

Dependence of switching on length of predator

The assumptions of the suitability model, namely, that the switching coefficient varies only with predator species and length and not with prey, are assumed to be fulfilled and are thus not tested. The dependency of the observed switching coefficient, *b*, on predator length is modeled as

$$b_{pr,l(pr)} = t_{pr} * \ln(l_{pr}) + b_{0,pr}$$

where $b_{0,pr}$ = The theoretical switching coefficient of a predator of length 1,

t_{pr} = Factor describing dependence of switching on length

It was also necessary to model the dependency of the part of b caused by the predator exhibiting switching at encounter, β, on predator length:

$$\beta_{pr,l(pr)} = \kappa_{pr} * \ln(l_{pr}) + \beta_{0,pr}$$

where $\beta_{0,pr}$ = theoretical β of a predator of length 1, κ_{pr} = factor describing dependency of β on length

Visibility

Modeling visibility is less straight forward, as this factor includes several rather subtle variables. Visibility is likely to be dependent on length of both prey and predator. The prey may change from schooling to solitary behavior or the other way around as it grows. It may also change its spatial distribution, both on local and North Sea scale. The same may be said for the predators, so the dependencies on the lengths are difficult to assess. As an approximation, visibility was assumed to rise or fall with lengths, not allowing for peak visibility at intermediate lengths. The expression included for visibility was thus

$$\ln\left(v_{i,l(i),pr,l(pr)}\right) = V_{0,i,pr} + v_{1,i,pr}\ln\left(l_{pr}\right) + v_{2,i,pr}\ln\left(l_i\right)$$

where V_0, v_1, v_2 = visibility - constants (within indices)

Model including dependence on ln(lengths) of predator and prey as polynomial

Together these assumptions give the model of ratios

$$\ln\left(\frac{F_{i,l_i}}{F_j}\right) = C_{ij,pr} + E_{ij,pr} * \ln(l_{pr}) + G_{ij,pr} * \left(\ln\left(l_{pr}\right)\right)^2 + H_{i,pr} * \ln\left(l_i\right)$$

$$+ o_{ipr}\left(\ln\left(l_i\right)\right)^2 + M_{i,pr}\ln\left(l_{pr}\right)\ln\left(l_i\right) + t_{pr} * \ln\left(l_{pr}\right) * \ln\left(\frac{T_{i,l_i}}{T_j}\right) + b_{0,pr}\ln\left(\frac{T_{i,l_i}}{T_j}\right)$$

The different factors include several components:

$$C_{ij,pr} = \ln\left(\frac{\varphi_{0,i,pr}}{\varphi_{0,j,pr}}\right) + \frac{\left(\ln(w_j)\right)^2 - \left(\ln(c_i)\right)^2 + 2\left(\ln(c_i) - \ln(w_j)\right)\left(\ln(c_{pr}) - \eta_{pr}\right)}{2\sigma_{pr}^2} + \beta_{0,pr} V_{0,ij,pr}$$

$$+ \ln\left(\frac{1 - p_i^B}{1 - p_j^B}\right) + B\left(\ln(c_i) - \ln(w_i)\right) - \ln\left(\frac{Q_i}{Q_j}\right) + b_{0,pr} \ln\left(q_{0,ij}\right)$$

$$E_{ij,pr} = \lambda_{ij,pr} + \frac{f_{pr}\left(\ln(c_i) - \ln(w_j)\right)}{\sigma_{pr}^2} + \kappa_{pr} V_{0,ij,pr} + t_{pr} \ln q_{0,ij} + \beta_{0,pr} v_{1,ij,pr}$$

$$G_{ij,pr} = \Gamma_{ij,pr} + \kappa_{pr} * v_{1,ij,pr}$$

$$H_{i,pr} = \frac{f_i\left(\ln(c_{pr}) - \ln(c_i) - \eta_{pr}\right)}{\sigma_{pr}^2} + \beta_{0,pr} v_{2,i,pr} + Bf_i + b_{0,pr} r_i$$

$$M_{i,pr} = \frac{f_i f_{pr}}{\sigma_{pr}^2} + \kappa_{pr} v_{2,i,pr} + t_{pr} r_i$$

$$o_{ipr} = -\frac{f_i^2}{2\sigma_{pr}^2}$$

Table 1

Species and length groups analyzed

All lengths in mm

Predator length groups

Species	lower length	upper length	lengthgroup
Cod	300	399	350
Cod	400	499	450
Cod	500	699	600
Cod	700	999	850
Whiting	200	299	250
Whiting	300	399	350

Prey length groups

lower length	upper length	lengthgroup
50	99	75
100	149	125
150	199	175
200	249	225
250	299	275
300	400	350

Prey lengthgroups included in analyses of ratios

Prey species	Lengthgroups
Cod	125, 175, 225, 275, 350
Haddock	125, 175, 225, 275, 350
Herring	125, 175, 225, 275, 350
Norway pout	75, 125, 175
Sprat	75, 125
Whiting	75, 125, 175, 225, 275, 350

Reference species and lengths

Species	Lengthgroups
Norway pout	75, 125, 175
Sprat	75, 125
Whiting	75, 125, 175, 225, 275

Table 2

Summary of the models tested

Key:
Empty cell=factor not tested
c=factor tested as categorial
l=factor tested as linear
ll=factor tested as log-linear

Analysis	basic	number of stomachs	length as polynomial
Area in which stomachs and trawl catches were compared	4-square	4-square	4-square
Factors tested for effect on k			
prey species	c	c	c
predator species	c	c	c
prey length	c	c	ll
predator length	c	c	ll
n(stomachs)		l	
prey*prey length	c	c	ll*c
prey*predator	c	c	c
prey*predator length	c	c	ll*c
prey*n(stomachs)		l*c	
prey length*predator	c	c	ll*c
prey length*predator length	c	c	ll
prey length*n(stomachs)		l*c	
predator*predator length			ll*c
predator*n(stomachs)		l*c	
predator length*n(stomachs)		l*c	
prey*prey length*predator	c	c	ll*c
prey*prey length*predator length	c	c	ll*ll*c
prey*prey length*n(stomachs)		l*c	
prey*predator*predator length			c*ll
prey*predator*n(stomachs)		l*c	
prey length*predator*predator length			ll*c*ll
prey length*predator*n(stomachs)		l*c	
prey length*predator length*n(stomachs)		l*c	
Factors tested for effect on b			
prey	c	c	
prey length	c	c	
predator	c	c	c
predator length	c	c	ll
n(stomachs)		l	
prey*prey length	c	c	
prey*predator	c	c	
prey*predator length	c	c	
prey*n(stomachs)		l*c	
prey length*predator	c	c	
prey length*predator length	c	c	
prey length*n(stomachs)		l*c	
predator*predator length			l*c*ll
predator*n(stomachs)		l*c	
predator length*n(stomachs)		l*c	

Table 2 continued

Summary of the models tested

Key:
Empty cell=factor not tested
c=factor tested as categorial
l=factor tested as linear
ll=factor tested as log-linear

Analysis	Roundfish areas	North Sea
Area in which stomachs and trawl catches were compared	Roundfish areas	North Sea
Factors tested for effect on k		
prey species	c	c
predator species	c	c
prey length	c	c
predator length	c	c
prey*prey length	c	c
prey*predator	c	c
prey*predator length	c	c
prey length*predator	c	c
prey length*predator length	c	c
prey*prey length*predator	c	c
prey*prey length*predator length	c	c
prey*predator*predatorlength	c	c
prey length*predator*predator length	c	c
Factors tested for effect on b		
prey	c	c
prey length	c	c
predator	c	c
predator length	c	c
prey*prey length	c	c
prey*predator	c	c
prey*predator length	c	c
prey length*predator	c	c
prey length*predator length	c	c

Table 3

Summary of fit of basic model of ratios

p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

Reference			Model				
species	length in mm	n(obs)	r^2	dimension	std	p	% dimension
Pout	75	610	0.526	42	4.42	0.639	0.0689
Pout	125	904	0.467	43	4.24	0.133	0.0476
Pout	175	341	0.461	28	3.63	0.854	0.0821
Sprat	75	381	0.438	43	6.48	0.637	0.1129
Sprat	125	320	0.398	7	7.09	0.490	0.0219
Whiting	75	184	0.689	60	3.98	0.657	0.3261
Whiting	125	529	0.372	37	4.63	0.936	0.0699
Whiting	175	461	0.303	10	5.53	0.716	0.0217
Whiting	225	434	0.348	25	5.31	0.716	0.0576
Whiting	275	281	0.364	24	5.41	0.103	0.0854

Slopes for analyses were no crossed effects with slope were found significant
up95=Upper 95% confidence limit
lo95=Lower 95% confidence limit

Reference					Probability of	
species	length in mm	slope	up95	lo95	slope=0	slope=1
Pout	175	0.220	0.287	0.153	<0.0001	<0.0001
Sprat	125	0.198	0.259	0.138	<0.0001	<0.0001
Whiting	125	0.204	0.245	0.163	<0.0001	<0.0001
Whiting	175	0.218	0.263	0.173	<0.0001	<0.0001
Whiting	225	0.142	0.207	0.077	<0.0001	<0.0001
Whiting	275	0.167	0.247	0.087	<0.0001	<0.0001

Table 4

Summary of fit of basic model of ratios

Proportion of total variance explained (r^2) by each significant factor

Empty cells denotes factors not having a significant effect

Reference species length in mm Factor	Pout 75	Pout 125	Pout 175	Sprat 75	Sprat 125	Whiting 75	Whiting 125	Whiting 175	Whiting 225	Whiting 275
ln(ibts)	0.2356	0.2058	0.2179	0.2429	0.1915	0.1241	0.1981	0.1926	0.1931	0.232
prey	0.0465	0.0525	0.0897	0.0363		0.1116	0.051		0.0579	0.0262
preylength	0.025	0.1046	0.0318	0.0164	0.1862	0.1302	0.0245	0.0877	0.0325	0.0159
predator	0.1234	0.0106	0		0.0203	0.0234	0.00003	0.00308		
predator length	0.0388	0.0122	0.0179	0.0477		0.0366	0.037	0.02	0.02	0.0219
ln(ibts)*prey	0.0162					0.00879				
ln(ibts)*prey length		0.01655		0.0114						
ln(ibts)*predator						0.00047				
ln(ibts)* predator length	0.00199	0.0221								
prey* prey length				0.0336		0.0162			0.0447	0.06823
prey*predator		0.0239	0.0273			0.0225				
prey*predator length	0.03896					0.1379	0.0494			
predator*prey length						0.00029	0.0121			
prey length*predator length		0.0185	0.07669	0.0494						
ln(ibts)*prey*predator						0.0495				
prey*prey length*predator						0.0275				

Table 5

Summary of fit of model of ratios including number of stomachs in the sample

p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

Reference			Model				
species	length in mm	n(obs)	r2	dimension	std	p	% dimension
Pout	75	610	0.468	48	1.062	0.608	0.079
Pout	125	904	0.409	49	1.055	0.221	0.054
Pout	175	341	0.374	19	0.956	0.235	0.056
Sprat	75	381	0.320	21	1.147	0.893	0.055
Sprat	125	320	0.389	19	1.212	0.036	0.059
Whiting	75	184	0.666	67	0.734	0.876	0.364
Whiting	125	529	0.303	23	0.998	0.765	0.043
Whiting	175	461	0.253	12	1.060	0.924	0.026
Whiting	225	434	0.272	16	1.026	0.267	0.037
Whiting	275	281	0.261	23	1.099	0.030	0.082

Slopes for analyses
*: Crossed effects between switching coefficient and prey, predator or their lengths exists
Switching coefficient=b+n(stomachs)*b_{stom}

Reference		Parameter values	
species	length in mm	b	b_{stom}
Pout	75	*	0.0072
Pout	125	*	0.00338
Pout	175	0.109	0.006
Sprat	75	0.1121	0.0033
Sprat	125	0.0512	0.00454
Whiting	75	*	0.00628
Whiting	125	0.1814	
Whiting	175	0.106	0.00313
Whiting	225	0.1489	
Whiting	275	0.1681	

Table 6

Summary of fit of model of ratios including number of stomachs as a factor

Proportion of total variance explained (r^2) by each significant factor

Empty cells denotes factors not having a significant effect

Reference species	Pout	Pout	Pout	Sprat	Sprat	Whiting	Whiting	Whiting	Whiting	Whiting
length in mm	75	125	175	75	125	75	125	175	225	275
Factor										
ln(ibts)	0.169	0.159	0.169	0.214	0.140	0.050	0.187	0.164	0.174	0.148
prey	0.033	0.031		0.032	0.132	0.079	0.045		0.023	0.035
preylength	0.022	0.078	0.069	0.011	0.019	0.124	0.023	0.045		0.013
predator	0.108		0.000		0.029	0.031	0.001	0.000		
predator length	0.028	0.022	0.014	0.023		0.022	0.009	0.020	0.011	
n(stomachs)	0.006	0.017	0.037	0.001	0.006	0.007	0.013	0.004	0.000	
ln(ibts)*prey						0.032				
ln(ibts)*prey length		0.015								
ln(ibts)*predator						0.001				
ln(ibts)* predator length	0.002					0.019				
ln(ibts)*n(stomachs)	0.013	0.011	0.015	0.007	0.027	0.052		0.020		
prey* prey length										0.065
prey*predator length	0.052	0.038				0.109				
prey*predator			0.010			0.030				
predator*prey length			0.030			0.006	0.011			
prey*n(stomachs)									0.047	
prey length* n(stomachs)	0.011	0.011			0.037					
predator* n(stomachs)		0.001								
predator length* n(stomachs)	0.024		0.039	0.033			0.016		0.016	
ln(ibts)*pred. length* n(stomachs)		0.025								
ln(ibts)*prey*predator						0.037				
ln(ibts)*prey*predator length						0.067				

Table 7

Summary of fit of model of ratios including effects of year, quarter and area

p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

Reference			Model				
species	length in mm	n(obs)	r2	dimension	std	p	% dimension
Pout	75	610	0.825	207	3.19	0.5322	0.339
Pout	125	904	0.754	261	3.34	0.0019	0.289
Pout	175	341	0.772	126	2.85	0.9668	0.370
Sprat	75	381	0.768	115	4.69	0.0001	0.302
Sprat	125	320	0.844	124	4.56	0.0001	0.388
Whiting	75	184	0.788	82	3.62	0.0050	0.446
Whiting	125	529	0.727	206	3.77	0.0226	0.389
Whiting	175	461	0.879	230	3.23	0.0001	0.499
Whiting	225	434	0.821	186	3.57	0.0359	0.429
Whiting	275	281	0.854	140	3.50	0.0183	0.498

Slopes for analyses were no crossed effects with slope were found significant
up95=Upper 95% confidence limit
lo95=Lower 95% confidence limit

Reference					Probability of	
species	length in mm	slope	up95	lo95	slope=0	slope=1
Whiting	75	0.182	0.278	0.086	<0.0004	<0.0001
Whiting	125	0.212	0.273	0.151	<0.0001	<0.0001
Whiting	175	0.169	0.261	0.077	<0.0004	<0.0001
Whiting	225	0.154	0.239	0.070	<0.0004	<0.0001
Whiting	275	0.142	0.265	0.018	<0.0252	<0.0001

Table 8

Summary of fit of model of ratios including effects of year, quarter and area

Proportion of total variance explained (r^2) by each factor

Empty cells denotes factors not having a significant effect

Reference species length in mm / Factor	Pout 75	Pout 125	Pout 175	Sprat 75	Sprat 125
ln(ibts)	0.2356	0.2058	0.2179	0.2425	0.1915
prey	0.0465	0.0525	0.0897		0.1647
preylength	0.025	0.1046	0.0318	0.0308	
predator	0.1234	0.0106	0		0.03703
predator length	0.0388	0.01217	0.0179	0.0477	0.0104
year	0.00073	0.0488	0.0455	0.0268	0.0643
quarter	0.0191	0.0049	0.0113	0.00713	
area	0.0795	0.0403	0.1182	0.2084	0.181
ln(ibts)*prey	0.0121				
ln(ibts)*prey length		0.0213		0.0336	
ln(ibts)* predator length	0.03896				
ln(ibts)*year	0.0134		0.0241		
ln(ibts)*area				0.0795	0.0555
prey* prey length					
prey*predator		0.0273			
prey*predator length					
prey*year			0.0471		
prey*quarter	0.0166		0.0348		
prey*area					0.0917
predator*prey length			0.0398		
predator length*prey length		0.0206			
prey length*year		0.0322			
prey length*quarter		0.0162			
predator*year	0.0198	0.0162			
predator*quarter					
predator*area	0.0436				
predator length*year	0.019	0.0194			0.04813
predator length*quarter			0.0164		
predator length*area	0.066	0.0637	0.0773	0.1251	
area*year	0.0348				
area*quarter	0.0311	0.0573			

Table 8 continued

Summary of fit of model of ratios including effects of year, quarter and area

Proportion of total variance explained (r^2) by each factor
Empty cells denotes factors not having a significant effect

Reference species length in mm / Factor	Whiting 75	Whiting 125	Whiting 175	Whiting 225	Whiting 275
ln(ibts)	0.1241	0.1981	0.1926	0.1931	0.232
prey	0.1116	0.051	0.0608	0.0579	0.0262
preylength	0.1302	0.0245	0.0426	0.0325	0.0159
predator	0.0234	0.00003	0.00352		
predator length	0.0366	0.037	0.0177	0.02	
year	0.00879	0.0105	0.1004	0.1105	0.0922
quarter		0.00924	0.00009	0.00326	
area	0.00047	0.1049	0.1728	0.156	0.2303
ln(ibts)*prey					
ln(ibts)*prey length					
ln(ibts)* predator length					
ln(ibts)*year					
ln(ibts)*area					
prey* prey length			0.0193	0.0258	0.0389
prey*predator					
prey*predator length	0.1388	0.0518	0.0171		
prey*year		0.0347	0.0396		
prey*quarter					
prey*area			0.1311	0.1235	0.1464
predator*prey length					
predator length*prey length				0.022	
prey length*year	0.0643		0.039	0.0634	0.0726
prey length*quarter					
predator*year					
predator*quarter		0.00586			
predator*area			0.00859		
predator length*year		0.0531	0.0295	0.0126	
predator length*quarter			0.00429		
predator length*area		0.1083			
area*year					
area*quarter		0.0378			

Table 9

Summary of fit of model of ratios including dependence on lengths as polynomial

p=Probability of normal distribution of residuals

% dimension= Model dimension in percent of the full model

Reference			Model				
species	length in mm	n(obs)	r2	dimension	std	p	% dimension
Pout	75	610	0.4885	21	4.512	0.650	0.034
Pout	125	904	0.437	20	4.301	0.152	0.022
Pout	175	341	0.4039	11	3.717	0.472	0.032
Sprat	75	381	0.3268	11	6.776	0.385	0.029
Sprat	125	320	0.4605	18	6.831	0.068	0.056
Whiting	75	184	0.5845	31	4.137	0.558	0.168
Whiting	125	529	0.3377	21	4.682	0.852	0.040
Whiting	175	461	0.2904	5	5.549	0.813	0.011
Whiting	225	434	0.2984	9	5.402	0.847	0.021
Whiting	275	281	0.2693	3	5.578	0.008	0.011

Slopes for analyses were no crossed effects with slope were found significant

up95=Upper 95% confidence limit

lo95=Lower 95% confidence limit

Reference					Probability of	
species	length in mm	slope	up95	lo95	slope=0	slope=1
Pout	75	0.3418	0.3808432	0.3027568	<0.0001	<0.0001
Pout	175	0.2146	0.2803188	0.1488812	<0.0001	<0.0001
Sprat	75	0.2226	0.2768724	0.1683276	<0.0001	<0.0001
Whiting	125	0.2025	0.2421704	0.1628296	<0.0001	<0.0001
Whiting	175	0.2251	0.2698272	0.1803728	<0.0001	<0.0001
Whiting	225	0.1528	0.213266	0.092334	<0.0001	<0.0001
Whiting	275	0.2171	0.2761156	0.1580844	<0.0001	<0.0001

Table 10

Summary of fit of model of ratios including dependence on lengths as polynomial

Proportion of total variance explained (r^2) by each significant factor

Empty cells denotes factors not having a significant effect

Reference species	Pout	Pout	Pout	Sprat	Sprat	Whiting	Whiting	Whiting	Whiting	Whiting
length in mm	75	125	175	75	125	75	125	175	225	275
Factor										
ln(ibts)	0.2356	0.2058	0.2179	0.2429	0.1915	0.1242	0.1981	0.1926	0.1931	0.2320
prey	0.0465	0.0525	0.0897	0.0363	0.1647	0.1116	0.0510		0.0579	
predator	0.1314	0.0343	0.0007	0.0057	0.0370	0.0067	0.0009	0.0003		
ln(prey length)	0.0073	0.0534	0.0230	0.0105	0.0143	0.1268	0.0146		0.0160	
ln(prey length)^2			0.0047					0.0757	0.0114	0.0219
ln(predator length)	0.0290	0.0076	0.0060	0.0060	0.0002	0.0422	0.0215	0.0099		0.0154
ln(predator length)^2	0.0005	0.0126		0.0029	0.0027	0.0029	0.0106	0.0119	0.0200	
ln(ibts)*predator		0.0125				0.0018				
ln(ibts)* ln(predator length)					0.0154	0.0005				
prey*ln(predator length)	0.0066					0.0365	0.0095			
predator*ln(predator length)		0.0001		0.0225		0.0019	0.0055			
prey*ln(predator length)^2	0.0275	0.0390			0.0185	0.0256	0.0260			
predator*ln(predator length)^2		0.0000			0.0084	0.0000	0.0000			
predator*ln(prey length)	0.0041	0.0110	0.0619		0.0079					
prey*predator						0.0305				
ln(ibts)*predator*ln(predator length)		0.0083								
prey*predator*ln(predator length)^2						0.0735				

Table 11

Summary of fit of model of ratios build on roundfish areas

p=Probability of normal distribution of residuals

% dimension= Model dimension in percent of the full model

Reference			Model				
species	length in mm	n(obs)	r2	dimension	std	p	% dimension
Pout	75	603	0.617	21	14.53	0.0001	0.035
Pout	125	841	0.650	59	11.71	0.9812	0.070
Pout	175	477	0.690	51	11.46	0.8098	0.107
Sprat	75	477	0.601	57	15.87	0.3592	0.119
Sprat	125	441	0.654	52	12.53	0.9037	0.118
Whiting	75	329	0.618	51	11.92	0.9004	0.155
Whiting	125	754	0.617	72	11.53	0.9665	0.095
Whiting	175	679	0.560	68	10.85	0.1246	0.100
Whiting	225	558	0.584	61	10.23	0.4050	0.109
Whiting	275	427	0.474	28	11.43	0.4538	0.066

Table 12

Summary of fit of model of ratios build on roundfish areas

Proportion of total variance explained (r^2) by each significant factor

Empty cells denotes factors not having a significant effect

Reference species	Pout	Pout	Pout	Sprat	Sprat	Whiting	Whiting	Whiting	Whiting	Whiting
length in mm	75	125	175	75	125	75	125	175	225	275
Factor										
ln(ibts)	0.3829	0.3229	0.1917	0.2658	0.2189	0.1466	0.2574	0.1954	0.3184	0.2322
prey	0.03802	0.07292	0.2938	0.0839	0.2355	0.0876	0.105	0.132	0.06	0.0441
preylength	0.02313	0.1635	0.0848	0.0318	0.0473	0.1275	0.0815	0.0542	0.0434	0.043
predator	0.1294	0.00163	0.00292	0.0941		0.06337	0.0058	0.0091		
predator length	0.02613	0.0235	0.0341	0.0194	0.0234	0.0329	0.0114	0.0382	0.0539	0.0783
ln(ibts)*prey				0.00818				0.02446	0.0267	
ln(ibts)*prey length		0.00393	0.00967			0.0205	0.0203	0.0107		0.0264
ln(ibts)*predator				0.00597	0.0194					
ln(ibts)* predator length				0.00374	0.0139	0.0199				
prey* prey length		0.00782	0.01207					0.0331	0.0274	
prey*predator	0.01696	0.02393	0.02448			0.0427				
prey*predator length				0.0485	0.0601	0.0513	0.0375	0.0384	0.0195	
predator*prey length		0.00815				0.0257	0.0447			
prey length*predator length		0.01571	0.0368	0.0399	0.0355			0.024	0.015	
ln(ibts)*predator*predator length							0.0537			
prey*prey length*predator		0.00587								
ln(ibts)*prey*predator length									0.0202	0.0503

Table 13

Summary of fit of model of ratios build on North Sea scale

p=Probability of normal distribution of residuals

% dimension= Model dimension in percent of the full model

Reference			Model				
species	length in mm	n(obs)	r2	dimension	std	p	% dimension
Pout	75	501	0.704	35	27.20	0.343	0.070
Pout	125	607	0.686	63	22.43	0.649	0.104
Pout	175	521	0.644	41	25.65	0.231	0.079
Sprat	75	517	0.709	60	25.37	0.098	0.116
Sprat	125	539	0.583	39	29.30	0.002	0.072
Whiting	75	457	0.671	33	26.07	0.293	0.072
Whiting	125	599	0.664	81	25.87	0.997	0.135
Whiting	175	522	0.796	93	19.34	0.908	0.178
Whiting	225	360	0.572	37	19.91	0.350	0.103
Whiting	275	300	0.494	12	20.79	0.697	0.040

Table 14

Summary of fit of model of ratios build on North Sea scale

Proportion of total variance explained (r^2) by each significant factor

Empty cells denotes factors not having a significant effect

Reference species length in mm Factor	Pout 75	Pout 125	Pout 175	Sprat 75	Sprat 125	Whiting 75	Whiting 125	Whiting 175	Whiting 225	Whiting 275
ln(ibts)	0.2594	0.126	0.1223	0.1068	0.1638	0.1812	0.1741	0.1297	0.265	0.356
prey	0.0432	0.171	0.3042	0.0953	0.1809	0.1211	0.2076	0.2379	0.0651	0.0421
preylength	0.0797	0.1558	0.0729	0.0846	0.0879	0.1086	0.1177	0.1193	0.0888	0.0599
predator	0.1818	0.00049	0.00628	0.2434	0.0253	0.0369	0.00418	0.0831		
predator length	0.067	0.0456	0.0237	0.0659	0.1037	0.1037	0.00932	0.0809	0.076	0.0359
ln(ibts)*prey		0.00743	0.013				0.0037	0.00215		
ln(ibts)*prey length		0.0231		0.0119			0.0034	0.00296		
ln(ibts)*predator			0.00473	0.0157				0.00392		
ln(ibts)* predator length		0.00504		0.0061	0.0119	0.0541	0.0047		0.0192	
prey* prey length		0.0202					0.0174	0.0232	0.0306	
prey*predator	0.0304		0.0469		0.0419		0.0452	0.0297		
prey*predator length				0.04459				0.0212		
predator length*prey length	0.0426	0.1033	0.0497	0.0351	0.0459	0.065	0.0503	0.028	0.0271	
ln(ibts)*prey*predator length		0.0277					0.0106			
prey*prey length*predator							0.0161	0.0238		
ln(ibts)*prey*predator length								0.00984		

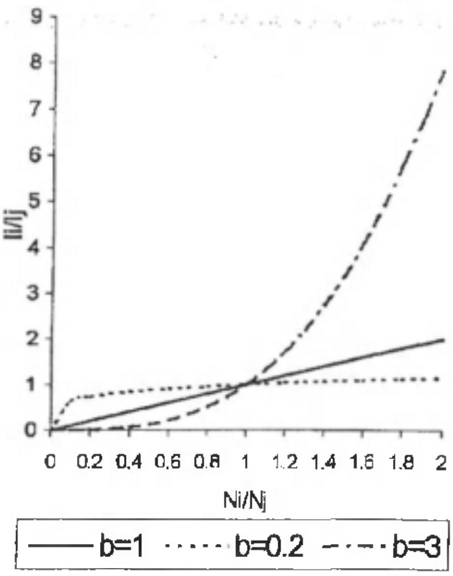

Fig. 1. Examples of ratio of one prey to another in the diet as a function og the corresponding ration in the surroundings. b=1 indicates no switching, b<1 indicates negative switching, b>1 indicates positive switching

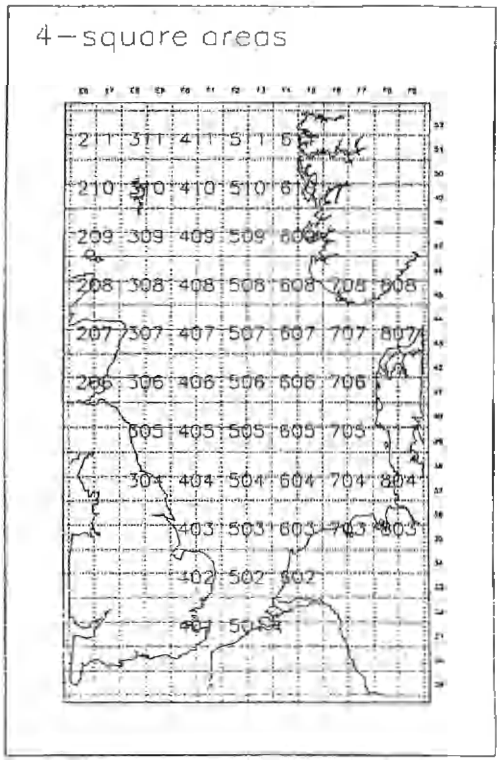

Fig. 2. 4-square areas in which trawl catches and stomach content were compared.

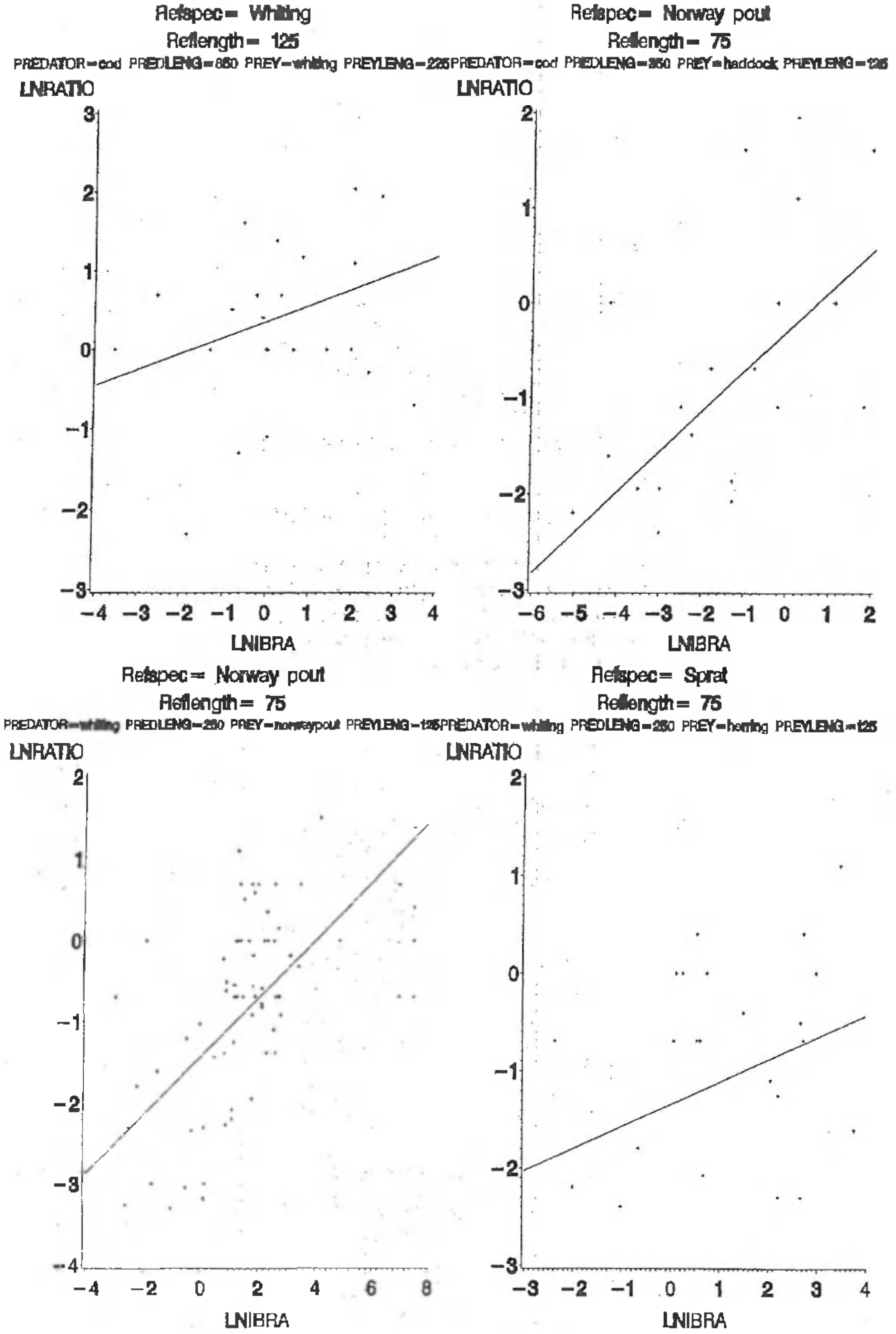

Fig. 3. Examples of ln(number of a particular prey in the stomach/number of reference in the stomach) as a function of ln(number of the particular prey in the trawl catch/number of the reference in the trawl catch). += Observations. Line= Predicted from basic model

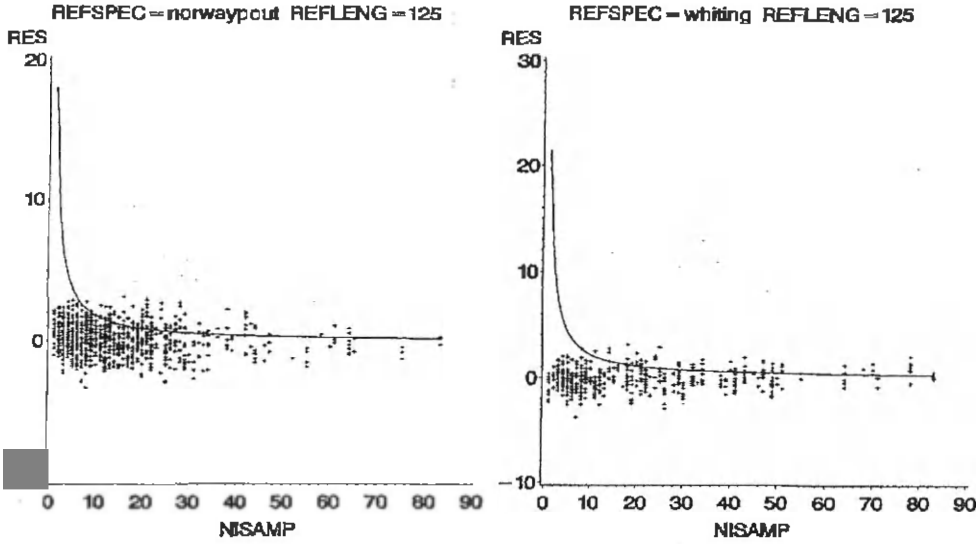

Fig. 4. Examples of residuals as a function of number of stomachs in the samlple. Line denotes σ^2/number of stomachs in the sample.

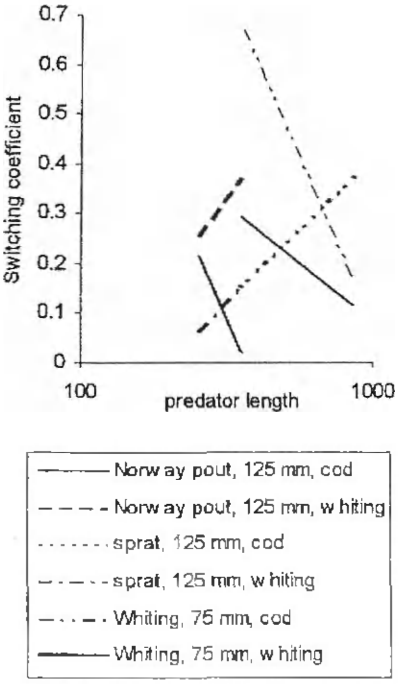

Fig. 5. Switching in the model describing dependence on length as polynomial. As a function of predator length for different references.

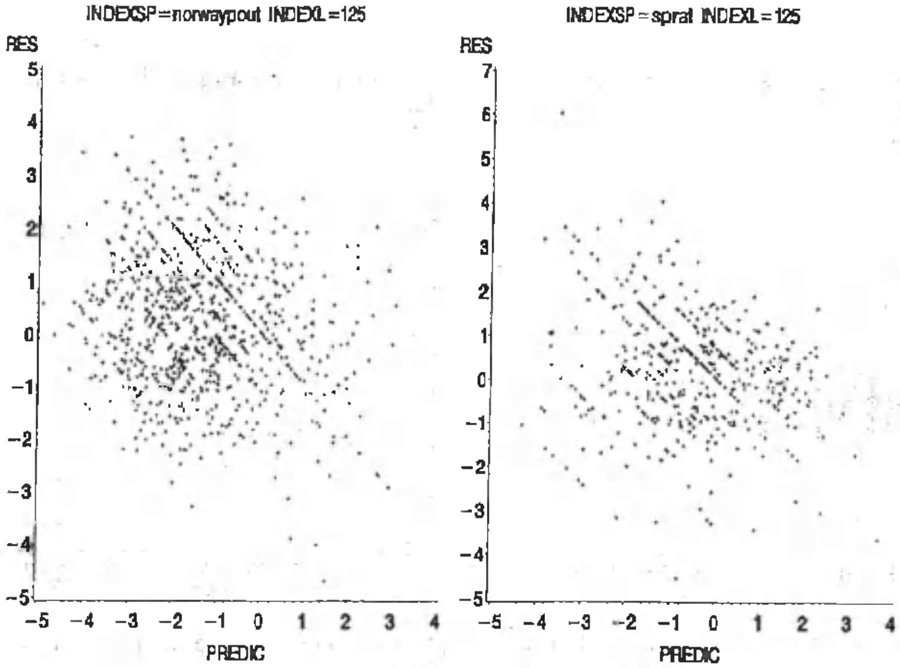

Fig. 6. Examples of plots of residuals as a function of predicted value of ln(stomach ratio) in the model built on roundfish areas.