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Prey switching and the implications for the use of predatory fish as bioindicators

Master thesis in biology

By

Anna Rindorf

Supervisor:
Professor Henrik Gislason
Copenhagen University

Investigations were carried out at
Danish Institute of Fisheries Research

Dept. of Marine Fisheries
Charlottenlund Slot
DK-2920 Charlottenlund

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1. Abstract

To investigate the dependence of diet composition of cod and whiting in the North Sea on relative prey density, several models were constructed. Prey abundance was estimated from survey catches. As trawl catches are highly variable, a model was built to estimate the mean catch. This model also corrected the catch for the significant effect of ship.

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. Several reasons for this are suggested, one of which is the effect of predator saturation. It was attempted to build a model incorporating this factor, but this model did not describe the data as well as the original model.

Using the estimated model of stomach composition, an index of sandeel was constructed. Two indices were calculated, one of which was based on the model developed to describe the composition of stomach content as a function of trawl catches. The predictions from this model showed a 63% correlation with abundance as estimated in the VPA. Predatory fish may thus give an indication of stock size of prey difficult to survey by conventional means.

2. 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 stability. Thus, 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 & Oaten, 1975).

Stability of the prey population can be influenced by several behavioral patterns of the predators. Thus, Murdoch and Oaten (1975) showed, 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 hass been examined by numerous authors (Chesson, 1984, Chesson, 1989, Kean-Howie et al., 1988, Manly et al., 1972, Murdoch et al., 1975, Murdoch & Marks, 1972, Murdoch & Oaten, 1975). Positive switching is generally found, when the pursuit of different prey requires different feeding modes or areas (Chesson, 1989, Murdoch et al., 1975). This has been explained as predators seeking to maximize their energy intake pr. time unit (Murdoch & Oaten, 1975). Another feature of positive switching appears to be, that preference is generally weak at equal prey densities (Murdoch & Oaten 1975). Positive switching may also be exhibited, where no apparent energy gain is related to this behavior. Thus, Manly et al. (1972) found positive switching in quail choosing between red and blue food items of identical energy value. Thus, learning or inherited behavioral patterns may also elicit this behavior.

Negative switching is less frequently observed, and the biological reasons for this behavior are less obvious. However, it has been recorded for fish predators foraging in an environment of depleteable prey densities (Kean-Howie et al., 1988, Reed, 1969, in Murdoch & Oaten, 1975). Murdoch and Oaten (1975) and Chesson (1984) hypothesized, that negative switching was found, when the mean preferences of samples consisting of several individually variable predators were examined. If some predators have specialized in one prey and others in other prey, a predator will still forage on this prey, though it may be less abundant than other prey. As the number of prey eaten by the species foraging on the most abundant prey is increased, the predators specializing in the least abundant prey will still eat only the prey in which they have specialized. In contrast to this, Abrams and

Matsuda (1993) suggest, that as a prey becomes more abundant, the relative predation-rate on this prey as compared to another prey changes. If prey actively seek to avoid the predator when predation-rate is high, rate will affect the relative encounter rates of the predator and the two prey. The model suggested predicts negative switching in this case. Yet another explanation is given by Kean-Howie et al. (1988). The authors observed sticklebacks feeding on fish larvae and small zooplankton. The sticklebacks exhibited negative switching, apparently because the large number of zooplankton confused the search image and caused the fish to eat less of the more abundant species. As the search image of the rarer prey is not confused, this prey becomes increasingly preferred as the density of the alternative prey rises.

The sensitivity of a prey species to predation pressure is particularly important, when trying to estimate a sustainable yield of the prey by commercial fisheries. Since maximum sustainable yield in a given area is greatly affected by recruitment to the fishery, a predator acting to increase variation in this factor enforces serious effects.

As most investigations in this area are carried out in the laboratory or in smaller confined areas of natural ecosystems, it is difficult to relate results in predator behavior from these experiments to a larger context. As an attempt to analyze predator behavior in the North Sea, switching has been tested as part of the Multi Species Virtual Population Analyses by Larsen & Gislason (1992). The authors found a tendency to negative switching, though this did not significantly improve model fit. 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, positive switching in the population will tend to make the MSVPA predictions of maximum sustainable yield of a prey species too low, as predation mortality will decrease as population decrease. On the other hand, negative switching will mean, that the predictions of maximum sustainable yield are too high, as the decrease in population density will be followed by an increase in predation mortality. This is a serious problem, as the estimate of maximum sustainable yield will become too high, and overfishing and subsequent collapse of stocks may be the result of such advice.

This paper compares the stomach content of cod and whiting with the species and size composition of the fish prey in the catch the International Bottom Trawl Survey. Stomachs were gathered in the North Sea during the stomach sampling projects carried out under the coordination of the International Council for Exploration of the Sea in the years 1981, 1985, 1986, 1987 and 1991.

To obtain unbiased estimates of trawl catch, a model was build to describe the 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 cod and whiting.

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 lengths and spatial scale on switching and suitability as defined in the suitability model presented by Larsen & Gislason (1992). Preliminary investigations indicated that predator saturation may produce artificially low switching coefficients, and to account for this, a model was built attempting to take the limited stomach size of the predator.

As sandeel are eaten in large amounts by predatory fish such as cod, haddock and whiting in the North Sea (Hislop et al., 1991, Kikkert, 1993), it is attempted to build an index for sandeel using the stomachs sampled during the ICES stomach sampling projects. The need for a such an index arises, as sandeel, though caught in vast amounts by commercial ships, is nevertheless rarely seen during trawl surveys (Gislason & Kirkegaard, 1996). The fishery on this species is the largest single-species fishery in the North Sea, with landings of around 1 million tonnes a year (Gislason & Kirkegaard, 1996). As sandeel is also an important food source for a variety of seabirds (Monaghan et al.,1989), the large landings have led to concern of the effect on the natural predators of of this species.

Numerous attempts have previously been made to use predator diet to construct indices of prey species. Investigations of piscivory birds include examination of foraging time (Miller & Davis, 1993), prey deliveries to chicks (Hislop & Haris, 1985), regurgiations (Cherel & Weimerskirch, 1995, Montevecchi et al., 1987, Montevecchi & Myers, 1995, Montevecchi & Myers, 1996) and number of chicks fledged (Monaghan et al., 1989). Regurgiations and otoliths from faeces of seals have been used to provide indices of prey species composition (Hammond et al.,1994, Klages, 1996), but investigations on this area have been less intensive than for seabirds.

Whereas nesting birds only forage in the vicinity of the colony km (Hamer et al., 1997, Honza, 1993), predatory fish are abundant in large areas. Thus, Lilly (1991, 1994) compared cod stomach content of capelin to acoustic surveys and found a high correlation.between a stomach fullness index for capelin and the index derived from acoustic surveys in the same area.

Pedatory fish may provide alternative indices of sandeel abundance. To validate the value of suchices, the model developed to describe the relative number eaten of each prey species and length waused to predict an index of sandeel abundance. This index wacompared to the abundance of sandeel estimated by Virtual Population Analyses. For comparison, an index of prey abundance in the stomachs introduced by

Lilly and Flemming (Lilly & Flemming, 1981, in Fahrig et al, 1993), was also calculated.

3. The suitability model

The suitability model is used in the MSVPA to describe the relative amount of a certain age group of a prey species eaten by a predator at a certain age as compared to another prey group.

3.1. Derivation of the model

The model is build on the assumption, that a predator having the choice of m different prey types occurring with the frequencies $n_1, n_2, n_3 \ldots n_m$ has the probability P_i of choosing a prey of type i (Larsen & Gislason, 1992) (Indices of predator species and age are omitted in the following for simplicity).

$$P_i = \frac{\alpha_i * n_i}{\sum_{k=1}^{m} \alpha_k * n_k}$$

where

α denotes the preference for prey i. $\alpha \in [0;1]$

P_i can be described as

This formula and others deductible from it have been suggested as a measure of selectivity by several authors (Chesson, 1978, Chesson, 1983, Ivlev, 1961 in Chesson, 1978, Manly et al., 1972). However, the disadvantage of the formula is the nonlinear dependence of P_i on n_i. Furthermore, the number of prey of all types present is often not known in field observations. This can be circumvented by examining the ratio of P_i to P_j rather than the absolute values of P.

The probability of eating prey i as compared to prey j is thus

$$\frac{P_i}{P_j} = \frac{\alpha_i * n_i}{\alpha_j * n_j} = \alpha_{ij} * \frac{n_i}{n_j}$$

where

$$\alpha_{ij} = \frac{\alpha_i}{\alpha_j}$$

Thus, if the total number of prey ingested is C, then

$$\frac{I_i}{I_j} = \frac{C * P_i}{C * P_j} = \frac{P_i}{P_j}$$

where

I_i = The number of species i ingested

3.2. Generalizing the model to population numbers and numbers eaten

To use the model on a North Sea scale, it is necessary to make some modifications, as the actual encounter rates are not known. What can however be estimated, are the population numbers and the number of prey eaten in selected years.

The relative encounter rate of the predator and prey *i* with respect to prey *j* is thus assumed to be a linear function of the relative abundance of the two species for a given predator species and length and prey species and length as suggested by Gerritsen and Strickler (1977):

$$\frac{n_i}{n_j} = \frac{v_i * N_i}{v_j * N_j} = v_{ij} * \frac{N_i}{N_j}$$

where

v_i = Visibility of i to the predator

N_i = Number of prey i present in the predators surroundings

The visibility of a certain prey can be thought of as a combination of the degree of spatial overlap between predator and prey and the vulnerability of the prey to the predator, where they are both present. The spatial overlap describes the extent to which, the prey and predator occurs at the same place at the same time. This can be influenced by the prey seeking refugees (areas where the predator is less abundant), or the predator and prey having different preferred depths or bottom types (Rose & Leggett, 1990, Bromley & Watson, 1994). The vulnerability is affected by several factors, e.g. the preys ability to hide and flee from predators, schooling behavior and others. Vulnerability could also be influenced by the predation rate on a prey as suggested by Abrams & Matsuda et al. (1993). This will give an indirect effect of alternative prey density on vulnerability, which is difficult to include in a model as comparatively simple as this.

The suitability used is thus a combination of the preference and the visibility:

$$\frac{I_i}{I_j} = \alpha_{ij} * v_{ij} * \frac{N_i}{N_j} = s_{ij} * \frac{N_i}{N_j}$$

where

s_{ij} = The suitabilit y of i as compared to j

3.3. Weight or number?

The model of suitability can be generalized to deal with weight of prey rather than number, which is convenient when estimating the diurnal ration of a predator (Daan, 1986, Larsen & Gislason, 1992). However, as trawl catches are given in number rather than weights, the ratio of one species to the other in the trawl by weight would have to be estimated from relationships between weight and length. Furthermore, the weight of the prey of a particular length caught in the trawl is not necessarily the same weight as the weight of ingestion of a prey of the same species and length. First, the predator may seek out fatter or slimmer fish, thereby increasing or decreasing the weight at length. Second, the trawl selection is likely to work to catch larger fish in a length interval more frequently than smaller ones, thereby overestimating the weight at length in the population if calculating the relationship from trawl catches. Building the model on numbers rather than weights eliminates this problem.

3.4. Incorporating switching in the model

In the MSVPA, the suitability of prey of one species and age as compared to prey of another species and/or age as calculated for each predator species and age over the whole North Sea is assumed to be constant. It is thus not allowed to vary from year to year or with the abundance of the prey. If the suitability varies with the prey abundance, the predator exhibits switching behavior.

This behavior can be incorporated in the model by making suitability a function of prey abundance as suggested by Larsen & Gislason (1992):

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

χ

$$\frac{I_i}{I_j} = s_{0,ij} * \left(\frac{N_i}{N_j} \right)^{b}$$

where

$s_{0,ij}$ = The suitability of i compared to j at equal densities of i and j

b = Switching coefficient. $b > 0$

for a given predator species and age group.

As this formula must hold for all combinations of prey, b cannot vary within predator species and size.

A switching coefficient<1 indicates negative switching, the predator striving to maintain its diet composition irrespective of the relative abundance of the prey. The lower the coefficient, the greater the ability of the predator to compensate for the changing prey abundance. A coefficient greater than 1 indicates positive switching, meaning that a certain prey density will cause the predator to switch its preferences from one prey to the other (Murdoch & Oaten, 1975). Above or below this relative prey density, the diet will consist more than proportionately of the most abundant prey. Again, the distance of the coefficient from 1 indicates the power of the switching behavior. In fig. 3.4.1 is shown examples of positive, negative and no switching.

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:

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

$$\Downarrow$$

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

if $\gamma_i = \gamma_j = \gamma$ then

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

where

β = Actual switching coefficient

γ = Visibility - potency

$\alpha_{0,ij}$ = Preference at equal densities

$v_{0,ij}$ = Relative visibility at equal densities

b-1 = $\beta * \gamma$

If the fish are randomly distributed, the encounter-rate and 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 $\gamma<1$. However, 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 the switching suitability, one would expect a different switching coefficient for different combinations of prey, except if the cause is confusion of the predators search image, in which case the effect should be of approximately same size for all prey.

3.5. The suitability model in relation to foraging theory

Most of the work done on foraging theory aims to find a set of "universal factors" that determine the preference of a predator for a given prey. Thus, it is appealing to assume, that there are rules determining the preference. Several theories exists, the most important ones being represented by the optimal foraging theory (Stephens and Krebs, 1986) and apparent size theory (Li et al., 1985, O'Brien et al., 1976). A group of theories more recently developed are the state dependent models (Hart & Gill, 1993, Mangel, 1992) in which the preferences are dependent on the internal state (hunger-level) of the predator.

3.5.1. Optimal foraging theory

Optimal foraging theory predicts, that the predator should always make the choice of prey, that maximizes its long-term fitness. Long term fitness is usually measured as energy intake pr. time unit. The simplest version of this theory predicts, that a predator should attack the most profitable (highest (energy content)/(handling time of prey)) at every encounter.

Ranking prey by profitability, only the most profitable prey should always be included in the diet. Only when not enough of the most profitable prey is present to saturate the predator should the less profitable prey be included.

Numerous investigations and experiments have been carried out to test the validity of this model (Bannon & Ringler, 1986, Eggers, 1977, Griffiths, 1975, Kaiser & Hughes, 1993, Werner & Hall, 1974). Good results are found when examining predators choosing between two prey presented at the same time (Werner & Hall, 1974). However, this is against model assumptions as prey encounter should be sequential and not simultaneous. When examining sequential encounters, the model fits the data less well (Hart & Ison, 1991).

As the preference is predicted to be equal for all prey included in the diet and zero for all others, the model of suitability should describe the stomach content of the two most profitable prey quite accurately. However, if examining two less profitable prey types, the ratio between these would to a large extent depend on, if more profitable prey is present and thus show little correlation between stock sizes and stomach contents. Thus, if the predators were only just getting enough food, they would eat all prey at encounter, and no selection would take place. The ratio in the stomachs would thus be proportional to the ratio in the surrounding waters. If the predators are not as hungry, the fit of the model will be better for some species (the more profitable ones)

than others. Furthermore, the estimated preference will vary with year and area as the amount of available food varies.

3.5.2. The apparent size model

Another model receiving much attention from the late 70's to the late 80's is the apparent size model. This model seeks to describe prey choice as a function of the predators ability to see the prey. Thus, the encounter-rate of the prey and predator depends on the visual capabilities of the predator and apparent size of the prey. A small prey close to the predator may appear larger, than a large prey at a greater distance. The model deals only with size selection, and selection between different species of similar size and shape is thus not accounted for. O'Brien et al. (1976) and Li et al. (1985) showed good correlation between model predictions and observed selection. However, Butler & Bence (1984) proved their assumptions to be wrong, and showed that the model in fact gave predictions significantly different from the observations. As light intensity and thereby visual capability varies with time of year, preference should vary with quarter, but less so with year and area.

3.5.3. State dependent models

The last category of models are the state dependent models. These models predict prey preference from optimal foraging combined with the saturation level of the predator. Thus, a saturated predator will be more particular in its prey choice than a hungry predator. Hart & Gill (1993) found a good fit of a state dependent model, describing data which the optimal foraging model failed to describe. However, as the preference is dependent on the saturation level of the predator, it is necessary to know the sequence in which the prey was ingested to estimate the preference. This is not possible when examining field observations, and so, the model is difficult to validate in these cases.

The suitability model used in the MSVPA assumes the relative preference of one prey to another to be constant from year to year, and so is inconsistent with optimal foraging theory. As relative preferences are not allowed to vary with light-intensity, the suitability model is also inconsistent with the apparent size model.

3.6. Adjusting the model to describe the correlation between stomach content and trawl catches

The suitability in the MSVPA is a North Sea average, though the predator is most unlikely to ever encounter prey in the relative frequencies calculated for the whole North Sea. This may introduce additional variation in the calculation of the suitability. In this project, 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 International Bottom Trawl Survey in that area. Furthermore, the predator is not likely to distinguish between fish prey at different ages but rather prey at different lengths. Thus, the model was build grouping prey by species and length instead of species and age as in the MSVPA. This has the advantage of making it unnecessary to estimate the age of the prey. As weight at length, age at length inferred from trawl catches may be biased, and in any event, there is great variation in aging of fish (Torstensen, 1994).

The relative number of one species caught in the trawl as compared to another species is not necessarily equal to the relative abundance's actually present in the water volume trawled (Engås & Godø, 1989, Ona & Chruickshank, 1986, Walsh, 1989). Trawl selection thus acts differently upon different species and certainly act differently on different lengths of fish. Neither is the ratio observed in the food necessarily the ratio in which the prey was ingested, as some prey may be digested faster than other (Jones, 1974). It was thus necessary to make some slight changes to the suitability model to allow for differences in catchability of fish to the trawl and digestibility of the prey caught by the predator.

The trawl catches are assumed to depend on the actual abundance of a species in that area (Cook, 1997):

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

where

$T_{i,l}$ = Trawl catch of species i at length l

$q_{i,l}$ = Catchability of i at length l. $q \in [0;1]$

$N_{i,l}$ = Number present in the volume trawled of i at length l

As a prey is counted as one prey at any time between ingestion and the time at which digestion renders prey unrecognizable, the average number ingested pr. day can then be calculated as

$$\overline{I_i} = \frac{F_i}{d_i}$$

where

i = Prey type

$\overline{I_i}$ = Mean number of prey i ingested in a day

F = Number of prey i recorded in the stomach content

d = Number of days a prey can be assigned to prey type i after being ingested

If this expression is transferred to lengths of prey rather than ages, the number of prey i at length l found in the stomach, F, is

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

where

F = Number of i at length recorded in the stomach

d = Number of days i at length l can be identified as belonging to that group

Combining these two models with the original suitability model, the expression becomes

$$\frac{F_i}{F_j} = s_{ij} * \frac{d_i}{d_j} * \left(\frac{q_i * T_i}{q_j * T_j}\right)^b = s_{ij} * \frac{d_i}{d_j} * \left(\frac{q_i}{q_j}\right)^b * \left(\frac{T_i}{T_j}\right)^b$$

for a given predator species and length (Indices of predator length and species omitted for simplicity).

Assuming s, d and q to be constant within prey species and length, the expression can be simplified to

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

where

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

Taking the natural logarithm of this expression gives

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

which is the model analyzed in this project.

3.7. Comparing suitabilities

As c does not measure suitability, but rather a combination of this and other factors, differences between c's can not be expected to automatically describe differences in suitabilities. However, special cases do exist, where the difference in c's can be interpreted in a meaningful way.

Comparing c_{ij} between predator species and/or size group given i and j are the same

gives

$$\frac{c_{p,ij}}{c_{o,ij}} = \frac{s_{p,ij} * \frac{d_{p,i}}{d_{p,j}} * \left(\frac{q_i}{q_j}\right)^b}{s_{o,ij} * \frac{d_{o,i}}{d_{o,j}} * \left(\frac{q_i}{q_j}\right)^b} = \frac{s_{p,ij}}{s_{o,ij}} * \frac{d_{p,i}/d_{p,j}}{d_{o,i}/d_{o,j}}$$

where

p, o = Predator species and size groups

It does not seem unreasonable, that the digestion rate should in- or decrease with predator length in a similar way for all prey in the stomach, and thus, the ratio between the number of days one prey remains recognizable to the number of days for another prey remain fairly constant within predator species. This reduces the expression to

$$\frac{c_{p,ij}}{c_{o,ij}} \cong \frac{s_{p,ij}}{s_{o,ij}}$$

where

p, o = Predator size groups within predator species

Thus, the suitability of a given prey as compared to another for one predator length as compared to another can be read directly from the analyses as the ratio between exp(intercept) of one predator length to another.

4. Statistical analyses

Statistical analyses are a necessary and valuable tool when building models for fish predation. The following chapter gives a brief overview of the methods used in this project.

4.1. General linear models

General linear models are models describing linear relationships between normal distributed observations and selected factors.

4.1.1. Formulating the model

Observe the stochastical variable y, belonging to a normal distribution with mean μ and variance σ^2:

$$y \in N(\mu, \sigma^2)$$

Generalizing to n observations, y becomes the n-dimensional vector

$$\underline{y} \in N(\underline{\mu}, \sigma^2 \underline{\underline{\Sigma}})$$

where $\underline{\underline{\Sigma}}$ is a matrix describing the variance and covariance of the observations. If the observations are independent and have the same variance σ^2, $\underline{\underline{\Sigma}}$ equals the unit-matrix $\underline{\underline{I}}$.

Now let μ be a linear function of a number of covariates, $\underline{x}$:

$$\mu = \underline{x\theta}$$

where

$\underline{\theta}$ = Parameter vector

Generalizing to n observations,

$$\underline{\mu} = \underline{\underline{x}}\,\underline{\theta}$$

that is, if $\underline{\underline{x}}$ has rank 3, then

$$\underline{\mu} = \theta_1 * \underline{x}_1 + \theta_2 * \underline{x}_2 + \theta_3 * \underline{x}_3$$

4.1.2. Estimation of parameters

The maximum likelihood estimator for $\underline{\theta}$ is the vector that minimizes

$$\left\|\underline{y}-\underline{\underline{x}}\underline{\theta}\right\|^2=\left(\underline{y}-\underline{\underline{x}}\underline{\theta}\right)'\underline{\underline{\Sigma}}^{-1}\left(\underline{y}-\underline{\underline{x}}\underline{\theta}\right)$$

where ' denotes the transposed

(Conradsen, 1984)

If $\underline{\underline{\Sigma}}=\underline{\underline{I}}$

$$\left\|\underline{y}-\underline{\underline{x}}\underline{\theta}\right\|^2=\left(\underline{y}-\underline{\underline{x}}\underline{\theta}\right)'\left(\underline{y}-\underline{\underline{x}}\underline{\theta}\right)$$

that is, the sum of the squared distances between the predicted and observed values of y. This is equal to minimizing the orthogonal distance between the observations and the model. The solution minimizing the sum of squared distances is

$$\left(\underline{\underline{x}}'\underline{\underline{\Sigma}}^{-1}\underline{\underline{x}}\right)\underline{\theta}=\underline{\underline{x}}'\underline{\underline{\Sigma}}^{-1}\underline{y}$$

if $\underline{\underline{x}}$ has full rank, this transforms to

$$\underline{\theta}=\left(\underline{\underline{x}}'\underline{\underline{\Sigma}}^{-1}\underline{\underline{x}}\right)^{-1}\underline{\underline{x}}'\underline{\underline{\Sigma}}^{-1}\underline{y}$$

If $\underline{\underline{\Sigma}}=\underline{\underline{I}}$, then the estimate of $\underline{\theta}$ is

$$E(\hat{\underline{\theta}})=\left(\underline{\underline{x}}'\underline{\underline{x}}\right)^{-1}\underline{\underline{x}}'\underline{y}$$

The estimate has the dispersion matrix

$$D(\hat{\underline{\theta}})=\sigma^2\left(\underline{\underline{x}}'\underline{\underline{\Sigma}}^{-1}\underline{\underline{x}}\right)^{-1}$$

The dependence of the x-variables may be categorical or linear. If x is categorical with the values x_1, x_2 and x_3, and there is one observation for each value of x,

$$\underline{\underline{x}}=\left[\underline{x}_1\,\underline{x}_2\,\underline{x}_3\right]=\begin{bmatrix}1&0&0\\0&1&0\\0&0&1\end{bmatrix}$$

The procedure for estimation of parameters is as above. Thus both linear and categorical dependencies may appear in the same model, without this having any effect on estimation procedures.

The central estimate for the residual variance is

$$\hat{\sigma}^2 = \frac{1}{n - rg\underline{\underline{x}}}\left(\underline{y} - \underline{\underline{x}}\hat{\underline{\theta}}\right)'\underline{\underline{\Sigma}}^{-1}\left(\underline{y} - \underline{\underline{x}}\hat{\underline{\theta}}\right)$$

$\hat{\sigma}^2$ is independent of the mean and therefor independent of $\hat{\underline{\theta}}$. It is also true that

$$\hat{\sigma}^2 \in \sigma^2 \chi^2\left(n - rg\underline{\underline{x}}\right)/\left(n - rg\underline{\underline{x}}\right)$$

If $\underline{\underline{x}}$ does not have full rank, it is not possible to estimate all the parameters without introducing bonds between them. The x-matrices and the bond together make up a generalized inverse, which can be used to solve the equations. The procedure is exemplified in the following.

We wish to measure the effect of a factor, α, on $y \in N\left(\mu, \sigma^2\right)$, using the model

$y = \mu_0 + \alpha_i$
$i = 1,2$
In a matrix, this becomes

$$\begin{bmatrix} y_{11} \\ y_{12} \\ y_{21} \\ y_{22} \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 \\ 1 & 1 & 0 \\ 1 & 0 & 1 \\ 1 & 0 & 1 \end{bmatrix} \begin{bmatrix} \mu_0 \\ \alpha_1 \\ \alpha_2 \end{bmatrix} + \underline{\varepsilon}$$

where

$$\underline{\varepsilon} \in N\left(0, \sigma^2\right)$$

We observe that $\underline{\underline{x}}$ has the rank 2. A linear bond between the parameters is therefor introduced:

$$\alpha_1 + \alpha_2 = 0$$

The model then becomes

$$\begin{bmatrix} y_{11} \\ y_{12} \\ y_{21} \\ y_{22} \\ 0 \end{bmatrix} = \begin{bmatrix} 1 & 1 & 0 \\ 1 & 1 & 0 \\ 1 & 0 & 1 \\ 1 & 0 & 1 \\ 0 & 1 & 1 \end{bmatrix} \begin{bmatrix} \mu_0 \\ \alpha_1 \\ \alpha_2 \end{bmatrix} + \begin{bmatrix} \underline{\varepsilon} \\ 0 \end{bmatrix}$$

The solution can then be found by inverting this new x-matrix as above.

4.1.3. Testing for lower dimension of model

We wish to test if the model M gives a significantly better description of the observations than the model H, where M denotes a subspace of H. If M is true, the maximum likelihood estimator of μ is

$$p_M(\underline{y}) = \underline{\underline{x}}_M \hat{\underline{\theta}}_M$$

Similarly, if H is true,

$$p_H(\underline{y}) = \underline{\underline{x}}_H \hat{\underline{\theta}}_H$$

is the maximum likelihood estimator of μ. The ML estimators for σ^2 are in the two cases

$$\hat{\sigma}^2 = \frac{1}{n}\left\|\underline{y} - p_H(\underline{y})\right\|^2 \text{ and } \hat{\sigma}^2 = \frac{1}{n}\left\|\underline{y} - p_M(\underline{y})\right\|^2$$

The test size, C_α, is the loss in explanation ability of the model when going from H to M compared to the residual variance. If model H does not give a significantly better description of the data than model M, this test size follows an F distribution with *(k-r, n-k)* degrees of freedom. Rearranging and applying Pythagoras' sentence, the critical area becomes

$$C_\alpha = \{(y_1,\ldots,y_n) \mid \frac{\left\|p_M(\underline{y}) - p_H(\underline{y})\right\|^2 / (k-r)}{\left\|\underline{y} - p_M(\underline{y})\right\|^2 / (n-r)} > F(k-r, n-k)_{1-\alpha}\}$$

where

α= Significance level

k = Dimension of model H

r= Dimension of model M

n= Number of observations

4.1.4. Weighting of analyses

In the ordinary general linear model, the variance of all observations must be the same. If however, some of the observations are based on multiple measurements, these observations will show less variance. Intuitively, an observation based on two measurements should have less variance than an observation based on one measurement. Thus, the analyses should be able to allow more variation in the case with one measurement. This is done by assigning weights to the observations, and is equal to counting the observation with weight 2 as if it occurred twice. However, the degrees of freedom used when testing for reduction of the model are still the number of observations and not the sum of weights.

The parameter vector in the general linear model is then calculated as

$$E(\hat{\underline{\theta}}) = \left(\underline{\underline{x}}' \underline{\underline{w}} \underline{\underline{x}}\right)^{-1} \underline{\underline{x}}' \underline{\underline{w}} \underline{y}$$

where

w = The diagonal matrix of weights

$\left(\underline{\underline{\Sigma}} = \underline{\underline{I}}\right)$

4.1.5. Checking model assumptions

In many cases, it is not possible to test the model assumptions of normal distributed observations with equal variances in advance, as this requires a minimum of 10 of observations in each cell.

As an alternative, the residuals, r, of the model can be examined, as these should be normal distributed with

$$r \in N(0,\sigma^2)$$

The distribution of the residuals can be tested for mean=0 and normal distribution. Furthermore, residuals should show no trend when plotted as a function of predicted value of the observations or as a function of any of the explaining variables. The word trend here also refers to increase or decrease in variation with the predicted values. This is a serious error, which can sometimes be circumvented by log-transformation of the data. If the residuals are not normal distributed, they should at least show a distribution, that resembles the normal distribution. This is important, as the general linear models are very sensitive to inhomogeneity of variances, but less so to deviations from the normal distribution (Conradsen, 1984, pp. 5.64-5.65).

4.2. Generalized linear models

Generalized linear models describe the dependence of observations belonging to a natural exponential distribution on categorical or linear variables or any combination of these.

4.2.1. The natural exponential family

The natural exponential family contains some of the most frequently used statistical distributions: binomial, Poisson, negative binomial, normal, gamma distributions and others. In this paper, only the binomial and normal distributions are used, and so only these will be treated further.

The deviance is the measure of error in the generalized linear model, just as the sum of squares is a measure of error in the normal distribution (Thyregod, 1998).

In the binomial distribution, the deviance is described by

$$d(y;\mu) = 2\left\{y\ln\left(\frac{y}{\mu}\right) + (1-y)\ln\left(\frac{1-y}{1-\mu}\right)\right\}$$

The deviance of the normal distribution is the sum of squares used in the general linear models:

$$d(y;\mu) = (y-\mu)^2$$

4.2.2. Formulating the model

The model may describe a categorical or linear dependence or any mixture of the two. If there are no linear dependencies and the distribution is normal, the analysis corresponds to the ANOVA. With only linear dependencies, it corresponds to linear regression.

A linear dependence does not necessarily mean, that

$$\mu = \alpha x + \beta$$

In some cases, the dependence is best described by

$$f(\mu) = \alpha x + \beta$$

$f(\mu)$ is called the link function and may be any function of μ as long as it does not involve unknown parameters. This is also convenient when the range of μ is limited, e.g. to positive values only. The deviance and

test for model reduction does not depend on the link function used. Also, if all the independent variables are categorical, the link has no effect. The logit=ln(p/(1-p)) can be a convenient link-function for observations that can assume values from 0 to 1. The logit link-function is used for both the binomial and normal generalized linear models in this project. In the binomial models, this is convenient, as it ensures, that all predicted probabilities are positive. As none of the factors are linear, it has no effect on tests.

The important difference between a generalized linear model with log link and a general linear model of log(y) is, that in the generalized model, y is normal distributed, whereas in the general model, log(y) is normal distributed. The two models are therefor not equal, but rather, the general linear model is a special case of the generalized linear model in which the link function is

$$f(\mu) = \mu$$

4.2.3. Estimation of parameters

The parameters in the generalized linear model are estimated by maximum likelihood methods. This is an iterative procedure, making the estimation computer time- and space-consuming. In short, the model must minimize the deviance.

In all the distributions in the natural exponential family apart from the normal distribution, the variance is given by the mean. However, there are cases, where the variance of the distribution is not sufficient to describe the variability of the observations. A dispersion-parameter can then be introduced to describe the difference between the observed variance and the variance of the distribution used. A family described by a natural exponential distribution and a dispersion parameter is called an exponential dispersion parameter family.

4.2.4. Residual deviance

The residual deviance is given by

$$D(y;\mu(\hat{\beta})) \overset{DEF}{=} \sum_{i=1}^{k} w_i d(y_i, \hat{\mu}_i)$$

where

$d(y;\hat{\mu}_i)$ = Deviance of the ith observation from the predicted value, μ_i

w_i = Weight of the ith observation

Another measure for the deviance of the ith observation is the Pearson residual given by

$$r_P(y_i;\hat{\mu}_i) \overset{DEF}{=} \frac{y_i - \mu_i}{\sqrt{V(\hat{\mu}_i)/w_i}}$$

Notation as above

Similarly, the scaled residual deviance is

$$D^*(y;\mu(\hat{\beta})) = \frac{D(y;\mu(\hat{\beta}))}{\sigma^2}$$

where

σ^2 = Dispersion parameter

4.2.5. Goodness of fit and estimation of the dispersion parameter

The goodness of fit can only be tested, if the dispersion parameter is known. In this case, and if the model gives an adequate description of the observations,

$$D^*(y;\mu(\hat{\beta})) \in \chi^2(k-m)$$

where

$(k-m)$ = The difference between the dimension of the full model and the dimension of the reduced model.

If the dispersion parameter is not known, it can be estimated by assuming, that the model provides an adequate description of the observations.

Using the pearson residuals, the estimate of the dispersion parameter becomes

$$\hat{\sigma}^2 = \frac{\sum_1^k r_P(y_i;\hat{\mu}_i)^2}{k-m}$$

Notation as above.

4.2.6. Test for reduction of model

The deviance can be analyzed in a similar way as the sum of squares in the general linear model. It can be split into contributions from the different effects in the model. If the dispersion parameter is known, the test size for the reduction of the model H_M to the model H_R is

$$G^2(H_M \mid H_R) = D^*(y;\hat{\mu}_M) - D^*(y;\hat{\mu}_R) = D^*(\hat{\mu}_R;\hat{\mu}_M)$$

If the model H_M does not provides a significantly better description of the observations than H_R, the test size is approximately χ^2-distributed:

$$G^2 \in \chi^2(m-r)$$

where

(m - r)= Dimension of H_M-dimension of H_R

If however, the dispersion parameter has to be estimated, the test size is

$$F_2(H_M \mid H_R) = \frac{D(\hat{\mu}_M;\hat{\mu}_R)/(m-r)}{D(y;\hat{\mu}_M)/(k-m)}$$

where

k = Dimension of the full model - 1 = Number of observation - 1

Other notation as above.

This test size is approximately F(*m-r, k-m*) distributed.

4.3. Type I, III and IV tests

In the SAS-software, the type I test gives the probability of the last parameter in the model line being equal to 0, given all other parameters coming before it in the model line have an effect (SAS Institute Inc., 1989a). The type III test gives the probability of each parameter being 0, given all other parameters in the model have an effect. Type III is thus independent of the order of the parameters in the model. Type IV is used for unbalanced data sets. It corresponds to type III, but takes the unbalance of the data set into account. In the balanced case, the type IV test equals the type III test. The types III and IV tests involves fitting several models, and in generalized linear modeling this requires both time and computer-space. In some cases, forward regression has therefore been used to estimate the models. When this is the case, it is noted in the methods-chapter.

4.4. Forward elimination

Forward elimination is carried out as shown in fig. 4.5.1 (Conradsen, 1984).

4.5. Significance level and software

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

5. Materials and methods

5.1. 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 (ICES, 1981a, ICES, 1996a).

5.1.1. Collection of IBTS-data

The IBTS is carried out each year in the 1st quarter, and since 1991 also in 2nd, 3rd and 4th quarter. The survey design is stratified-random, trawling at random positions within an ICES-square (50 km*50 km)(ICES, 1981b, ICES 1996a). The aim is to trawl at least twice in each square, but due to weather and other factors, this aim is not always attained. The number of hauls taken in each square in the years examined is seen in fig. 5.1.1.1. The number of ship participating in the survey in each year and quarter is seen in table 5.1.1.1. There is generally little overlap in time and space between ships, as around one third of the squares are only sampled by one ship at a given time (fig. 5.1.1.2). Gear, rigging and trawl-time is standardized (GOV-trawl, codend meshsize 10 mm, trawl time 30 min.) to minimize the difference in fishing power between ships (ICES, 1981a).

As much of the catch as permitted by time and weather is measured, sampling fish at random where the whole catch cannot be measured. The minimum number of fish sampled from each species is 50, except for herring, where the minimum sample size is 100. The length of the fish in the sample is measured to nearest cm below for the gadoid species and to nearest 0.5 cm below for sprat and herring. To minimize the number of parameters to be estimated in the following models, the fish were divided into 50 mm length groups from 0 mm to 300 mm. Fish between 300 mm and 400 mm were allocated to the same group, as there were few prey above 300 mm. Size groups are referred to by their midpoints.

5.1.2. Model for numbers caught in the IBTS

As an analysis cannot have several values of an independent variable for the same value of the dependent variable, it was necessary to obtain

one estimate of relative abundance within each area. It was not possible to examine the ratio of one prey to another within the hauls taken in the stomach sampling program, as haul number was not included in this data set. 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. This will gather all information at once and thereby predict the catches with the least possible variance. Thus, a model should give an estimate of trawl catches that has less variance than a simple average. Another advantage of a model is, that confidence limits of predictions can be calculated, though this is not done in this project.

It is often assumed, that number caught pr. haul in a square is lognormal distributed (ICES, 1981b). However this distribution cannot be used, where the number caught is zero. One way to circumvent this problem is to model the ln(number caught + 1). This is not entirely satisfactory, as the difference between catching zero and 1 is reduced from indefinite to ln(0.5). This may not be serious, if there are few hauls, where nothing is caught, but the higher the proportion of small catches, the greater the error. To obtain a sufficient number of observations (hauls) in each cell (a cell being all hauls taken by one ship in a given area, year and quarter), the squares were gathered in 4-square areas (fig. 5.1.2.1). This furthermore had the advantage of increasing the overlap between ships, reducing the number of areas only sampled by one ship at a given time to one fourth of all areas (fig. 5.1.2.2). The distribution of ln(number caught+1) was examined within each of these cells, and the distribution was tested against the hypothesis of normal distribution of observations within a cell (only cells with more than 5 observations included). The result of the test of all cells is shown in fig. 5.1.2.3. The normal distribution can be rejected in 5% of the cells (α) without the theory of normal distribution within the cells being rejected. However, for all species, less than 61% of the cells could be assumed to be normal distributed, with the percentage being as low as 34% for norway pout (the column at p=0.0 in fig. 5.1.2.3). If the data had been completely normal distributed within all cells, the columns of fig. 5.1.2.3 should be of equal height, apart from the first and the last column, which should be half the height of the others.

As a consequence of the uniqueness of zero catch, it was decided to build two models: One describing the probability of catching something (none or some) and another describing the number caught given something is caught. The distribution of ln(number caught), given at least one fish of a given species and length is caught, was significantly different from a normal distribution in only 9% (mean value, range 5.5%-12.5%) of the cells (a cell being as above) (first column in fig. 5.1.2.4). Examining these values, it must be kept in mind, that a normal distribution in all cells would still lead to 5% of the cells being significantly different from a normal distribution, as this is what the significance level signifies. On the basis of these

considerations, it was decided to model ln(number caught) than ln(number caught+1) when analyzing the catches.

One problem when building the models is the correlation between cells: A large catch of a species at a particular length is often accompanied by large catches of the adjacent length-groups (fig. 5.1.2.5). To make the observations as independent as possible, a model was therefore build for each species and size group apart. It is likely, that catches in adjacent 4-square areas are also correlated, but nevertheless this was not taken into account in the analyses.

A number of size groups are omitted from the models, as they are caught in very low numbers. Furthermore, only the length groups also found in the stomachs were considered. The remaining length groups for each species is shown in table 5.1.2.1.

5.1.2.1. 0-1 model

The 0-1 model describes whether or not something is caught of a certain species and size group. Each haul is seen as a trial, and the outcome is 1, if the particular species and size group is present in the haul (regardless of the numbers caught) and 0 otherwise. The probability of catching something in a 4-square area is then modeled as a generalized linear model with all independent variables categorical.

The model tested was:

$$\ln\left(\frac{p_{i,j,k,m}}{1-p_{i,j,k,m}}\right) = a_i + y_j + q_k + sh_m + ay_{ij} + aq_{ik} + ysh_{jm}$$

where

i, j, k, m = area, year, quarter and ship, respectively

p = Probability of catching something

a = Area - effect

y = Year - effect

q = Quarter - effect

sh = Ship - effect

One model was build for each species and size-group. For simplicity, indices of species and length are omitted from the formula. The logit link function was used, as this assured, that none of the predicted probabilities became negative.

The crossed effect between year and quarter could not be tested, as all other years than 1991 were sampled only in the 1st quarter. The crossed

effects between ship and area and ship and quarter are omitted, as they complicate interpretation and prediction. The effect of these were nevertheless tested for significance given all other tested effects were included in the model.

To investigate, if the ship parameter was an artefact of the unbalanced data set and would thus aggravate model predictions, a model ignoring the ship effect was also build. This was similar to the model taking ship into account, only the two factors including ship were omitted from analyses.

5.1.2.2. Model for number caught

It was decided to model ln(numbers caught) as a general linear model with the same explaining variables as the 0-1 model. Due to the unbalanced sampling design, type IV analysis was used to eliminate the non-significant effects. The model tested was:

$$\ln(no_{i,j,k,m}) = a_i + y_j + q_k + sh_m + ay_{ij} + aq_{ik} + ysh_{jm}$$

where

no = Number caught

Other notation as above.

One model was build for each species and size-group. For simplicity, indices of species and length are omitted from the formula. As in the 0-1 model, the significance of the crossed effects between ship and area and ship and quarter were tested in a model including all other effects. None of these crossed effects were included in the models used for predictions. Furthermore, a model ignoring the ship effect was build. This was similar to the model taking ship into account, only the two factors including ship were omitted from analyses.

5.1.2.3. Estimated catch

Both the 0-1 model and the model for the numbers caught show a significant effect of the ship used for most species and lengths. Predictions were therefore standardized to one ship (Cirolana) by subtracting the ship effect of the ship actually taking the sample and adding the ship effect of Cirolana. To examine, whether this improved the correlation with the stomach ratios, a model was also build, in which the ship effect was not accounted for. Apart from the ship-effect, the procedure was the same for the two models.

The ln(*no*) was assumed to be lognormal-distributed, and predicted values were corrected for the skewness in the lognormal distribution before taking the antilog. The predicted number was obtained by multiplying the expected value of number caught with the predicted probability of catching something to obtain the estimated catch in a given year, quarter and area of a particular species and size group:

$$E(\hat{T}_{sp,l}) = \hat{p}_{sp,l,i,j,k,l,m} * \exp(\ln(no)_{sp,l,i,j,k,m} + \tfrac{1}{2} * \hat{\sigma}_{sp,l}^{2})$$

where

sp,l = Species and length, respectively

m = ship = Cirolana for all predictions

$E(\hat{T})$ = Estimatet catch pr. trawlhour

$\hat{p}$ = estimated propability of catching something

$\ln(\hat{no})$ = Estimated ln(number caught)

$\hat{\sigma}^2$ = Estimated variance on the model for ln(number caught)

As the variance of both p and ln(*no*) is known, it is possible to estimate the variance of the predictions, if the covariance between the two is calculated. However, as calculating the resulting variance on the estimated ratio between two species or length groups involves estimating both this covariance and the covariance between the estimated number of the two groups, this quickly becomes rather complicated. In any event, this variance can not easily be taken into account in the software procedures used. As the variance on the ratio found in the stomachs furthermore was thought to be much larger than the variance on the IBTS-ratios, the IBTS predictions were considered to be without error in the following analyses.

5.1.3. Estimated number of 1-year olds

The percentage of 1-year olds in each length group was calculated from the fish aged in each survey. As this was not the overall aim of this project, as a rather crude estimate, it was decided to calculate the percentages as

$$p_{1,sp,l,y,q,r} = \frac{(no_{1,sp,l,y,q,r})}{(\sum_{i=nages}^{1} no_{i,sp,l,y,q,r})}$$

where

sp,l,y,q,r = Species, length, year, quarter and roundfish area, respectively.

p_1 = Proportion being 1 year old

no_1 = Number of 1 - year olds

$nages$ = Number of agegroups

The proportion of 1-year olds was thus assumed to be constant for a given species and lengthgroup within a roundfish area, year and quarter.

The catch of a length group was summed within roundfish areas (fig. 5.1.2.6) and then multiplied by the proportion of 1-year olds in that roundfish area:

$$predicted_{1,sp,y,q} = \sum_{l=nl(sp)}^{1} \left(\sum_{r=9}^{1} p_{1,sp,l,y,q,r} * \left(\sum_{a=narea(r)}^{1} E(T_{sp,l,y,q,a}) \right) \right)$$

where

a = 4 - square area

$nl(sp)$ = Number of length groups in species sp

$narea(r)$ = Number of areas in roundfish area r

$predicted$ = Predicted catch of 1 - year olds

Remaining notation as above.

This gives the total expected catch of 1-year olds, if Cirolana trawled once in each 4-square area. Only the areas trawled in at all times were included in the sum. As sprat were not age determined in 1981, no predicted catch of 1-year olds were calculated for this species in that year.

5.2. 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, Robb et al., 1994).

5.2.1. Collection of stomach data

Samples were collected during all quarters in 1981 and 1991, and during 1st and 3rd quarter in 1985, 1986 and 1987. 15 ships from 8 countries participated in the surveys, though all ships did not participate in all years and quarters. All ships trawled using a demersal GOV trawl (ICES, 1991). Generally, two hauls were taken within each ICES-square.

The stomach samples used in this project are from the predators cod and whiting (all years) and haddock (1981 and 1991). The desired number of fish sampled from each length group in each haul is seen in table. 5.2.1.1. Where less predators were caught, all predators were sampled. Where more predators were caught, fish were sampled from the trawl using a stratified random design, taking the desired number at random from each size group (ICES, 1991a, ICES, 1992).

The stomachs were divided into the following categories: empty, with food, with skeletal remains and stomachs showing signs of regurgiation. Where part of the stomach had been forced out of the mouth by the expansion of the swimbladder or the fish had obviously been feeding in the trawl, stomachs were excluded from the analyses. As only stomachs containing food have importance for the ratio between different prey types, only these were considered in the analyses of ratios. A total number of 37370, 29939 and 91093 stomachs were sampled from cod, haddock and whiting, respectively. When examining the stomach content only, all of these were considered, but when comparing stomach data and IBTS data, only the 1st quarter of 1981, 1985, 1986 and 1987 together with all quarters of 1991 could be used, rendering the total number of stomachs sampled and compared to IBTS at 22465 and 57440 for cod and whiting, respectively. Haddock was not compared to IBTS, see section 5.2.5 for the reasons for this. The distribution of stomach samples on predator lengths is shown in fig. 5.2.1.2.

Stomachs containing food were pooled into one sample within haul, predator species and –sizegroup, or, in a few cases, examined individually. The samples not examined at sea, were as strictly as possible examined by the same country. Cod, haddock and whiting stomachs were thus analyzed by The Netherlands, Germany and Scotland, respectively, in 1981 and 1991 and by The Netherlands and Scotland in the remaining years. The fish prey were identified to species, or, where digestion had made this impossible, to the lowest possible taxonomic group. Only the prey species cod, haddock, herring, norway pout, sandeel, sprat and whiting are considered in the calculation of ratios, as (apart from sandeel) these species all have been caught and measured regularly in the IBTS. Prey, that were too digested to be measured, weighed or classified to the taxonomic groups

used here (all sandeel considered together, all others at species level), were ignored.

5.2.2. Examination of food composition

The food was divided into the groups annelida, mollusca, crustacea, echinodermata, fish and other invertebrates. The percentage of the total stomach content weight coming from each group was calculated.

The fish prey were divided into the most frequently occurring species and families together with the two larger groups flatfish and other fish (not among the most frequently occurring species).

5.2.3. Length distribution of fish prey

The mean length of fish prey of each species (all sandeel considered together) for a given predator species and length was calculated, as was the variation in prey length. The variation was calculated as

$$\hat{\sigma}^2_{sp} = \sum_{i=1}^{i=n} (l_{sp,i} - \overline{l_{sp}})^2$$

where

sp = Species

l_i = Length of the i'th prey

$\overline{l_{sp}}$ = Mean length of species sp

Indices of predator species and length omitted for simplicity.

5.2.4. Partial fullness index

The partial fullness index, PFI, as introduced by Lilly and Flemming (Lilly & Flemming, 1981, in Fahrig et al, 1993), was calculated as

$$PFI_i = \frac{1}{n}\sum_{j=1}^{n}\frac{W_{i,j}}{L_j^3} * 10^4$$

where

i = prey species and sizegroup

j = sample no

n = number of stomachs

W = weight of i in g

L = length of predator in cm

The length is used, because length to a lesser extent than weight is influenced by changes in condition, weight of liver, gonads and stomach content. The index is analogous to Fulton's condition factor (weight pr. length^3) (Fahrig et al, 1993).

As an attempt to build a PFI for the 1-year olds rather than for length classes, the prey caught by the predator in a given roundfish area, year and quarter were assumed to have the same age-distribution as the fish of that length group caught in the trawl surveys. This is not necessarily correct, as trawl catches due to the different selection of different lengthgroups (Engås & Godø, 1989), will tend to show a higher mean length of a length class than is actually present. As fish grow as they age, this will overestimate the proportion of the length class being older than 1 year. However, this was assumed not to introduce errors serious enough to completely change the PFI of one year as compared to another. Furthermore, the small prey sizes eaten by the predators are mostly 1-year olds in the 1st quarter. Thus, the PFI's were summed and multiplied by the proportion of 1-year olds as described in section 5.1.3. This PFI of 1-year olds was then compared to the predicted catch and VPA-estimate of that ageclass for all species but sprat. For sprat, the PFI was compared to the survey index calculated by ICES as a VPA is not carried out for this species. As sandeel changes its behavior and thereby presumably its availability to the predators, over the course of the year, a PFI was also estimated for each length group in the 3rd quarter. This PFI was compared to VPA estimates of number of 0-year olds in the 1st quarter (haddock, herring and whiting), 3rd quarter (norway pout and sandeel) or number of 1-year olds in the following year (cod). The PFI's of the different prey lengths were summed into "less than length"-groups, and the less than length-group having the highest correlation with the VPA- or ICES-estimates for a given predator was compared to this.

5.2.5. Calculation of the stomach ratio

As the predator haddock, apart from sandeel, eat only norway pout to any extent, ratios could not be build for this species. It was therefore excluded from all analyses of ratios.

The predators where divided into 100 mm length groups for predators shorter than 500 mm. The size groups to which the predators were assigned during the stomach sampling projects varied from year to year, with the 1981-sampling using the broadest size groups (ICES, 1991). For large predators, the 1981 length groups (500-700 mm, 800-1000 mm, above 1000 mm) were thus used to make comparison with the other years possible. The size groups are referred to by their midpoints. Predators, for which fish prey did not make up a large part of the diet (cod less than 300 mm, whiting less than 200 mm)(fig. 6.2.1.1), were excluded. Also, large predators, that were caught and sampled infrequently (cod greater than 1000 mm, whiting greater than 400 mm, see fig. 5.2.1.2), were excluded to minimize the bias caused by an unbalanced sampling design. In any case, these predators are of limited value as indicators of prey abundance, as they are only caught occasionally. The remaining predator length groups are shown in table 5.2.5.1. The same length groups for the prey as described in section 5.1.1 were used.

Examining the ratio within samples led to very few observations. It was therefore decided to examine all stomachs within predator species, sizegroup, 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. The diet then expresses outcomes of the same sampling procedure, and can be thought of as watching the same predator foraging several times over in a constant environment. All samples were thus pooled within area, year, quarter, ship, predator species and –sizegroup. This was done for the areas 4-square area, ICES roundfish area and the whole North Sea. The total number of stomachs in the pooled samples were calculated. The prey species and -sizegroups, that most often occurred together with other species (of the ones examined in this project, sandeel not included) were chosen as reference species and size-groups. The ratios of all other prey species- and size-groups to these reference groups were calculated. The reference groups chosen where: norway pout at 75 mm, 125 mm and 175 mm, sprat at 75 mm and 125 mm and whiting at 75 mm, 125 mm, 175 mm, 225 mm, 275 mm.

Using different reference groups should, according to the suitability model, only affect the suitability factor, and thus give the same significant effects.

5.3. Combination of predicted IBTS catches and stomach data

The IBTS predictions and the stomach data were combined on 3 different spatial scales: 4-square areas, roundfish areas and the whole North Sea. For the 4-square areas, the IBTS-predictions could be compared directly with the stomach data. For roundfish areas, the IBTS predicted ratios were found by summing all predicted catches in that area. Where 4-square areas were in 2 or more roundfish areas, the predicted catch in the 4-square area was split between roundfish area according to the area of the 4-square area lying in each roundfish area. For the whole North Sea, all predicted catches were summed for the particular species, length group, year and quarter. The 4-square areas that were not sampled by the IBTS in all years and quarters of 1991 were excluded from the roundfish- and North Sea- calculations for all years and quarters. This was done to make predicted catch comparable between years. For each reference, the ratios to the other species and sizegroups were calculated and compared to the corresponding ratios in the stomach samples in that area (area being 4-square area, roundfish area or the North Sea). The ratios compared were thus

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

where

$area$ = The area in which the ratios were compared

i = prey species and lengthgroup

ref = reference group

pr = predator species

$l(i)$ = length of i

k = Constant within indices

$T_{i,area}$ = Predicted trawl catch of i in that area

Remaining notation as in section 3.6

5.4. Comparison of ratios

Initial plots of the ratio in the stomach samples as a function of the ratio in the IBTS catch indicated, that the variance rose with the ratio in the IBTS catches. It was therefore decided to log-transform all ratios, and the analyses were done on ln(stomach ratio) and ln(IBTS-ratio). One analyses of ratios were done for each reference group apart, to avoid correlation between observations. All analyses were done as mixed models (both linear and categorical factors tested) in the glm-procedure in SAS. Type IV sum of squares was used to test for significance of

effects. 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.

A sample consisting of several subsamples (stomachs) taken under identical conditions would normally be weighted by the number of subsamples when performing the analyses. However, stomachs sampled from predators collected from the same haul can not be considered to be independent subsamples, as these predators presumably have been foraging in the same environment. This effect gives a large intra-haul correlation between stomach contents as shown by Warren et al. (1994) and Bogstad et al. (1995). This means, that an analysis should not be weighted by the actual number of stomachs but by some smaller number. The decrease in the weight that should be given to the sample is dependent on the intra-haul correlation coefficient. However, this factor is not known, and as stomachs have not been examined individually, it was not possible to estimate it. To use this approach, it would furthermore be necessary to examine the ratio in each haul rather than in each area. As the number of fish eaten is not infinite, this would mean, that many hauls could not be used in analyses, as none of the reference groups were present. It was thus considered more appropriate to ignore this haul effect and examine all stomachs taken within a 4-square area together. This however still leaves the problem of how to include the number of stomachs in the analyses. As an approximation, it was decided to weight the analyses by the number of stomachs in the sample used in calculation of the ratio. As empty stomachs did not provide any additional knowledge on the ratio between species, the number of stomachs in a sample was calculated as the number of stomachs containing food in the sample.

As shown by Chesson (Chesson, 1984), pooling stomachs from variable predators may result in the population showing switching, though individual predators do not exhibit this behavior. The effect of the number of predators pooled on the switching coefficient may be positive or negative, with a negative effect the most likely outcome (only negative effect on the switching coefficient was observed in the cases examined by Chesson). The effect is dependent on the number of stomachs pooled and not just whether pooling takes place or not. To examine if pooling of the stomachs had any effect on the switching coefficient found in the analyses, two models were build including the number of stomachs in the sample and ln(number of stomachs in the sample), respectively, as a linear variable in the model of ratios. These two analyses were thus not weighted by the number of stomachs. Apart from these two, all analyses were weighted by the number of stomachs in a sample.

The dependency of the suitability on length of predator and prey was modeled as categorical, and the parameter values investigated to see if any pattern was revealed. However, due to the noise in the data, no pattern was evident. Nevertheless, prey and predator length were

modeled as categorical in all the models except the model including the dependence on these as a polynomial.

5.4.1. 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 their 1st and 2nd order effects of these were tested for significance. The model was:

$$\ln\left(\frac{F_i}{F_{ref}}\right) = b_{ijk} * \ln\left(\frac{T_i}{T_{ref}}\right) + b_{ijm} * \ln\left(\frac{T_i}{T_{ref}}\right) + py_i + l_j + pd_k + pl_m +$$

$$pyl_{ij} + pypd_{ik} + pypl_{im} + lpd_{jk} + lpl_{jm} + pylpd_{ijk} + pylpl_{ijm}$$

where

i, j, k, m = Prey species, prey length, predator species and predator length, respectively

$b_{ijk}, b_{ijm}, py_i, l_j, pd_k, pl_m, pyl_{ij}, pypd_{ik}, pypl_{im}, lpd_{jk}, lpl_{jm}, pylpd_{ijk}, pylpl_{ijm}$ =

Constants within indices

n = Number of stomachs in the sample

Remaining notation as above

5.4.2. Investigations of the effect of number of stomachs in a sample

To examine if the number of stomachs in the sample have an effect on the slope of the ln(stomach ratio) as a function of ln(IBTS ratio), two models were build in which the number of stomachs in the sample were included as a factor: One model examined the effect of number of stomachs in the sample as linear, another model examined the effect as log-linear, that is, the factor included was ln(number of stomachs). This was done to examine, whether an effect of number of stomachs were due to a few very large samples "pulling" the analyses to one side.

The models were thus:

$$\ln\left(\frac{F_i}{F_{ref}}\right) = b_{ijkn} * \ln\left(\frac{T_i}{T_{ref}}\right) + n * b_{ijkm} * \ln\left(\frac{T_i}{T_{ref}}\right) + py_i + l_j + pd_k + pl_m + d_{ijk} * n$$

$$+ d_{ijm} * n + pyl_{ij} + pypd_{ik} + pypl_{im} + lpd_{jk} + lpl_{jm} + pylpd_{ijk} + pylpl_{ijm}$$

Notation as above

In the model including number of stomachs in the sample as ln(n), n must be replaced by ln(n).

5.4.3. IBTS model without ship effect

To examine the effect of correcting the IBTS catches from differences between ships on the correlation between the predicted IBTS ratios and the stomach ratios, a model testing the same effects as the basic model was build comparing ratios in the stomach with the IBTS catches not corrected for ship effect. Otherwise the model was as the basic model.

5.4.4. Effect of year, quarter and area

To test if the dependence of the stomach ratios on the IBTS-ratios differed between areas, years and quarters, analyses were made on 4-square area testing the effect of prey species and length, predator species and length, ln(IBTS-ratio), year, quarter and 4-square area. Their 1st order crossed effects were tested. Year, quarter and area were tested as categorical variables.

5.4.5. Dependence on length as polynomial

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 $\ln(w_{predator}/w_{prey})$ such that a predator has the same preference for a prey of twice the preferred sizeratio as half the preferred ratio. The model describing the preferred ratio of prey size to predator size is

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

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

where

pr, i = Predator and prey, respectively

w_i = Weight of i

$g_{pr,i}$ = Preference coefficient

η_{pr} = Preferred size ratio of the predator

σ_{pr} = Coefficient describing the particularity of the predator in its choice of prey

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. The detailed calculations are included in appendix A. Thus, only the model assumptions and the resulting model is described here.

5.4.5.1. 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

5.4.5.2. Predator species preference

The relative preference of one prey species to another should 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 certain species peaks at a particular predator length.

The dependence of species preference on predator length is thus

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

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

modeled as

5.4.5.3. 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,

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

$$\Updownarrow$$

$$\ln q_i = \ln q_{0,i} + r_i * \ln l_i$$

where

$q_{0,i}, r_i$ = Constants.

l = Length of fish i

catchability (q) of a fish to the trawl is modeled as

5.4.5.4. 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, $w_{0,i}$:

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

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

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

where

Λ = Constant

Q_i = Rate of elimination of species i in the stomach of the predator

l_{pd} = Length of predator (in cm)

d_i = Number of days prey i can be allocated to species

5.4.5.5. 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

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

where

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

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

is modeled as

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:

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

where

$\beta_{0,pr}$ = The theoretical β of a predator of length 1

B_{pr} = Factor describing dependence of β on length

5.4.5.6. 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 (as is the case for herring, see section 6.2.3). 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,

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

$$\Downarrow$$

$$\ln\left(v_{i,l(i),j,pr,l(pr)}\right) = \ln\left(v_{i,l(i),pr,l(pr)}\right) - \ln\left(v_{j,l(j),pr,l(pr)}\right) =$$

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

where

V_0, v_1, v_2 = Visibility - constants (within indices)

not allowing for peak visibility at intermediate lengths. The expression included for visibility was thus

5.4.5.7. Final model

Together these assumptions give the model of ratios

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

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

where

i, j, pr = Prey species, reference and predator species, respectively

l_i = Length of i

C, E, G, H, o, M = Constants within indices

t_{pr} = Factor describing the dependency of switching on predator length

$t_{pr} = 0 \Rightarrow b_{0,pr}$ = Common switching coefficient for all predators

$t_{pr} \neq 0 \Rightarrow b_{0,pr}$ = Theoretical switching coefficient for a predator of length 1

Remaining notation as above.

5.4.6. Analyses at different spatial scales

To examine the effect on the model of comparing the ratios at different spatial scales, a model was build comparing ratios in roundfish areas and another model build comparing ratios in the whole North Sea. The factors tested were the same as in the basic analyses on 4-square areas.

5.4.7. Total catch of a species as predicted by the model of ratios

The model including length as polynomial has the advantage, that no crossed effects between prey species and prey length are found. This makes it possible to calculate the intercept of a given combination of prey, prey length, predator and predator length, by assuming that the abundance of the prey is a given value in one area at one time. As the intercept is not dependent on time and area in this model, this intercept should be constant within prey, prey length, predator and predator length. The slope varies only with predator species and length in the polynomial model, and can thus be calculated without knowing the abundance of the prey. Knowing the intercept and slope of the relationship between ratios, the predicted ratio in the IBTS can be

$$\ln\left(\frac{\hat{T}_i}{T_j}\right)_{area} = \frac{\ln\left(\frac{F_i}{F_j}\right)_{area} - \hat{c}_{ij}}{\hat{b}}$$

where b denotes the slope and c the intercept
estimated as

Indices of predator species and length are omitted for simplicity.

As no crossed effects between prey species and prey length are found significant, it is not necessary to know the relative abundance of the lengthgroups of the prey in question in the area chosen as index area. Thus, an area and a prey length is chosen as the index, and the abundance of prey in this area is set to 100. From this, the intercept is calculated, and the ratio in the IBTS estimated. Knowing the number caught in the IBTS of the reference species, the predicted number of sandeel caught, had the trawl been able to catch the sandeel can be calculated as

$$\hat{T}_{i,l,area} = \hat{T}_{j,area} * \exp\left(\ln\left(\frac{\hat{T}_{i,l}}{T_j}\right)_{area}\right)$$

From this, the predicted average catch can be calculated and compared to the VPA estimates.

5.5. Saturation model

It was found in the above analyses, that the number of stomachs in a sample had a significant positive effect on the ratio in the stomach when data was compared on 4-square level. This could be caused by the sample reaching a maximum or minimum value for the ratio, that is, saturation of the predator, as visualized in fig. 5.5.1.1. As predator

stomachs are of finite size, it seems reasonable, that for small samples, the total number of fish in the stomachs is limited. Thus, if a predator of a certain length can hold a maximum number of 4 equally sized fish prey in the stomach, the maximum ratio in the stomach will be 3:1 (a total of 4) and the minimum ratio 1:3, that is, 3 and 1/3, respectively. If the predicted ratio is much above 3, then a predator conforming to the model would eat only the prey species and none of the reference. However, though this conforms to the model, it does not result in any observed ratio, as both species must be present for a ratio to be calculated. This is a problem when modeling data in this way, acting to dampen the extreme values for the ratios. Thus, a low slope could be due to the lack of very high and very low values of the ratio.

It was sought to determine, whether there actually is a saturation of the samples by three different approaches.

First, the maximum weight of the stomach content of a given predator length is estimated, and the percentage saturation calculated, assuming that all predators are able to eat the maximum recorded weight in that lengthgroup. The percentage saturated should however be taken as a minimum value, as the maximum stomach content is likely to be found in predators in the upper end of the length interval and therefor higher than the maximum stomach weight for the smaller predators in the length group. Thus, predators in the lower end of the length interval are saturated at lower weight of stomach content than predicted by the model.

Second, the percentage of the predators estimated to be unable to eat another prey had the predator encountered it, is estimated. This is done by estimating the weight at ingestion of the prey from the heaviest specimens present in the stomachs.

As these two approaches provide no knowledge of whether the ratios are affected by saturation, it is also examined, if the maximum and minimum ratio is dependent on the space left in the stomach (as calculated from the maximum stomach content weight estimated for each predator length), given the predator have eaten the other food present in the stomach.

5.5.1. Maximum weight of stomach content

The maximum stomach content is modeled as a fixed percentage, c, of the total weight of the predator, as the mean weight of the stomach content is generally well described in this way (Hislop et al., 1991). If predator weight is further modeled as a potency function of the length of the predator, the model becomes

$$\max(W_{pr,pl}) = p_{pr} * W_{pr,pl}$$

$$\Updownarrow$$

$$\ln(\max(W_{pr,pl})) = \ln(p_{pr}) + \ln(W_{pr,pl})$$

Substituting

$$W_{pr,pl} = c_{pr} * pl^{f_{pr}}$$

$$\ln(\max(W_{pr,pl})) = \ln(p_{pr}) + \ln(c_{pr}) + f_{pr} \ln(pl)$$

where

pr, pl = Predator species and length, respectively

$W_{pr,pl}$ = Weight of total stomach content

p_{pr} = Constant within predator species.

$0 < p_{pr} < 1$

The observations analyzed in the model was the maximum weight of the total stomach content recorded for each predator species and length. The maximum average stomach weight of all samples was used when finding the maximum weight of stomach content. The smallest length groups were omitted from the analysis, as the midpoint of the length interval probably did not describe the mean length of the predators in this length group (due to trawl selection, the mean length of the fish examined is likely to be higher than the interval midpoint). This left 6 observations for cod and 4 for whiting to be analyzed in the model. As an approximation, $\ln(\max(W_{p,pl}))$ was assumed to be normal distributed. The model tested was thus:

Type IV analysis was used to eliminate insignificant variables. The predictions were corrected for the skewness in the log-normal

$$\ln(\max(W_{p,pl})) = d_p + f_p * \ln(pl)$$

where

d, f = Constants

Other notation as above
distribution as described in section 5.1.2.3.

With the maximum weight of the stomach content predicted by this model, it was estimated, that less than 1% of the predators were 75% saturated or above.

5.5.2. Weight of prey at ingestion

Even if the predator is not fully saturated, as prey come in whole portions, the predator may nevertheless be too full to eat another prey. To investigate how many of the predators were unable to eat another prey had they met one immediately before being caught, the weight of each prey at ingestion must first be estimated along with the available

$$\hat{avai}(W_i) = \max(\hat{W}_{p,pl}) - \frac{stom(W_i)}{n_i}$$

where

i = sample

$avai(W_i)$ = Weight available for more food

$\max(\hat{W}_{p,pl})$ = Maximum weight of stomach content estimated from the above model

$stom(W_i)$ = Total recorded weight of stomach content in sample i

n_i = Number of stomachs in sample i

space in the stomach. The last factor can be calculated as

Where there was more than one stomach in the sample, the recorded stomach content was divided by number of stomachs in the sample. Thus, all stomachs were assumed to contain the average weight for the particular sample. The other extreme would be to assume, that virtually all of the stomach content was found in all but one stomach, leaving this stomach as empty as possible. The available space would then be the total available space, and not the available space pr. average stomach. Of the two extremes, it seemed most appropriate to assume, that each stomach contained the average weight of the stomach content found in the sample.

Having estimated the space available in the stomach, whether or not a predator could have eaten one more prey was estimated as

$\hat{avai}(W_i) > w_{prey} \Rightarrow$ The predator could have eaten another prey

$\hat{avai}(W_i) < w_{prey} \Rightarrow$ The predator could not have eaten another prey

where

$prey$ = Prey species and length

w_{prey} = Weight of prey at ingestion

Weight of prey at ingestion is not known, and the length-weight relations normally used for calculations of weight are based on fish caught in trawl. Due to trawl selection, few fish are caught in the smaller lengthgroups, and the ones that are caught tend to be in the

upper end of the length interval, thereby giving a biased weight estimate for that lengthgroup. Relations calculated from trawl catch may also differ from length-weight relations for the prey of the predator, if the predator tend to eat fatter or slimmer fish, than are caught in the trawl.

As an alternative, prey weight can be estimated from stomach content: The heaviest prey in each lengthgroup is probably either the most recently ingested, in the upper end of the length interval or both. When using the weight length relationship calculated from the heaviest prey in each lengthgroup to estimate the prey weight at ingestion, one will therefore rather over- than under-estimate the percentage of the population unable to eat one more prey. Thus, digestion would work to lower estimated weight at length and the relatively broad length intervals to increase estimated weight at length.

To estimate the weight of prey at ingestion, for each prey length group the greatest observed weight of an individual prey was recorded. Where several prey were pooled before weighing, the sample mean weight was used when comparing to find the maximum value.

The weight of the prey at ingestion was modeled as a potency function of prey length:

$$\max\left(stomw_{i,j,k}(l)\right) \approx w_{i,j,k}(l)$$

$$w_{i,j,k}(l) = c_{i,j,k} * \ln(l)^{f_{i,j,k}}$$

$$\Updownarrow$$

$$\ln(w_{i,j,k}(l)) = \ln(c_{i,j,k}) + f_{i,j,k} * \ln(l)$$

where

i,j,k = Prey species, predator species and predator length, respectively

l = Length of prey

$stomw_{i,j,k}(l)$ = Maximum recorded weight of i at length l in the stomach of j at length k

$w_{i,j,k}(l)$ = Weight at ingestion of i at length l eaten by j at length k

Having found the maximum weight of a given prey and length eaten by a predator species and length group, these values were used to build the model. The model tested was

$$\ln(\max(stomw_{i,j}(pl,l))) = py_i + pd_j + pypd_{ij} + a_{ij} * \ln(l) + b_{ij} * pl$$
$$+ c_i * pl * \ln(l) + d_j * pl * \ln(l)$$

where

i, j = Prey species and predator species, respectively

l = Prey length

pl = Predator length

$\max(stomw_{i,j}(pl,l))$ = Maximum weight of i at length l eaten by predator j at length pl

py, pd, a, b, c, d = Constants within indices

Where the dependence on predator length and ln(prey length) was modeled as linear.

Max(*stomw(l)*) is allowed to vary between predator species and length group, as one species or length group may seek out "fatter" prey than the other. This may also cover some of the variation caused by larger predators predominantly eating prey in the upper end of the length interval. The effect of predator length should, if present, show some kind of consistency, as there is no reason to think, that one predator length group is dramatically different from the two adjacent length groups. The dependence of maximum weight on predator length was thus modeled as linear. ln(max(*w(l)*) was assumed to be normal distributed and the model was analyzed as a general linear model. Type IV analysis was used to eliminate variables that did not have a significant effect. The predictions were corrected for the skewness in the log-normal distribution as described in section 5.1.2.3.

The estimated weights at ingestion were compared with the available space in the average stomach as calculated above, and the estimated percentage of predators unable to eat one more prey calculated.

5.5.3. The dependence of maximum and minimum ratio on sample size

Yet another way to examine the saturation problem is to investigate, whether the maximum and minimum ratio observed depends on the estimated remaining space in the stomachs. As a stomach has a limited size, the maximum ratio would be the maximum number of the prey possible, given that one prey of the reference species is present. The same applies to the minimum ratio, if reference and prey are switched. Thus, all the following remarks goes for minimum ratios as well if prey and reference are switched, as a minimum ratio is in fact the inverse of a maximum ratio.

The room available for the prey in the sample i is

$$avai(W_i) = n_i * \max(W_{p,pl}) - W_i(other) - w_{ref}$$

where

i = sample number

p,pl = Predator species and length

n = number of stomachs in sample i

$W_i(other)$ = Weight of food other than prey and reference

w_{ref} = Weight of reference

Notice, that this is the room available in the whole sample and not as before, in the average stomach. Though there is not room for one more prey in each stomach when examined as if they all contained the average stomach content, there may be room for one more prey in the sample, which may be the reason for the positive effect of number of stomachs in the sample on the switching coefficient (see section 5.4).

Due to digestion, not all prey have the estimated weight at ingestion. The two extremes of reference weight are:

- The reference has been ingested just before the predator was caught and have the weight estimated from the model of weight at ingestion
- The reference is almost completely digested and the weight of it is therefor very small.

To be used in the later models, maximum and minimum ratios must be as independent of the observed ratios as possible. If the weight of the reference was used directly, this would not be the case, as this will depend on the digestion stage of the reference. If several reference prey were observed, the weight of reference would not be clear: If the total weight of the reference (no matter the number) was used, this would not be independent of the ratio. Rather, high weight of reference would correspond to high number of reference present. Using the mean value of the reference would probably also give a dependence on number of reference: A high number of references would tend to lower the mean weight, as it is likely, that several of the specimens will be almost completely digested. If they were not somewhat digested, there would not be room for so many of them. Instead, the model was build in the two extremes mentioned above and then compared.

With the available room for prey being as mentioned in section 5.5.2, the maximum ratio, max(r) would occur, when one specimen of the reference was present, and the remaining room filled by the prey in

$$\max_i(r) = \frac{\max_i(no(j))}{\min_i(no(ref))}$$

where

r = Ratio in the stomach

j, ref = Prey and reference, respectively

i = Sample number

$no(j)$ = Number of j in the sample

As

$\min(no(ref)) = 1$

$\max_i(r) = \max_i(no(j))$

question:

Thus, the predator is "allowed" to include other food in the diet, and the weight of this other food is not modeled. According to the suitability model, the amount of other prey should not affect the ratio between the two species considered.

The maximum number of prey j, that can be contained in sample i, occurs when all the space not taken up by other food is filled by the prey up to the maximum stomach weight in each sample:

$$\max_i(no(j)) = \frac{avai(W_i)}{\overline{w_j}}$$

where

i = Sample number

$\overline{w_j}$ = The average weight of j in the stomach

The maximum ratio now becomes:

$$\max_i(no(j)) = \frac{avai(W_i)}{\overline{w_j}}$$

$$\max_i(r) = \frac{n_i * \max(\hat{W}_{p,pl}) - W_i(other) - w_{ref}}{\overline{w_j}} \Leftrightarrow$$

$$\ln(\max_i(r)) = \ln(n_i * \max(\hat{W}_{p,pl}) - w_{other} - w_{ref}) - \ln(\overline{w}_{ji})$$

Notation as above.

As a simple approximation, the average weight of prey in the stomach is modeled as a potency function of the length. The expression then becomes:

$$\ln(\max_i(r)) = \ln(avai(W_i)) - (a_j + b_j * \ln(l_j))$$

as

$$\overline{w_j} = \exp(a_j) * l_j^{b_j}$$

where

a, b = constants

l_j = length of prey

for a given predator and predator length.

Other notation as above.

a and b should be constant within predator, predator length and prey species. However, as they depend on the prey weight at ingestion and the digestion rate, they are likely to vary with prey, predator and predator length.

Thus, a model describing the maximum ratio measured as a function of the available space should give a linear dependency of max(r) on ln(*avai*(*W*)) with slope=1. To test, if the maximum ratio measured was in fact dependent on the available space as described by this model, the maximum observed ratio for each combination of reference, prey, prey length, predator, predator length and sample size (=a cell) was found. The object of the analyses was not to describe the ratio in all samples at this point, but rather to investigate if there was a dependency of the highest recorded ratios on the space available in the stomach. If this is not the case, it is unlikely, that saturation of the predator affects the ratio between prey in the stomachs.

Where the number of stomachs was greater than one and the ratio was found to be less than (number of stomachs in the sample-1), the observation was not used in analyses. Such an observation cannot be the maximum ratio, as there must be room for at least one prey pr. stomach, given the prey is observed in any stomach. If there is not room for one prey in each stomach, other prey must take up the available space. Samples dominated by other prey are likely to provide little information about the prey and reference examined. Another reason for this procedure was the desire to minimize the number of observations used in this analysis. As estimated maximum and minimum ratios were later used in the logit model described in section 5.5.4, these should be as independent as possible of the data set examined in section 5.5.4. Thus, the fewer observation used in both analyses, the better.

The set of observations was thus the maximum ratio observed for each cell as mentioned above, provided the value was larger than (number of stomachs-1) where the number of stomachs was greater than one. For each observation, the available space was calculated by two approaches.

In the first model, the space taken up by the reference was assumed to have an insignificant effect.

$$avai(W_i) \cong \max(\hat{W}_{p,pl}) - W_i(other)$$

This may be thought of as a predator first eating the reference species, and then eating the prey, rendering the reference almost completely digested at the time of capture of the predator. It may also be the case, if the prey is much larger than the reference. In this model, the estimated weight at ingestion is not used. The advantage of this method is therefore also, that additional error from the estimation of prey weight at ingestion is not introduced.

In the second model, the space taken up by the reference prey was taken into account when estimating the maximum/minimum ratio:

$$avai(W_i) = \max(\hat{W}_{p,pl}) - W_i(other) - \hat{w}_{ref}$$

where

$\hat{w}_{ref}$ = Estimated weight of reference at ingestion

This may be thought of as the predator ingesting the reference just before capture of the predator or the reference group being large compared to the prey.

The models analyzed were thus:

$$\ln(\max_{i,j,k,m,n}(r)) = c * \ln(avai(W_i)) + py_j + pd_k + d_{jk} * pl + f_{jk} * \ln(l) + g_j * pl * \ln(l)$$

where

i, j, k = sample, prey species and predator, respectively

l = Prey length

pl = Predator length

c, py, pd, d, f, g = Constants within indices

The dependency on predator length was modeled as linear to avoid marked differences between predator length groups arising from the unbalanced sampling design, and as some consistency in the maximum ratio as a function of predator length should be expected. The ln(max(r)) was assumed to be normal distributed, and the model was analyzed as a general linear model. Type IV analysis was used to eliminate the insignificant variables.

The model for the minimum ratio is the same, only reference and prey switch places:

$$\ln(\min_{i,j,k,m,n}(r)) = c * \ln(avai(W_i)) + py_j + pd_k + d_{jk} * pl + f_{jk} * \ln(l) + g_j * pl * \ln(l)$$

where

i, j, k = sample, reference species and predator, respectively

l = Reference length

pl = Predator length

c, py, pd, d, f, g = Constants within indices

However, instead of a slope of 1, this model should yield a slope of –1.

The available space for the models of minimum ratios are calculated as

$$avai(W_i) = \max(\hat{W}_{p,pl}) - W_i(other)$$

and

$$avai(W_i) = \max(\hat{W}_{p,pl}) - W_i(other) - \hat{w}_{prey}$$

where

$\hat{w}_{prey}$ = Estimated weight of prey at ingestion

for the two models, respectively.

As maximum ratios between different species rarely occur at the same time, they are not dependent on each other in the way the total set of ratios are. The maximum ratios were therefore analyzed in the same model and not as before in one model for each reference.

When comparing the two models, the model taking the weight of the reference into account had a slightly better fit than the model ignoring the weight of the reference. This model was therefor used to estimate the maximum and minimum ratios in the following. Both models had slopes very close to 1 and –1 for maximum and minimum ratios, respectively. It thus appears, that saturation may have an effect on the ratios.

5.5.4. The logit model

As an attempt to include saturation in the analyses, a new model was build, taking saturation into account. At high or low ratios in the IBTS, the predicted ratio in the stomachs should approach the maximum or minimum ratio estimated asymptotically. At intermediate ratios in the IBTS, the model should approach the suitability model, as saturation should play a minor role in this case. These demands are met by a logistic curve with minimum and maximum of maximum and minimum ratio estimated and 1st difference maximum of b. The formula for this is thus

$$\ln\left(\frac{F_i}{F_{ref}}\right) = (\max(r) - \min(r)) * \frac{\exp(4 * b * \ln\left(\frac{T_i}{T_{ref}}\right) + a_{ij})}{1 + \exp(4 * b * \ln\left(\frac{T_i}{T_{ref}}\right) + a_{ij})} - \min(r)$$

where

i = Prey species and length

a_{ij} = Constant. Corresponds to c_{ij}

Other notation as in section 5.4.1.

Indices of predator species and length omitted for simplicity.

As this expression is not linear in $\ln(T_i / T_j)$, it was necessary to transform the stomach ratios to analyze the model on the present software. The formula was thus rewritten as

$$normrat = \frac{\ln\left(\frac{F_i}{F_{ref}}\right) - \min(r)}{\max(r) - \min(r)}$$

$$\Updownarrow$$

$$normrat = \frac{\exp(4 * b * \ln\left(\frac{T_i}{T_{ref}}\right) + a_{ij})}{1 + \exp(4 * b * \ln\left(\frac{T_i}{T_{ref}}\right) + a_{ij})}$$

$$\Updownarrow$$

$$\ln\left(\frac{normrat}{1 - normrat}\right) = 4 * b * \ln\left(\frac{T_i}{T_{ref}}\right) + a_{ij}$$

Notation as above.

Indices of predator species and length omitted for simplicity.

The normrat thus follows a logistic curve with maximum 1 and minimum 0, and can be modeled as a generalized linear model with logit link. The normrat's were calculated using the maximum and minimum ratio estimated as a function of the estimated available space as described in the models above.

However, as the maximum and minimum ratios are estimated from a model seeking to minimize the sum of squares, some observed ratios will invariably lie above the maximum or below the minimum ratio. These were then set equal to the maximum and minimum, respectively, as values less than zero and above 1 are not allowed in the analyses. The normed ratios were thus

$$\frac{\ln\left(\frac{F_i}{F_{ref}}\right)_i - \min\hat{}(r_i)}{\max\hat{}(r_i) - \min\hat{}(r_i)} \in [0;1] \Rightarrow normrat = \frac{\ln\left(\frac{F_i}{F_{ref}}\right)_i - \min\hat{}(r_i)}{\max\hat{}(r_i) - \min\hat{}(r_i)}$$

$$\frac{\ln\left(\frac{F_i}{F_{ref}}\right)_i - \min\hat{}(r_i)}{\max\hat{}(r_i) - \min\hat{}(r_i)} > 1 \Rightarrow normrat = 1$$

$$\frac{\ln\left(\frac{F_i}{F_{ref}}\right)_i - \min\hat{}(r_i)}{\max\hat{}(r_i) - \min\hat{}(r_i)} < 0 \Rightarrow normrat = 0$$

where

i = Sample number

The variable normrat was analyzed as the dependent variable in a generalized linear model, normal distribution and logit link function.

$$\ln\left(\frac{normrat_{i,j,k,m}}{1 - normrat_{i,j,k,m}}\right) = c_{i,j,k} * \ln\left(\frac{\hat{T}_i}{T_{ref}}\right) + c_{i,j,m} * \ln\left(\frac{\hat{T}_i}{T_{ref}}\right) + py_i + l_j + pd_k +$$

$$pl_{ml} + pyl_{ij} + pypd_{ik} + pypl_{i,m} + lpd_{jk} + lpl_{jm} + pylpd_{ijk} + pylpl_{ijm}$$

where

i, j, k, m = Prey species, prey length, predator species and predator length, respectively

c = Switching koefficient

py, l, pd, pl = Constants within indices

The model analyzed was

One analyses was carried out for each reference group, and analyses were weighted with number of stomachs in the sample. The degrees of freedom were not corrected for the dimension of the models used when estimating maximum and minimum ratio. Forward selection was used to determine the variables with significant effect.

6. Results

6.1. Examination of trawl catches

6.1.1. 0-1 model

It was not possible to test the validity of the model, as the dispersion parameter was not known, but had to be estimated.

6.1.1.1. With ship effect

A summary of the models are given in table 6.1.1.1

The deviation explained by the model ranges from 33% to 59% (mean 47%) of the total deviation. This is a fair explanation, though there is still a large amount of unexplained variation.

The percentage is above average for prey in smallest length group (75 mm), where explanation ranges from 54% to 59%. In the case of haddock, the percentage explained increases with the length of the group, being low for the smallest length group (125 mm). For cod, the explanation seems to decrease slightly with length. The percentage explained is generally slightly higher for norway pout and sprat, but this seems to be due to the higher explanation for small lengths.

All the models but one are slightly overdispersed, with the estimated dispersion parameter ranging from 0.99 to 1.13 (mean=1.061). A dispersion parameter close to 1 indicates, that the variation is almost completely described by the binomial model, and the modeling of caught or not caught as a binomial model thus seems reasonable.

4-square area has a significant effect in all models, and explains as much as 48% of the variation in the model for haddock at 275 mm. This factor explains the largest part of the deviation for any one factor for all species other than cod. The contribution to the model explanation is greatest for haddock and norway pout, species found mainly in the northern part of the North Sea. Year has a significant effect on all models, and quarter on all but 5 models. The larger cod shows a large effect of year and, when included in the model, also the crossed effect between ship and year.

The models for haddock are almost completely explained by the area factor. Quarter has a large effect only on the smallest length group, 125

mm. For the largest length group year and the crossed effect between year and area explains almost a fifth of the deviation. Ship effects never exceed 5% of the deviation.

For the remaining species, ship and ship-year effects explain a rather large part of the deviation, topping with sprat, where these effects explain above 20% of the deviation. In many groups, the ship effect exceeds the effect of year, year-area, quarter and quarter-area.

Thus, the most important factor appears to be the area in which the haul is taken. However, this effect changes from year to year, and for some of the models, also from quarter to quarter. Year effect is small for all species but cod, indicating that species other than cod tend to change distribution of catches over the years rather than increase or decrease the probability of catching something over the entire North Sea. The probability of catching all species but haddock is greatly influenced by ship.

6.1.1.2. Test for significant crossed effects of ship and area and ship and quarter, respectively

The crossed effects between ship and area and ship and quarter had significant effect on 15 and 8 of 21 models, respectively (table 6.1.1.2). This is probably due to the large residual variation in the model, and could indicate further ship differences or be a product of different ships not trawling at the same time, though they may have been in the same area. As can be seen by comparing fig. 5.1.1.2 and fig. 5.1.2.2, two ships trawling in the same area at the same time will often have trawled in different squares. A crossed effect between ship and area may thus be an effect of square within 4-square area.

6.1.1.3. Without ship effect

A summary of the models is given in table 6.1.1.3. 9 of the models now yield different significant effects (apart from ship and ship crossed with year, which are excluded from all analyses) than the model for the same group including ship effect. Only in one model (herring at 275 mm) does effects formerly excluded become significant. In the remaining 8 model, model dimension is decreased more than just the degrees formerly contributed by ship and crossed ship effect, in particular by excluding crossed effects between area and year (4 models) and area and quarter (2 models). This is presumably due to the increase in residual deviation, which decreases the F-value used when testing.

6.1.1.4. Comparison of the two models

The model including the ship effect gives a better or just as good explanation of the deviation in all cases but one (herring, 275 mm) (table 6.1.1.4). The improvement in explanation of the deviation ranges from 0% to 140% for haddock at 125mm (and 225 mm) and whiting at 225 mm, respectively. In half the cases (excluding haddock), the improvement is higher than 50%. It thus seems, that there is a large difference between ships in the probability of catching something, and that this effect should be included in the model.

The overdispersion is increased slightly from 0.99 to 1.13 (mean=1.061) to 1.02 to 1.26 (mean=1.097) when ship effect is excluded. Dispersion is thus generally increased when excluding ship effect, indicating a better fit of the model distribution in the model with ship effect.

6.1.2. Model for numbers caught

6.1.2.1. With ship effect

The models generally explain from 44% to 65% (mean 52%) of the total variation (table 6.1.2.1). The fit is slightly better for the smallest lengthgroups (75 mm and 125 mm) than the larger. The models for cod above 150 mm and herring explain slightly less than and the models for haddock, sprat and whiting slightly above the average. All together, this level of explanation is considered to be fair, remembering the large number of factors, that probably have an effect but are excluded from the model. Among these are depth, date within a quarter and time of day at which the trawl was taken. Wind, current and temperature may also have an effect.

As in the 0-1 model, 4-square area explains the greatest part of the variation for all species and length groups except 2 (cod at 225 mm and herring at 350 mm). The percentage explained by this factor ranges from 15% to 38% for cod at 225 mm and haddock at 275 mm, respectively.

For most species and size-groups, the crossed effect between year and area is the 2nd most important factor, explaining from 9% to 19% when included in the model. The crossed effect between area and quarter is almost as important. As the effects from year and quarter are much smaller, the difference between the years seem not as much to be how much is caught but rather where the catch is taken.

The quarter effect and the crossed effect between area and quarter is strongest for small cod, haddock and whiting as well as norway pout in

all size classes. For herring, the opposite appears to be the case, as quarter and crossed effects with quarter show increasing importance with increasing length-group.

Ship show a moderate effect for cod with no obvious increase or decrease with length. For haddock, the ship effects are small as was the case in the 0-1 model. Herring, norway pout and whiting all show smaller effects of ship and ship crossed with year than was the case in the 0-1 model, the effect on number caught being greatest for small lengths. Sprat catch is greatly influenced by ship effects, these explaining 10% of the total variation.

6.1.2.2. Inspection of residuals

Only in 10 and 8 of the 26 groups can the residuals be assumed to be normal distributed for the model with and without ship effects, respectively (table 6.1.2.2). However, the distributions of the residuals seem to be symmetric and resemble the normal distribution when inspected by eye. The distributions are skewed, but to different sides for different models. The residuals from the analyses of cod and sprat are positively skewed, whereas the residuals from haddock and norway pout are negatively skewed. The residuals of herring and whiting are negatively skewed for lengthgroups below 200 mm, and positively skewed for the remaining lengthgroups. Positive skewness indicates, that the lognormal distribution is not sufficiently skewed to describe the data, negative skewness, that the lognormal distribution is too skewed (observations show less increase in variation with mean than the lognormal distribution).

Examples of residual plots are given in fig. 6.1.2.2. Inspection of plots of the residual as a function of predicted value reveals no tendencies towards increasing variation with increasing mean. The discreteness of the variable (number caught) does however give the plots a number of "stripes", which are caused by the jump from ln(1) to ln(2) and so forward. This pattern is most obvious for groups, were few fish are caught. It is not considered to impair the analyses.

Though the assumptions of the model are thus not fulfilled for all analyses, the models are not considered to have systematic errors, as the residuals show no trends. As the residuals are thus not too badly behaved, the models are considered to give a better estimate of the number caught than a simple average would have given.

6.1.2.3. Test for significant crossed effects of ship and area and ship and quarter, respectively

The crossed effects between ship and area and ship and quarter had a significant effect in 4 and 8 of the 21 models (table 6.1.2.3). The crossed effect with area is only found in the species and lengths, where this effect is significant in the 0-1 model as well. The opposite is true for the crossed effect between quarter and ship, as this is generally not found for the same species and lengths as was the case for the 0-1 model. There are markedly fewer models showing a significant crossed effect between area and ship than was the case for the 0-1 model. This may indicate, that the number caught varies less between squares within an area, than does the probability of catching something. It may also be due to the larger residual variation allowed in the normal distribution.

6.1.2.4. Without ship effect

Model summary is seen in table 6.1.2.4. One model show a decreased dimension (greater than what is due to excluding ship effects), while for two models, the dimension is increased. Apart from this, the results correspond to the above (excluding the ship effects).

6.1.2.5. Comparison of model with and without ship effects

In all but three cases, the ship effects improve the model, both as measured by the r^2 and the standard deviation around the model (table 6.1.2.5). There is no clear tendency towards improving or aggravating the distribution of the residuals by excluding the ship effect. The standard deviation is however lessened, and the r^2 increased almost unanimously when including the ship effect. It was therefore decided to use the model including the ship effects.

6.1.3. Comparison of 0-1 model and model for numbers caught

The model for numbers caught generally have more significant effects and thereby higher dimension, than the 0-1 model. In 7 models, a factor found not to be significant in the number-model was found significant in the 0-1 model, but comparatively, all number-models but 1 included more significant effects than the corresponding 0-1 model.

Explanation was however also better, the models for numbers accounting for 5% more, on average, of deviation. Only haddock showed higher explanation for the 0-1 model than the model of numbers caught for 4 of the 5 size-classes.

When considering the high explanation of crossed effects with area, the large amount of parameters estimated should be taken into account. In these cases, examination of the F-values or the probabilities for these can give a more appropriate picture of their significance for the model as a whole. The probabilities show, that these crossed effects often only just are included in the model. This may be part of the explanation of the differences between the models for the different species and sizegroups.

In general, the models are considered to describe the catches fairly well, taking all the other factors, that may have an effect into account, as mentioned in section 6.2.2.1.

The large effect of area and the crossed effect between area and year implies, that the most important factor determining if something is caught, and given something is caught, how much, is where the haul is taken. The effect of year is generally much smaller, as is that of quarter. Differences between year class strength thus to a lesser extent affects the catch than the fishing position and the difference in distribution of the catches (and thereby presumably the stock) over the years.

Quarter mainly have an effect on small length groups. This is as expected, as these grow quickly, and therefore quickly "outgrow" the small length classes. Thus, small fish present in the 3rd quarter may very well have grown and be recorded in the next lengthclass in the 4th quarter. In the 1st quarter, the smallest lengthgroup may be caught in very low numbers, as the new yearclass has not yet settled and therefore is not available to the trawl.

The crossed effects between year and area and quarter and area may similarly be caused by two factors: The small fish may drift or actively swim from one area to another (the last being relevant only for small distances) or the changes in catch may be due to fish growing faster in one area than another. Any combination of the two may be the actual case. The difference in growth is probably important, as a small length group will often be caught predominantly in the southern part of the North Sea in one quarter, and predominantly in the northern part in the next quarter as shown in fig. 6.1.3.1. Especially for herring, the drift of young fish is important. Small herring are caught in the Southern North Sea, near the Dutch coastline. As the herring length increases, catches move clockwise around the North Sea, ending in the northern part, where the largest herring are taken (fig. 6.1.3.2).

The large area-effect on haddock and norway pout is quite understandable, as these species are confined to the northern part of the North Sea (fig. 6.1.3.3). For sprat, the same applies, only this species is

confined to the southern part. Catches of cod and whiting are rather evenly distributed, though there are regional differences for these species as well.

It is interesting, that haddock shows virtually no effect of ship. If the ship effect is due to lack of overlap or the differences in time of survey between the different ships (surveys are carried out over as much as 2 months (ICES, 1981b)), one would expect the same effect on haddock as on the other species. Also, haddock is known to move upwards at the sound of the ship (Ona & Chruickshank, 1986) and this effect would be expected to be different from ship to ship. In the case of cod, the trawl selection seems more dependent on the ground gear used than evasive actions upwards or to the sides (Engås et al., 1988). As the ground gear is the same for all ships, a ship effect on cod catches would be expected to be smaller than the effect on haddock.

The smaller length groups are generally better described than the larger in both models. This could be due to a more even distribution of the smaller fish on the scale sampled by the trawl. Thus, if smaller fish are patchily distributed on a smaller scale, they will appear evenly distributed when sampling on a large scale.

6.1.4. Predictions of the model

The total number caught in the North Sea as predicted by the model including the ship effects is seen in fig. 6.1.4.1 for the 5 years and in fig. 6.1.4.2 for the 4 quarters of 1991. As only two and three length groups are modeled for sprat and norway pout, respectively, there is little information in examining catches of these two species as a function of length. They are therefore excluded both from examination of yearly and quarterly catches. Catches of the 350 mm group are plotted as 0.5*estimated catch, as this group is twice as broad as the others.

6.1.4.1. Yearly catches in the 1st quarter

For all species, the distribution of the catch on the different lengthgroups varies from year to year. All 4 species show a peak length above average in 1981, which could correspond to this year being a year with higher growth for all, e.g. because of more abundant food, higher temperature or other factors. However, this is the only year, in which peak length is increased for all species. All other years, some species show increase while others show decrease, thus leaving no clear over-all picture.

Not one species show the exact same length distribution of catches in two years. As predators exhibit some degree of length preference, if for no other reason, then because of physical constraints, it is not reasonable to expect the suitability of age 1 species i to age 1 species j to be the same in different years, as the two species may have quite different length distributions in different years. As the predators considered here are as small as 20 cm, it is of great importance if the age 1 group have a peak length of 10 cm or 15 cm.

6.1.4.2. Quarterly catches in 1991

As the yearly catches, the length distribution of the quarterly catches vary markedly. All species show an increased peak length of catches from 1st to 2nd quarter, presumably as the 1-year olds grow. In 3rd and 4th quarter, a new peak appears, indicating that the 0-year olds become available to the trawl at this time. As fish of different species thus do not grow at the same rate, the suitability of age 1-group of one species as compared to another species can not be expected to be constant over the year.

6.1.4.3. Comparison of predicted catch of 1-year olds to VPA estimates.

The predicted catch of 1-year olds is plotted as a function of VPA-estimates in fig. 6.1.4.3. The correlation is never higher than the correlation between the index calculated by ICES and the VPA (table 6.1.4.1). This index is calculated as the geometric mean of ln(number caught+1) within a square. The arithmetic mean of all squares is then calculated, and this is the ICES IBTS index. The index does not correct for ship effects. As the VPA is tuned by the ICES index, the correlations between this and the VPA can not rightfully be compared to the correlations between the catch predicted from the model build here and the VPA. The predicted catch only deviate substantially from the ICES index for norway pout and sprat (fig. 6.1.4.4). This is as expected, as both species show a large effect of ship on catch.

6.2. Examination of stomach contents

6.2.1. Diet composition

The diet composition varied between predators and predator length groups (fig. 6.2.1.1). For all three predators, crustacea and fish make up the prevailing part of the diet, though less so for haddock than cod and whiting.

All predators exhibit a gradual switch from crustacea being the dominant prey at small predator lengths to fish prey dominating at large predator lengths. For the predator lengths used in analyses of ratios, fish make up above 50%-80% of the diet, with the smaller percentages found for medium size cod. Thus, no more than 50 % of the food is non-fish, and in most length groups, the percentage is as low as 20%. As a model should give a better description of prey eaten regularly than prey eaten sporadically, the high percentage of fish in the diet should improve the fit of the suitability model.

6.2.2. Fish prey

When examining fish prey only, the fish species considered in the analyses make up the greater part of all fish prey (by number) for the predator species and size groups included (fig. 6.2.2.1) in analyses of ratios. When gathering information for an index, it is important, that the total number of the particular prey recorded is high. In this respect, it is of little help to examine a predator eating only the particular species, if this predator is only rarely caught. It is thus clear by comparing fig. 5.2.1.2 and fig. 6.2.2.1, that though large predators eat large amount of fish prey, they are caught infrequently, and the total number of fish prey found in this group is small. Small predators, though caught more frequently, have few fish prey in the stomachs and therefor are equally unsuitable.

In all three predators, sandeel make up a substantial part of the diet. Haddock eat only few other fish species to any extent, namely flatfish and, for haddock between 200 mm and 800 mm, norway pout. As flatfish are caught infrequently in the IBTS, these can not be used to build a model. This leaves norway pout as the only species found both in the stomachs and the IBTS. Ratios between prey species can thus not be examined for this predator.

The relative frequency of sandeel in the stomach of cod increases with predator length up to a predator length of 350 mm. Here, a maximum of around 35% of the fish prey is reached, and this proportion is held

fairly constant up to a predator length of 450 mm. For larger predators, the proportion of sandeel in the diet decreases down to around 10% for cod at 1100 mm. Gobidae make up a large part of the diet for small cod, but their importance quickly decreases with length, reaching less than 10% for cod above 400 mm. Cod makes up a very small part of the diet, but is nevertheless included in the calculation of ratios. Norway pout is present in cod above 200 mm, increasing its importance to a maximum of 20% in cod at 600 mm. For greater lengths, the proportion decreases, leaving around 5% in cod at 1100 mm. Sprat makes up a small part of the fish prey, lying at 2% to 6%, the higher proportions being found in cod above 700 mm. Haddock, other fish and flatfish excluding sole make up a fairly constant part of the fish prey for cod above 200 mm, with proportions of 4-8% each. The proportion of whiting and herring increases with length of predator, ranging from 0% for the smallest cod to 10% each for cod above 1000 mm. Sole makes up a fairly constant proportion of the fish for cod smaller than 500 mm. For larger predators, the proportion increases quickly, ending at above 20% for predators at 1100 mm.

Whiting does, in contrast to cod, not have flatfish to any extent in the stomach. The single most important fish prey is sandeel for all lengthgroups but 50 mm and 350 mm. As the 50 mm and 600 mm group consists of very few stomachs (see fig. 5.2.1.2), they have been omitted in the following. The proportion of sandeel rises with length up to a maximum of above 50% in whiting at 250 mm. For larger whiting, the proportion decreases, ending at 30% for predators at 450 mm. Sprat and herring make up 2-6%, the highest proportion being found in whiting at 450 mm. The proportion of norway pout increase with length of predator, ranging from 8% at 150 mm to 25% at 450 mm. Haddock is only found in significant proportions in whiting at 450 mm, reaching a proportion of 12%. Gobidae is found mainly in predators at 150 mm, its importance decreasing rapidly with length of predator, and disappearing completely in predators above 400 mm. Cannibalism is very important in predators at 300 mm, making whiting the single most important fish prey in this length group, but only make up a small part of the diet for other predator lengths.

For both of the predators cod and whiting, there appears to be marked changes in prey preferences with length of predator. The proportion of the diet consisting of a certain prey species appear to peak at a certain predator length for several prey species, e.g. whiting eaten by whiting. Both species eat gobidae in large numbers as small predators, but these prey are completely excluded from the diet as the fish grows. In all but the smallest lengthgroups, sandeel is the dominant prey, followed by norway pout for both predators. As norway pout is included when building the model, the model should be able to describe the fact that one species is much more frequent than the others. Thus, generalizing the model to describe the number of sandeel in the stomachs should not be impaired by the fact, that sandeel is the dominant fish prey (by numbers).

Only the fish prey used in the analyses of ratios are considered from this point on.

6.2.3. Length composition of fish prey

The length distribution of the fish eaten is unimodal for all prey, predators and predator length groups. The peak length is generally the same for all prey species, and in all cases varies no more than 50 mm (one size group) between species within predator group. There is an increase in peak length with predator length for all prey species (fig. 6.2.3.1).

The mean length of prey increase with predator length, but not with the same rate for all prey species (fig. 6.2.3.2). Thus, the increase in mean length is small for sandeel eaten by whiting compared to the other species, and the mean length for norway pout, sprat and sandeel eaten by cod seems to reach a plateau at a prey length of 100 mm. The remaining species show similar increase in mean length with predator length. The difference is probably partly due to the norway pout, sprat and sandeel reaching lower lengths than the other species. For the predator whiting, the difference between species is less pronounced. This is probably due to the smaller range of predator lengths for whiting, since by comparing with cod, it seems that cod at these lengths do not eat norway pout, sprat and sandeel above 100 mm to extent.

The standard deviation of the prey length also rise as a function of predator length (fig. 6.2.3.3). However, the rise seems to depend solely on length and not on predator species, as the two predators show similar values. As the mean length, the standard deviation for norway pout, sprat and sandeel reach a plateau at around 40. The value is a bit lower for sprat, and higher for sandeel. This corresponds to sandeel and norway pout being present in a larger size range than sprat. The standard deviations of the gadoid species are generally larger, as these species are present in a larger size range and apparently also eaten in a larger range of sizes.

The rise in mean length and standard deviation of the length distribution of the prey is in accordance with Andersen & Ursins (1977) model of prey size selection. Theoretical plots of prey length distribution as calculated from Andersen & Ursins size selection model is seen in fig. 6.2.3.4. They are based on equal abundances of all prey lengths, and the observed distribution in an environment, where the less preferred prey is more abundant than the most preferred, the length distribution of the prey should be broader. This is as observed.

6.2.4. Partial fullness index

The partial fullness indices (fig. 6.2.4.1) should be compared with the distribution of the prey as inferred from the predicted trawl catches (fig. 6.1.3.2 and fig. 6.1.3.3). The PFI's cover a larger area than the IBTS catches. Even in areas where no norway pout of this length are caught by the trawl in a particular year, they are still found in the stomachs of the predators. In general, the coherence between the spatial distribution of the PFI's and the trawl catches are not impressive. This could be due to the trawl catches not reflecting the actual distribution, or it may be, that the amount of a prey eaten does not show a straight forward dependence on the number present. In any event, this result is different from Lilly's results examining the stomach content of shrimp (Lilly et al., 1998). Here, Lilly found a fair correlation between the spatial distribution of commercial catches and PFI's. Another difference from Lilly's results, is that the PFI's found here are a factor 10 larger. The reason for this is unclear, but is probably a problem of units or of the power ten must be lifted to before multiplying this with the index.

The distribution of the PFI of sandeel at 75 mm are shown in fig. 6.2.4.2. The predators do not show the same pattern, as cod have the highest PFI's near the coast of England, haddock at the southern limit of its distribution and whiting in the far north. To use the PFI's to indicate the quantitative distribution of sandeel, the results from the three predators should be correlated.

6.2.4.1. Comparing the PFI of yearclass 1 in the 1st quarter to VPA estimates.

The correlation of PFI's of the predator whiting is above 0.50 for all prey but whiting (table 6.2.4.1, fig. 6.2.4.3). However, when examining the correlation between the PFI of whiting as prey and the predicted catch in the IBTS, the correlation is as high as 0.73 (fig. 6.2.4.4). Cod shows a lesser correlation between PFI's and VPA estimates, with only the prey cod, sandeel and sprat having correlations above 0.5. As for the predator whiting, PFI's of whiting as prey shows good correlation with predicted catch in the IBTS. For comparison, Fahrig et al. (1993) found a correlation of around 0.3 when comparing acoustic surveys of capelin abundance to PFI's of the predator cod at this scale. When examing the same two species, Lilly (1991) found a correlation of 0.93 for Soviet surveys but only 0.22 for Canadian surveys. Thus, a low correlation may be due to low coherence of survey results with the actual abundance.

It may be possible to use the 1st quarter PFI's of cod to indicate the year-class strength for cod and whiting, provided that the predicted catch of whiting is an estimate of year-class strength. The predator whiting could provide an index of sprat abundance and less reliable estimates of the other species. Cod eaten by whiting shows a good fit,

but this is dependent on relatively small amounts of cod in the stomachs (with a PFI of zero for two of the years), and is thus not likely to be reliable.

Sandeel has a correlation of around 0.53 for both predators. This is not a very high correlation, considering the low number of data points used. However, it may still be considered a better estimate than none.

6.2.4.2. Comparing the PFI's in the 3rd quarter to VPA estimates of 0-group abundance.

The predator-prey combinations that show high correlation in the 1st quarter generally have lower correlation in the 3rd quarter (table 6.2.4.1). One noticeable exception is herring, for which the correlation is increased to above 0.9 for both predators. Whiting eaten by whiting increases its correlation, which may indicate, that the VPA may give a better estimate of what is present in the predators surroundings in the 3rd quarter than the 1st quarter.

The high correlation for herring indicates that the predators largely eat this species when encountered, and that an index may be build from the stomach content describing the abundance of 1-year olds in the following year. The value of the PFI as an indicator of sandeel recruitment is less promising. With an r^2 value of 0.23 and –0.02 for cod and whiting, respectively, the PFI either is influenced little by prey abundance, or the VPA does not give a realistic picture of the recruitment for this species

As correlation of sandeel PFI's and VPA-estimates is greater in the 1st quarter than the 3rd quarter, this may indicate, that sandeel is more available in the 1st quarter. This is consistent with observations of sculpin and flatfish preying on the pacific sand lance made by Hobson (1986). The predators prey most intensively on this prey at the period where the sand lance leaves the school to bury in the sediment or exits the sediment to join the school. This limits the number of sandeel eaten to the amount that can be ingested in the relatively short period when sandeel leave the school or sediment. In the summer, this will be a few hours at dawn and dusk. In the winter, sandeel spend most of their time buried in the sand, only changing locations occasionally (Whitehead et al., 1984). This will give the predators the opportunity to feed on sandeel buried during daylight, either by striking into the sand or by striking when a sandeel emerges to change position. Another reason could be, that the estimate of 1-year olds in the 1st quarter is a better estimate of the actual abundance than the number of 0-year olds in the 3rd quarter. Due to the calculation methods of the VPA (Hilborn & Walters, 1992), the estimates of the youngest yearclasses generally have a higher uncertainty, so this could be an explanation. However, it

can not be determined from the present data which of the causes is the most likely.

6.2.5. Observation of ratios

Unfortunately, eating one of the species here considered, does not necessarily mean eating several of the species. As observation of at least two prey groups is necessary to calculate a ratio, the data set is reduced severely. To include the ratios in the analyses, the particular reference and prey must also be present in the IBTS. This is not the case for any prey below 25 mm and only for three species at 75 mm, and this further reduces the number of observations. As seen in the PFI's, the prey is often found in the diet in a larger area, than it is caught in the IBTS, so apparently, the size selection in the IBTS is not the sole cause of the problem.

The resulting models have from 184 to 904 observations (4-square area, IBTS model with ship). The observations are not evenly distributed between prey groups, some references occurring more frequently with some prey groups than others (fig. 6.2.5.1). In general, prey of one length group often occurs together with the adjacent lengthgroups. Apart from this, there is a tendency for the reference sprat to occur together with herring and whiting, while the reference norway pout mostly occur together with haddock (examining other species only). This is probably due to the extension of the spatial overlap between the species: Thus, haddock and norway pout are most abundant in the Northern part of the North Sea, whereas small herring and sprat mostly are found in the southern part. The reference whiting is distributed over most of the North Sea, and show almost the same number of simultaneous observations with all the prey species considered. Though there are many observations of ratios to the reference norway pout at 75 mm, a large part of the observed ratios can not be used in analyses, as the IBTS does not show a corresponding ratio. More than any other reference, the results for this reference will rely on observations of ratios within the same species, as between 41% and 52% of the observations are between different lengthgroups of norway pout. This problem is less pronounced for the other references, the within species observations here ranging from 25% to 35% of the observations. Sprat show similar problems as norway pout, many of the ratios being excluded because of missing ratios in the IBTS. Whiting at 75 mm has a larger proportion of ratios missing due to lack of one of the species in the IBTS than the other species. The model for this reference therefor relies more heavily on what is caught by the trawl than the models for the other references. Generally, the problem with missing IBTS ratios is greatest for small prey and/or reference, as these are only rarely caught by the gear used. The observations of whiting at other lengths than 75 mm as a reference generally are less influenced by missing IBTS ratios than the other groups, and also less influenced

by within species ratios. It therefor appears the most reliable of the references.

6.3. Analyses of ratios

Examples of ln(stomach ratio) as a function of ln(ibts ratio) is found in fig. 6.3.1.1.

6.3.1. Basic analyses

A summary of the analyses is given in table 6.3.1.1-6.3.1.3. Selected predicted and observed values of ln(stomach ratio) as a function of ln(IBTS ratio) are shown in fig. 6.3.1.1.

Between 30% and 69% (mean 44%) of the weighted variation is explained by the models. This a fair explanation, considering the amount of effects, that could have an effect but are not included in the analyses. The model dimension varies, ranging from 7 df at the least to 60 df at the most, corresponding to 2.2% to 33% of the dimension of the full model. A model having a dimension of 33% of the full model is probably over-parameterized in the sense, that it will have little ability to describe a repetition of the experiment.

6.3.1.1. Examination of residuals

In none of the models is the distribution of the residuals significantly different from a normal distribution with mean 0. There is a tendency for variation to decrease with predicted value for the reference sprat at 125 mm, and for variation to rise with predicted value for whiting above 175 mm (fig. 6.3.1.2). The lines on the plots of residuals as a function of predicted value are caused by the discreteness of ratios, when the number of relevant prey in the sample is small. This is not considered to impair analyses. No trend is apparent when plotting residuals as a function of ln(IBTS ratio), indicating that it is not unreasonable to assume a linear relationship between this factor and ln(stomach ratio).

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. 6.3.1.3). However, the residuals should be distributed with a variation of $\sigma_i^2=\sigma^2/w_i$ (the curve plotted on fig. 6.3.1.3)(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 indicates, that the variation in stomach content will not be reduced to zero by taking

infinitely large samples. Rather, some level of variation is reached, where increasing sample size does not decrease variation. This could be 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. Thus, the increased number of stomachs in a sample does not correspond to an increased number of hauls, and the variation is reduced by less than the number of stomachs.

6.3.1.2. Significant effects

The significant factors in each model and the total explanation of the effects and the crossed effects with them can be seen in table 6.3.1.2 and 6.3.1.3, respectively.

Due to the many differences between the model, interpretation of the significant effects is difficult. Thus, only the slope and its crossed effects (the switching coefficient and the factors that have an effect on this) is examined closely in the basic models. The intercepts predicted from these models are highly variable, and show little consistency when plotted as a function of prey or predator length. As they should not vary freely, but rather be some continuos function of prey and predator length, they are not interpreted here. Instead, the intercepts and slopes derived from the model describing this factor as a polynomial function of prey and predator length are examined in section 6.3.5.

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 (the slope) is only allowed to vary with predator and predator length. It may be due to a dependence of visibility on abundance. Another cause for these effects could be the highly unbalanced data-set, that is, the effects are artifacts of the model and not actual biological effects. A difference in slope between predators and predator length groups occurs at whiting at 75 mm and norway pout at 75 mm and 125 mm, respectively. This is in not in conflict with the suitability model.

As mentioned above, the model for 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%. Also, when calculating the slope for all combinations of prey and predator in the model for whiting at 75 mm, several combinations reveal powerful negative correlation, the slope falling to as low as –1.14. As the ratio in the stomach cannot possible rise as the ratio in the IBTS falls, this model is considered fairly unrealistic. It is furthermore based on the smallest number of observations for any of the models (184), 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 others.

The slope is significantly different from 0 and 1 in all models ($p<0.0001$), where no crossed effects with slope are found significant. The upper limit for the 95% confidence limit for the slope (where no crossed effects are found) has a maximum value of 0.29. The lowest 95% lower confidence limit is 0.077. The average slope weighted by number of observations used in each model is 0.192. This gives a dependence of the ratio in the stomach on the ratio in the IBTS as shown in fig. 3.4.1 ($b=0.2$), when transformed back to stomach ratio as a function of IBTS-ratio. As seen in the figure, a slope of 0.19 indicates powerful negative switching.

6.3.2. Investigations on the effect of number of stomachs in a sample

The object of these investigations was to determine, if the number of stomachs in the sample had a tendency to lower the switching coefficient, as the sample size was increased. If this is the case, the low switching coefficient found in the basic analyses may be caused by the pooling of stomachs as suggested by Chesson (1984).

6.3.2.1. Number of stomachs included as a variable

The models explain between 25% and 67% of the total variation (mean 37%) (table 6.3.2.1). The model dimension varies, ranging from 12 df at the least to 67 df at the most, corresponding to 2.6 and 36% (mean 8.6%) of the full model, respectively. The dimension of the model for the reference group whiting at 75 mm is 36% of the dimension of the full model, and is thus very high in this analyses also.

6.3.2.1.1. Examination of residuals

The residuals are significantly different from a normal distribution with mean 0 in two models (sprat 125 mm and whiting 275 mm). There is no trend in the residuals when plotted as a function of the predicted value or ln(IBTS ratio) in the sample. When plotted as a function of number of stomachs in the sample, the pattern is the same as noted above in section 6.3.1.1.

6.3.2.1.2. Significant effects

The effects found to be significant differ from one model to the next as was the case for the basic model (table 6.3.2.2). However, the ln(ibts ratio) always has a significant effect, explaining from 5% (whiting at 75 mm) to 21% (mean 15.7%). In all models except whiting at 75 mm, this is the largest part of the variation explained by any one factor.

The number of stomachs in the sample have an effect on all models but one, explaining from virtually 0% to 3.7% (mean 1%), and when included, number of stomachs always 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% (mean 5.5%) when included in the model.

Contradicting the theory of the suitability formula holding for all combinations of reference group and prey, there is a significantly different slope in the different prey and/or prey length groups for whiting at 75 mm and norway pout at 125 mm. For the other reference groups, such a difference in the slope can however not be detected.

There is a relatively large 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, thus increasing the slope with the number of stomachs in the sample (fig. 6.3.2.1). For norway pout at 125 mm, one predator lengthgroup shows a negative effect of number of stomachs on slope, but the remaining groups all show positive effects (fig. 6.3.2.2). The low switching coefficient is thus not due to artificial lowering by pooling of stomachs (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.

There may however be alternative explanations for this. The effect of number of stomachs on the switching coefficient could first of all 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. However, it might also be caused by the limited stomach size of the predator (section 5.5.1). A saturated predator will thus attain a maximum (or minimum) ratio, which cannot be exceeded. When performing a regression on the values, the solution minimizing the sum of squares for different saturation levels are shown in fig. 5.5.1. It is clear, that the increased maximum and minimum ratio (increased stomach size) results in a higher slope. Increasing the sample size gives the same result, as this increases the maximum ratio and decreases minimum ratio.

If the predator reaches a maximum or minimum 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. If there is such an effect on these data, it is not strong enough to be visible

at this scale (fig. 6.3.2.1). 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 (fig. 6.3.2.2). Whether a model taking saturation into account will fit the data better is examined later in the project. For the following analyses, it has been assumed, that the effect of number of stomachs in the sample on the slope is due to the smaller random variation in a larger sample, and the number of stomachs in the samples are thus used as weights in the analyses of ratios.

6.3.2.2. ln(number of stomachs) included as a variable

To examine if the effect of number of stomachs in the sample was due to a few very large samples "pulling" the effect in this direction, a series of analyses were done with ln(number of stomachs in the sample). A summary of the model can be seen in table 6.3.2.3. Model explanation was improved in two cases while decreased in the remaining 8 cases as compared to including number of stomachs in the sample untransformed. It decreased model dimension in all but these two cases and the residual standard deviation was increased in all but one case. The total explanation of number of stomachs in the sample and crossed effects with this was generally lower in the analyses with ln(number of stomachs) (lower in 7 of 10 analyses). As the variation explained by ln(number of stomachs) was lower than by number of stomachs, the analyses including the number of stomachs was considered to fit the present data better.

6.3.3. IBTS model without ship effect.

The summary of the models is given in tables 6.3.3.1 and 6.3.3.2.

When building a model of the ratio in the stomachs as a function of the IBTS ratios predicted from the model excluding ship effects, model explanation is only changed to any extent in three cases (table 6.3.3.3). In all three cases, the model including the ship effect gives higher r^2. All other models show a less than 2% change in r^2. The model build on IBTS models including ship-effect, gives an improved explanation for all reference groups of 75 mm, the improvement being greatest for whiting. Model dimension is however simultaneously increased, also to the greatest extent for whiting at 75 mm.

Another measure of model fit is the residual variation. This is lower in 4 models including ship effect, and higher in 6 models. The mean change is however a slight decrease (std(without ship)-std(with

ship)=0,021) in residual variation when including ship effect. Once again, for reference groups at 75 mm, the models are improved as measured by a decreased standard deviation.

The mean change in model dimension is a small decrease when including ship effect, with 4 models having a lower dimension, 3 being unchanged and 3 having a higher dimension when including ship effect. A change in dimension may however have several causes: An increase in random variation will make factors less significant when tested, and may therefor lead to exclusion of otherwise significant factors. However, with a data-set as unbalanced as this, increase in variation from one source may lead to other sources giving a significant effect when tested. The result may also be caused by variation being greater on the uncorrected IBTS values: Greater variation on the IBTS catches for some groups will tend to decrease slope for these. This could be an explanation of the greater number of models showing significant crossed effect between prey length and slope in the analyses of the uncorrected data. However, this should decrease the percentage of the variation explained by the ratio in the IBTS in the uncorrected analyses, and this is only the case for 5 of the 10 models. For sprat at 75 mm and whiting at 75 mm, the decrease in r^2 for ratio in the IBTS is 5.0% and 5.2%, respectively, when using the uncorrected IBTS predictions. These two groups also show a large effect of ship on catches, 38% and 11% improvement of model of ln(number caught), respectively. Sprat at 125 mm also shows a large effect of ship on catches, but nevertheless has a lower r^2 for ratio in the IBTS when correcting the IBTS data for ship. As the reference group is present in all ratios in the model, the ship effect on this group is very important, but if the particular reference is observed with a few prey groups, these may have an effect that is equally important. This can however not be the explanation for the difference between the two sizes of sprat, as these show almost identical number of observations in all prey groups (they generally occur simultaneously).

As the residual variance is decreased in 6 of 10 cases when correcting the IBTS predictions with ship, the predictions including ship effect are used in the following analyses.

6.3.4. Effects of year, quarter and area.

Model explanation is increased to 73% to 88% (mean 80%) of weighted variation when including the factors year, quarter and area (tables 6.3.4.1 and 6.3.4.2). Model dimension is however also increased, making the model dimension 28-50% of the full model (mean 39%). The residuals, though still one-topped, are no longer normal distributed in 8 of the 10 models. Residual plots show no trends, except perhaps a tendency to greater variation at high and low

predicted values. Residual variation is decreased in all models as compared to the basic models (table 6.3.4.3).

The only three factors tested, that are not found significant in any of the models, are slope crossed with quarter, slope crossed with predator and prey length crossed with area (table 6.3.4.2). Crossed effects between slope and area are only found for sprat. Here, the slope becomes negative in several cases, and for sprat at 75 mm, the mean slope if averaged over areas (regardless of number of observations in each area) is only –0.17. This may be caused by the IBTS catches providing a less accurate index for abundance for this species than for the others, as 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 there are significantly different slope in different years (norway pout at 75 mm and 175 mm). Both models yield a slope that is significantly lower in 1981 than the other years. It is in fact so low, that it is negative for all combinations of prey and reference, apart from the model for norway pout at 75, where a positive slope is found for norway pout as prey. As noted above, a negative slope seems highly unlikely. The high number of crossed effects make interpretation of the effect of year, quarter and area difficult, and so, this is not attempted here.

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 factors actually having an effect are associated factors such as depth, temperature, light intensity, bottom texture, mutual interference of predators and abundance of other food. A combination of these then turn up as crossed effects between area, year, quarter and the remaining factors in the model. The biological interpretation of the crossed effects is thus doubtful, and as the models do not provide any great simplification of the observations, year, quarter and area are not included in any other models.

6.3.5. Dependence on length as polynomial.

The models explain from 26% to 58% of the total variation (mean 39%) (table 6.3.5.1 and 6.5.3.2). This is a slight 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 6.5.3.3). The residuals are not significantly different from a normal distribution in any models but the one for the reference whiting at 275 mm. The residuals plotted as a function of the predicted value and of the independent variables show no trends. The residuals plotted as a function of number of stomachs in the sample show similar patterns as described in section 6.3.1.1.

The models once again gave different significant factors. However, the model including all effects found significant in at least one analysis became

$$\ln\left(\frac{F_{i,l_i}}{F_j}\right) = C_{ij,pr} + E_{1,ij} * \ln(l_{pr}) + E_{2,j,pr} * \ln(l_{pr}) + G_{ij,pr} * \left(\ln(l_{pr})\right)^2 +$$

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

where

E_1, E_2 = Constants within indices

Remaining notation as in section 5.4.5

Thus, the term of $\ln(l_{pr})*\ln(l_i)$ has a coefficient of zero in all analyses, and the coefficient of $\ln(l_i)^2$ does not vary within analyses. The factors are generally difficult to interpret, as they are a combination of several other factors. However, the parameters t_{pr}, $b_{0,pr}$ and o are not too complicated to make a meaningful interpretation possible. These parameters and the parameter H_{pr} should further satisfy the demand of constancy over all analyses.

6.3.5.1. Switching and the dependence of switching on predator length

The switching coefficient shows no consistent pattern with predator length when comparing the models for different references (fig. 6.3.5.1). The significance of the factor may thus be due to model estimation techniques and the unbalance of the data-set. Thus, one of the models showing this effect is the model for whiting at 75 mm, which has a high number of significant factors in all analyses. 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. Thus, the largest reference is eaten only by the largest predators, and a trend in switching as a function of predator length should be apparent when plotting switching coefficient as a

function of reference length. Such a trend is however not present (fig. 6.3.5.2), 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, where crossed effects with the switching coefficient are absent. The coefficient appears to be in the range of 0.9 to 0.38, which is the lowest and highest 95% lower and upper confidence limit, respectively. The predators thus exhibit powerful negative switching.

6.3.5.2. Interpretation of the parameter *o*

Recall that the parameter *o* is the combined effect of the predator particularity and the exponent for the conversion of prey length to

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

where

f_i = Exponent of the weight - lenth relationship of the prey

σ_{pr}^2 = A coefficient describing predator particularity in Andersen and Ursins model weight (Appendix A):

Thus, the value of *o* should always be negative.

In 4 models, *o* is found to be significantly different from zero. In two of these, *H* is not significantly different from 0, and the value of *o* may thus be biased by the dependency on $\ln(l_i)$. This leaves two models where both *o* and *H* is significantly different from 0. The values of o should not depend on the reference, and are not found to be significantly different (table 6.3.5.4). None of the 95% confidence limits include positive values. The particularity can be estimated by assuming that f=3 for all prey species. This gives a particularity of 5 and 11 for the analysis of norway pout and whiting, respectively. Calculating the 95% confidence limits give a particularity in the range of 3 to 41. This is higher than the value of 1.1 found by Ursin (1973) and the value of 2.4 found by Hahm & Langton, 1984. The last value must be taken as a maximum, as this experiment did not take the differential abundances of prey lengthgroups into account. The value found here is also higher than the estimated 2.0 used by Gislason & Helgason (1984). This indicates, that the predators are less size selective than found in these experiments. However, this may be due to the large degree of negative switching, witch is bound to affect the intercept of the model.

6.3.5.3. Comparison of parameter estimates of H_{pr} from the different models

If there is an effect of both prey length and prey length squared, excluding one of the factors will affect the estimation of the other, as the model tries to compensate for the lack of the quadratic expression by changing the linear dependency. Values of H are therefore most likely to depend on whether o is found to be significantly different from 0 or not. This is exactly what is observed, as the estimates of H are not significantly different in the two analyses including both this factor and o (table 6.3.5.5). The remaining estimates of H are likely to depend on the average length of the prey, as the model will seek to fit the linear term to the linear term plus the contribution of the squared term. Thus, the estimates are varying, and not the same in all analyses.

6.3.5.4. Comparison of suitability of a given prey combination as a function of length

Recall from section 3.7, that c of one predator length for the prey i and j can be compared to c of another predator length for the same prey:

$$\frac{c_{pr,pl1,ij}}{c_{pr,pl2,ij}} \cong \frac{s_{pr,pl1,ij}}{s_{pr,pl2,ij}}$$

$$\Updownarrow$$

$$\ln\left(\frac{s_{pr,pl1,ij}}{s_{pr,pl2,ij}}\right) \cong \ln c_{pr,pl1,ij} - \ln c_{pr,pl2,ij}$$

Inserting the model found gives

$$\ln\left(\frac{s_{pr,pl1,ij}}{s_{pr,pl2,ij}}\right) \cong C_{ij,pr} + E_{ij,pr} * \ln(l_{1pr}) + G_{ij,pr} * \left(\ln\left(l_{1,pr}\right)\right)^2 + H_{pr} * \ln\left(l_i\right) + o\left(\ln\left(l_i\right)\right)^2$$

$$-\left(C_{ij,pr} + E_{ij,pr} * \ln(l_{2,pr}) + G_{ij,pr} * \left(\ln\left(l_{2,pr}\right)\right)^2 + H_{pr} * \ln\left(l_i\right) + o\left(\ln\left(l_i\right)\right)^2\right) =$$

$$E_{ij,pr} * \left(\ln\left(l_{1,pr}\right) - \ln\left(l_{2,pr}\right)\right) + G_{ij,pr} * \left(\left(\ln\left(l_{1,pr}\right)\right)^2 - \left(\ln\left(l_{2,pr}\right)\right)^2\right)$$

Unfortunately, plotting the relative suitabilities found in this way reveals great dependency on length of reference (fig. 6.3.5.3). This indicates, that the species suitability is not independent of length of reference, as should be the case according to the formula above. This is most likely to be caused by the limited overlap between prey length and predator length. Thus, increasing the preferred prey length also means decreasing preference for small prey. As is seen from fig. 6.3.5.3, the

relative suitability of the reference whiting at 75 mm falls (suitability of other prey increase) dramatically with predator length.

The calculated values of the intercept c range from –6.3 to 5.3, with the numerically largest values found for large cod. This corresponds to one prey being as much as a 500 times more abundant in the stomachs than the trawl (relatively). This implies very strong selection. Unfortunately, the values can not be compared to literature values, as the intercept is strongly influenced by the slope, and as the intercept here is not the suitability, but a combination of several factors.

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

6.3.6. Analyses at different spatial scales

6.3.6.1. Roundfish areas

A summary of the fit of the models is given in tables 6.3.6.1 and 6.3.6.2. 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 (table 6.3.6.2). It does however also increase the dimension of the model by as much as 10% of the full model dimension (sprat at 125 mm). Taking both factors into account, only two models have a higher relative dimension at roundfish area than 4-square area. The proportion of the total variation explained by the model is increased in all models, the improvement ranging from 9% to 26% (mean 17%).

6.3.6.1.1. Examination of residuals

The residuals are not significantly different from a normal distribution in the models for all references but norway pout at 75 mm. There is a weak tendency for residuals to fall with the predicted value of the ln(stomach ratio), indicating that it is not quite reasonable to model dependency of ln(stomach ratio) as a linear function of ln(IBTS ratio) at this scale (fig. 6.3.6.1). 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 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 in section 6.3.1.1. Thus, had the variation of the observations actually decreased by (number of stomachs)$^{-1}$ as a function of number of stomachs, the residual variation of the roundfish area model should be of comparable size to the variation in the basic model. As it is, standard deviation is increased by 250% on the average by increasing the spatial scale. An alternative would be not to include the number of stomachs as a weight in the analyses on a higher spatial scale. However, if including the number of stomachs sampled in a roundfish area as a factor similarly to the analyses in section 6.3.2.1, the number of stomachs still have significant effects on slope. Thus, the problem remains how to include the number of stomachs in the best way. The weighting problem should however not impair the comparison of r^2 and parameter estimates, so the problem is ignored in the following.

The crossed effects with slope make it difficult to compare the parameter estimates for this factor with estimates from the basic model. The models for norway pout at 125 mm and 175 mm does however not have a great number of crossed effects with slope in either model. Here, the slope varies only with prey length, and for norway pout at 125 mm, with predator length (fig. 6.3.6.2). 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.

Another way to compare the effect of the ratio in the IBTS is to compare the proportion of the total variation explained by this factor. Here, there is a general increase when building the model on roundfish areas, though one model show a decrease of 12% (norway pout at 175 mm). This increase is probably due to a further decrease in individual variation as more stomachs are pooled. However, it is of little informative value, as there is a general problem with the model description of the data as indicated by the residuals.

6.3.6.2. North Sea

Model explanation is further increased when increasing the spatial scale to the whole North Sea as compared to roundfish areas (tables 6.3.6.4, 6.3.6.5 and 6.3.6.6). However, with only 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 therefore 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 (whiting at 75 mm), explanation is higher in the North Sea model than in the basic model. Model dimension is increased in 7 of the 10 models as compared to the basic models.

6.3.6.2.1. Examination of residuals

The residuals are not significantly different from a normal distribution in all but the model for sprat at 125 mm. The plots of residuals as a function of predicted ln(stomach ratio) shows a decreasing tendency for sprat and whiting at 75 mm (fig. 6.3.6.3). The comments in section 6.3.6.1.1 refer to these plots as well. The plots for the other references show no trends. The residual variances cannot be compared to the variances of the basic and roundfish area-models due to reasons given in section 6.3.6.1.1.

6.3.6.2.2. Significant effects

Half the models are in conflict with the suitability model, as they have significant crossed effects between slope and prey, slope and prey length or both. 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).

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 build on another spatial scale. The proportion of the variance explained by ln(IBTS ratio) is generally lower on North Sea than Roundfish area and in the basic model (lower in 8 models and 6 models, respectively).

The improvement in total model description when increasing the spatial scale seems to come largely from a greater number of significant effects. This is a general problem, when variation is increased in an unbalanced set of observations. The model on roundfish areas does not describe the data set well, and should not be used. The model on North

Sea scale have limited biological meaning, as ratios are also calculated between species not overlapping in distribution. Must the scale be increased, the model at North Sea scale nevertheless describes the data most accurately of the two.

6.3.7. Predicted abundance of sandeel from the model of ratios

The predicted abundance-index of sandeel in the 1st quarter varies between references and predator lengths. This should not be the case, but is due to the large variation in the data. The references showing the best correlations are norway pout at all lengths and whiting at 75 mm (table 6.3.7.1, fig. 6.3.7.1). Of these, only the two smallest groups of norway pout have a correlation significantly different from zero. The correlation between the estimates using these two references and the VPA estimate is 0.62 and 0.63, for 75 mm and 125 mm respectively. This is somewhat higher than the correlation between the PFI and the VPA. The reference lengths showing the best correlation are thus the ones of similar size as the sandeel. This is probably largely due to the higher number of observations of ratios between similar sized prey. Sprat could not be expected to show a good correlation of the prediction and VPA of sandeel, as this species is concentrated in a rather small part of the southern area, and thus is unlikely to give a reliable estimate for the abundance of a prey in the whole North Sea.

6.4. Saturation model

6.4.1. Maximum weight of stomach content

The maximum weight of the stomach content can very well be described as a function of fish length (fig. 6.4.1.1, table 6.4.1.1). Thus, the model describes 98.8% of the total variation with only one variable having a significant effect.

The resulting model was

$$\ln\left(\max(W_{pr,pl})\right) = \ln(0.005489) + 2.82\ln(pl)$$

The parameter value of ln(length) is 2.82, which is close to 3, which is the potency usually found (Jensen & Sparholt, 1992). This indicates,

that maximum stomach content probably is a percentage of body weight and that this percentage varies little with length. The condition factor listed by ICES (1990c) is around 0.01. Assuming this values for both cod and whiting, the maximum stomach content is 55% of the weight of the predator. This is obviously unrealistic, and this value is not even the mean but the median value, as the skewness of the log-normal distribution is not taken into account. The problem here is probably, that the estimated maximum stomach content is for the largest predator present in the length group.

There is no significant difference between the parameters for the two predators, which may only mean, that the actual differences are too small to be significant in a data set of this small size. The residuals show no trends with expected value, and their distribution is not significantly different from a normal distribution ($P<0.40$).

The model predicts that less than 1% of the predators are more than 75% saturated, but as a saturation level of 50% of total biomass is clearly unrealistic, this only means, that the 1% are definitely saturated. The percentage holds little information on whether the rest of the population is saturated or not.

6.4.2. Maximum weight of prey in the stomachs

The model of maximum prey weight has a very good fit ($r^2=0.96$), with the explanation being slightly lower than for the model of maximum stomach content (fig. 6.4.2.1, table 6.4.2.1). Had there been major differences in digestion state between different sized individuals of the same species, one would not have found such high explanation of the total variation. The residuals show no trends, but are not normal distributed ($p<0.03$). However, the distribution still appears symmetric.

The resulting slopes and intercepts for each combination of prey and predator is seen in table 6.4.2.2. There is a small increase in prey weight with predator length, but only the intercept is affected and not the slope. The intercepts in the table are therefore standardized to a predator of 350 mm. The slopes for the predator whiting are 0.87 smaller than the slopes for cod. As the intercept for cod lie closer to the expected values (2.83 as compared to 2.96 found for cod in cod stomachs from the Baltic Sea (Jensen & Sparholt, 1992), there seems to be a problem with estimating the prey weight for whiting in this way as is also indicated by the enormous intercept values. In the early stages of digestion, weight of remaining prey can be assumed to be an exponential function of weight at ingestion as shown Salvanes et al. (1995). If this is the case, the weight of the prey can be expressed as

$$w(t) = w_0 * \exp(-r * t)$$

where

t = Time elapsed since ingestion of prey

$w(t)$ = Weight of prey at time t

w_0 = Weight of prey at ingestion

$-r$ = Digestion rate

Substituting a potency function of prey length for prey weight, this becomes

$$w(t) = (c * l^b) * \exp(-r * t)$$

$$\Updownarrow$$

$$\ln(w(t)) = \ln c + b * \ln(l) - r * t$$

where

c, b = Constants within prey species

l = Length of prey at ingestion

$-r$ = Digestion rate.

Thus, to get an effect of digestion on b (slope), r would have to be dependent on weight as well, and this to a large extent to give the values observed. It does not seem very likely, that this is the case. Rather, the results could be caused by whiting eating most prey in the lower end of the largest length intervals used, rendering the mean value of the length interval to be a too high estimate of the mean length of the prey in this length class. This is probably a lesser problem for cod, as this predator eats a larger range of prey sizes, thus leveling this effect out.

Using the estimated weight of prey at ingestion, it was calculated, how large a proportion of the population was unable to eat another prey, had the predator encountered one. For each ratio, it was calculated if there was room for one more prey. The resulting proportion of the predators used in analyses unable to eat another prey for each reference group is shown in fig. 6.4.2.2. The proportion of the stomachs unable to contain another prey is highest for the two smallest lengths of reference. This may be caused by these being eaten more frequently by small predators, which are saturated at lower stomach weights. In comparison, the largest reference group is eaten only by predators above 500 mm, and these are not likely to be easily saturated. The percentage of the stomach space that must be free to ingest another prey is much lower than for the small predators. 9-14% of the stomachs used when analyzing the smallest references are apparently unable to eat another prey, and as this is quite high, saturation may have affected

the ratios, given the estimated weights at ingestion and maximum weight of stomach content describe the actual values of these parameters.

6.4.3. The dependence of maximum and minimum ratios on sample size

The third approach to the saturation-problem was to investigate, if the maximum and minimum ratio recorded for each sample size were dependent on the calculated space available.

6.4.3.1. Weight of reference has no effect on maximum ratio

The resulting model was

$$\max(r)_{i,pl} = 1.172 * \ln(avai(w)) + f_i * \ln(l) + c_{i,pl}$$

where

i, l, pl = Prey species, prey length and predator length, respectively

$\max(r)_{i,pl}$ = Maximum ratio of a predator of length pl eating prey i

f, c = Constants within indices

The model explained 72% of the total variation with a dimension of 4% of the full model (table 6.4.3.1). The residuals were significantly different from a normal distribution ($p<0.0006$). Residuals tend to decrease with predicted value, but show no trend when plotted as a function of $\ln(avai(w))$ (fig. 6.4.3.1). The slope was slightly (but significantly) higher than 1.

The maximum ratio falls as a function of predator length (fig. 6.4.3.3). This may be due to other factors changing with predator length. Thus available space is likely to rise with predator length as is mean length of the prey ingested. If the slope was overestimated, this would give a dependency on predator length as the observed, as available space is likely to rise with predator length.

The model thus describes the data well, but there is a problem with distribution and trend in the residuals.

6.4.3.2. Weight of reference has an effect on maximum ratio

The model including the weight of the reference was

$$\max(r)_{i,pl} = 1{,}227 * \ln(avai(w)) + f_{i,pl} * \ln(l) + c_{i,pl}$$

Notation as above.

The model explains a slightly higher percentage (73.8%) of the variation than the model excluding the weight of the reference (table 6.4.3.2). Model dimension is simultaneously increased, but the result is nevertheless a fall in standard deviation from 0.819 to 0.805. Residuals are not significantly different from a normal distribution with mean 0 (p=0.124). They show the same trends as in the model not taking weight of reference into account (fig. 6.4.3.2).

The slope is increased, though not significantly so. The slope is still significantly above 1 (95% confidence limits 1.162-1.293). It is interesting, that decreasing the available space by the weight of the reference increases the "value" of the remaining available space. The trend in the parameter value of predator length is less clear, but still appears to be present (fig. 6.4.3.3). This is however difficult to interpret due to the crossed effects present.

6.4.3.3. Weight of prey has no effect on minimum ratio

The resulting model was

$$\min(r)_{ref,pl} = -1.137 * \ln(avai(w)) + 0.427 * \ln(l) + c_{ref} + d_{pl}$$

where

ref, l, pl = Reference species, reference length and predator length, respectively

$\min(r)_{i,pl}$ = Minimum ratio of a predator of length pl eating reference ref

f, c, d = Constants within indices

This model explains 70.4% of the total variance, leaving a standard deviation of 0.776 unexplained (table 6.4.3.3). Residuals are significantly different from a normal distribution ($p<0.0004$) and positively skewed. When plotted as a function of predicted value, the residuals show increasing variation as predicted value is increased (fig. 6.4.3.4). They show no tendency when plotted as a function of ln(avai(w)), indicating that the log-transformation of this factor is reasonable. The parameter values for predator length increase with predator length, and, as they are negative, decrease numerically with predator length. The explanation for this is assumed to be the same as

mentioned in section 6.4.3.1. This theory is supported by the fact, that the parameter values for predator length decrease slightly when slope is decreased (fig. 6.4.3.6).

6.4.3.4. Weight of prey has an effect on minimum ratio

This model became

$$\min(r)_{ref,pl} = -1.191 * \ln(avai(w)) + 0.446 * \ln(l) + c_{ref} + d_{pl}$$

where

ref, l, pl = Reference species, reference length and predator length, respectively

$\min(r)_{i,pl}$ = Minimum ratio of a predator of length pl eating reference ref

f, c, d = Constants within indices

The explanation of this model is slightly higher than for the model excluding weight of prey (70.7% compared to 70.4%)(table 6.4.3.4). The same factors are found to be significant, and thus standard deviation is decreased to 0.772. The residuals are still significantly different from a normal distribution (p=0.0014), though less so than in the model excluding weight of prey. Skewness is simultaneously decreased to –0.00099, which is very close to zero. The variation of the residuals still increase with predicted value, but show no trends when plotted as a function of the independent variable (fig. 6.4.3.5).

6.4.3.5. Comparison of the two models

In all the models, length of prey/reference has less impact than would be expected if all prey had just been ingested. As prey is most likely to be somewhat digested, this is in accordance with expectations. All the models have difficulties with describing small maximum ratios or large minimum ratios. This is as expected, as these ratios are likely to be controlled by factors other than predator saturation. It is however unfortunate, as this means, that the predicted maximum and minimum ratios of small samples have large variation.

The slopes are numerically higher than predicted, though only slightly so. If this is due to the unbalanced data (larger predators eat large prey) or the result of some biological effect is difficult to say. The effect of predator length could be a result of the unbalanced data as mentioned in section 6.4.3.1. If this is the case, the actual slope is closer to one than the observed. Thus, it can not be rejected, that the models provide an adequate description of the data, especially for numerically large observed ln(ratio).

The fact, that the slope is close to the expected value of 1 indicates, that the ratio is in fact dependent on the space available in the sample. This

indicates, that saturation of the predators may present a significant problem.

6.4.4. The logit model

All the logit models but one describe the variation in the data worse then the basic models (table 6.4.4.1). One model comes out with 4 crossed effects, but otherwise the model dimension is low with few factors having a significant effect. The slope of the model (the slope of the curve at the normed ratio 0.5) is not increased by a factor 4, as would be expected, if the reason for the low slope in the basic model was the minimum and maximum ratio being reached (table 6.4.4.2). As a matter of fact, the slope is decreased as compared to b, that is, to less than four times the expected value.

It does thus not improve the model to incorporate saturation of the predators in this way. The reasons for this can be several: There may not be any saturation, or the noise introduced when trying to estimate the upper and lower level of the ratios clouded the signal, so no clear trace is left. It is nevertheless interesting, that the effect of ln(IBTS-ratio) is still strong enough to come out significant in all models.

As mentioned in section 6.4.3.5, the models for maximum and minimum ratios have difficulty describing small predicted ratios. As these are the cases, where the limitation of the ratios is likely to play a significant role, this may be part of the reason for the poor correlation between the logits and the ln(IBTS-ratio).

7. Discussion

The areas investigated in this project can be divided into three larger areas: A model describing trawl catches, a model of stomach contents and n attempt to construct an index of sandeel abundance from predator stomach content. The discussion is therefore arranged in these three categories.

7.1. The model for IBTS-catches

The models generally describe the data well, taking the variability of the catches into account. However, most of the analyses show large ship-effect on catches, even though gear and trawling procedure have been standardized as much as possible. This is unfortunate, as it makes it difficult to compare catches from different ships without building a model to account for this factor. Sprat generally show little correlation between survey catches of 1-year olds and commercial catches of two year olds in the following year (ICES, 1990), and the large ship effect on the catch of this species could be part of the reason for this. However, it cannot be concluded from the present data, whether the predicted catches corrected for ship effects give a better estimate of the abundance of 1-year olds, than the traditional index calculated from the IBTS catches. To investigate this, the VPA should be tuned with each index separately over a larger range of years and the weight of the index results on the final population estimate should be examined in both cases.

The ship effect on catches is not necessarily caused by an actual effect of ship. Rather, it may be caused by a combination of factors co-varying with ship, such as date and trawl position within an area. This may explain the models showing crossed effects between ship and area, as it seems unlikely, that the ship effect should vary with area. Ship effect could vary with year and quarter, as the trawl is worn, adjusted or replaced, as even minor changes in gear rigging may have large effects on catches (ICES, 1981a). Another explanation could be, that the ship effect depends on the abundance of the species. If this is the case, it becomes virtually impossible to standardize to one ship and thus impossible to compare catches between ships. However, it does seem more likely, that the crossed effects are due to factors other than ship. Thus, position within an area affects depth, temperature and salinity. The two last factors will furthermore be influenced by date, as will the number of fish present in each length.

Depth is an important factor due to several reasons. Thus, the depth distribution of the species are different, cod being a typical demersal fish whereas herring and sprat are pelagic species and whiting seem to

be semi-pelagic when feeding (Daan et al., 1990). Time of day changes the distribution of several species, e.g. herring and sprat, which are found deeper in the watercolumn during daylight and closer to the surface during night. The fish may also perform evasive actions at the sight of the trawl (Walsh, 1991) or vessel lights (Aglen & Misund, 1990). However, this effect should not be too different from ship to ship as all hauls were taken between 15 min. to sunrise and 15 min. past sunset (ICES, 1981a).

Temperature and salinity may have a large effect on distribution, if some species tend to avoid certain temperature/salinity ranges or actively seek them, e.g. to avoid predators (Rose & Leggett, 1990). The number removed due to death and migration is dependent on the time elapsed since hatching, and thereby on both temperature and date. As both time and temperature have an effect on the number of fish that have grown from one length group into another, these two factors act at several levels to influence catches. However, though temperature has an important effect on growth and this factor has an effect on the number caught in each length group, this should not affect the predicted catch of 1-year olds, as the proportion of 1-year olds is estimated for each year separately. This leaves the effect of temperature on local distribution, which should be included in a model, if attempting to determine the causes of the ship effect.

The lack of ship effect on the catches of haddock could indicate, that the effect of date is not the cause of the ship factor, as a date effect should affect all species. It could also suggest, that the ship effect was due to a difference between the north and south parts of the North Sea. However, if this was the case, a similar lack of ship effect should be found for norway pout and sprat. As this is not the case, the ship effect is unlikely to be caused by large scale spatial differences.

The analysis of ratios did not indicate clearly whether the model including or excluding ship effect showed the better correlation with ratios in the stomach, as the differences were small. Thus, for this project, standardizing to one ship probably had little effect on analyses of ratios other than for the smallest references.

The biological interpretation of the model predictions is not straightforward. The models are designed to describe the catches in an area, but if this is actually a linear function of what is present remains to be determined. It is generally assumed, that the trawl will catch a certain percentage of the fish present of a given species and size (Cook, 1997). However, it is virtually impossible to test if this is actually the case. Video cameras attached to the trawl opening is one method to approach the problem, but this would have to be combined with acoustic surveys to examine the proportion of fish leaving the trawl area by the sight or sound of the ship and the gear (Ona & Chruickshank, 1986, Walsh, 1989). Furthermore, the trawl does not stop fishing in the period from the trawl is set until it reaches the bottom and in the period when the trawl is hauled back in. It may thus

catch some pelagic fish on the way down and up. The extent of this will depend on depth, as the period in which the trawl is not in contact with the bottom is longer at greater depths.

Even if the model does predict 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 present 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.

7.2. The suitability model

7.2.1. 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 impossible to determine the weights that should rightfully be assigned to each sample when performing the analyses.

The effect of number of stomachs when included in the model as a variable 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. If the effect of the number of stomachs is caused by an increased number of predators as a response to an increased abundance of prey, this will give the effect of available space (which is an increasing function of number of stomachs) on maximum and minimum ratio observed in the analyses of these. One way to test this theory would be to build the model of ratios including a factor describing predator abundance in that area. 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). However, if predator interference had a large effect, one would expect the maximum ratio to rise with the number of stomachs up to a certain point. At this point, corresponding to the density of predators at which mutual interference would start, the slope of the dependency would

decrease. This is not the case here, when the analyses of maximum ratio were done for samples containing less than 5, 10, 15 stomachs and so on. No indication of a decreased slope at high number of stomachs was detected. Thus, predator interference may not have a negative effect on the ratio, though the weight of each prey ingested may be decreased (Daan et al., 1990).

7.2.2. The effect of time and space on suitability and switching

Whether the suitability is constant over time and space cannot be determined from the present analysis. It appears to be changing, but this may just as well be an indicator of other factors affecting the suitability changing over time and space. The areas are not of equal depth, and this is likely to change the visibility of one species compared to another. A pelagic and demersal prey species, say, herring and cod, may thus be present at the same place an time in a shallow area, whereas a deep area containing the same relative frequencies is likely to have a different apparent frequency depending on which depth the predator is at. Furthermore, bottom texture has an effect on the distribution of both prey and predator (Hobson, 1986, Bromley & Watson, 1994). Thus, as is the case with the models of trawl catches, if one wishes to interpret the parameters and significant effects in a biologically meaningful way, factors such as depth, bottom texture, temperature and salinity would have to be added to the model.

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.

It is interesting to note, that 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, even if switching and suitability is allowed to vary from year to year.

7.2.3. The 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, indicating that this is in fact a reasonable model. However, to conclude this with more certainty, the model should include a larger number of sizeclasses, as the signal is likely to be clouded by the quite large size intervals. It is interesting, that the particularity of the predator is in fact smaller when taking the differential availability of prey in the different sizes into account than when examining the stomach content without considering prey abundance as noted by Ursin (1973). Thus, the greater particularity found here may indicate, that the IBTS is unable to describe the differences in abundances accurately. On the other hand, it is difficult to compare values of selection found in analyses not including switching with the analyses done in this paper. If the IBTS model does in fact under estimate the difference in abundance of adjacent length groups, this could give the negative switching found, when examining each prey species separately. However, the largest and smallest ratios are found between very abundant species and less abundant species, not within species, as is also indicated by the large correlation between catch of adjacent lengthgroups.

Thus, due to the large amount of unexplained variation in the model and the high degree of correlation between parameters, caution should be taken when interpreting the values. 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 project are on length basis rather than age basis.

7.2.4. Spatial scale

The models tend to get very complicated when spatial scale is increased. Thus, the model on North Sea scale reveal factors that do not comply with the suitability model. It does describe the data better as measured by r^2, but it is difficult to separate this from the fact, that the models are build 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 will be very sensitive to differences in distribution and thereby changes in overlap between predators and prey and different 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. Thus, prey only distributed in certain parts of the North Sea will be more sensitive to year to year differences in distribution than prey more evenly distributed. The reference most evenly distributed is whiting at 175 mm and 225 mm, but as one model has a high and the other a low dimension, it cannot generally be said,

that the evenly distributed references conform more closely to the model.

That dependence of predator diet on the abundance of prey is greatly affected by the scale at which data are compared is demonstrated by Rose & Leggett (1990) and is thus as expected.

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.

7.2.5. 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 from the observed values for cod 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 are 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, though not the lowest observed in both cases. If the low switching coefficient for sandeel found by Larsen & Gislason is actually present in the data set, this will make the use of predators as indicators of the abundance of this species very difficult. Due to the low switching coefficient, the number of sandeel in the stomach will vary little with stock numbers. This is in accordance with the relatively low correlations between PFI's and VPA estimates of sandeel abundance.

It is interesting, that the switching coefficient tested by Larsen & Gislason in no cases become significantly different from zero. 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 was here 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 week. 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 foodsupply.

The strong negative switching found may be caused by a number of factors. First, the predators may exhibit negative switching at encounter of the prey. Usually this will mean, 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 collapses of prey stocks, and is likely to show high mortality if one of the prey types needed is absent. Evolutionary, this is a very dangerous tactic to follow in an environment as changing as the sea, and thus does not seem likely.

Another possible explanation is the theory adopted in the state dependent models (Mangel, 1992, Hart & Ison, 1993): Predators become more picky in their prey choice as they get less hungry. Thus, a predator showing a very large or very low ratio must necessarily have eaten large numbers of one species, and may thus not be very hungry. This could cause the predator to ignore all prey, but the preferred. 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 prefered prey should always be eaten, provided the predator is not too full (Hart & Ison, 1993). If a high correlation between the PFI and the trawl index is an indicator of high prey profitability, the highest slopes should be found for whiting compared to cod, herring and sprat. The highest slope found for whiting at 75 mm is in fact 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). Thus, there appears to be some support for the optimal foraging theory, if the most profitable prey can be found by examining the correlation between PFI's and VPA. However, as the two estimates are from the same data-set, the two indicators of the most profitable prey can not rightfully be

compared, as they are not independent. Thus, other investigations will have to be carried out to examine, if the low switching coefficient is due to the predators foraging according to optimal foraging theory rather than the suitability model.

A second factor that may cause the apparent switching is the dependence of visibility on relative prey density. As noted in section 3.4, prey may become less visible to the predator as prey density is increased, if this causes schools to increase in size. Schooling provides good protection from predators (Hobson, 1986), so this may be a possible explanation. 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, schooling species such as 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 models including a 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 availability of other prey in a complex way. However, this effect would still be expected to be similar for species with similar behavior and does not explain the large differences 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, as mentioned in section 7.3.1 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 build here is wrong, either because it eliminates important factors that should be considered or because prey choice can not be described in this way.

For example, 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. This will be the case, if the predator forages according to optimal foraging theory.

Another problem could be, that the suitability is held constant over the years. Thus, 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 can not be the reason for the low slope.

The observations in the model are the ratios between the number of two prey given both are present. This may dampen 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 dampen the very low and very high ratios. It does seem, that saturation has an effect on the high and low ratios, and this should be included in a future model. The model build to incorporate saturation introduced additional variance, and no clear results were found. The effect of saturation should thus be included in some other way in a future model.

The ideal approach would be to include all prey eaten and thus all ratios in the same model. This would make it unnecessary to build a new model for each reference, and such a model could be build to include saturation, if the data was assumed to follow a multinomial distribution. However, this is not straight forward, as ingesting a small prey is not equal to ingesting a large prey in the multinomial sense. In any event, such a model would still be unable to cope with the pooling of stomachs into large samples.

It seems most likely, that the negative switching found here is either caused by predator switching, density dependence of prey visibility or by the lack of some important factors in the 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 optimal foraging theory and state dependent models, provided less switching (stronger dependence on abundance) is found for the more profitable prey. This may be the case her, and some evidence is thus provided for high prey abundance in the North Sea, if either of the three theories describe predator diet choice. The high abundance of prey is supported by the dependence of the maximum recorded ratio on the number of stomachs in the sample.

A future investigation should try to determine, if other effects than the ones considered here may be important for prey choice. It should also investigate the visibility factor more closely, and compare this to the spatial structure of schools and patches of fish.

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 thus 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. It also means, that scientific advice on maximum sustainable yield is in fact too high. 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.

7.3. The use of predatory fish as indicators of prey abundance

The partial fullness index may give an indication of the spatial distribution of the species, for which the PFI corresponds well to the VPA estimate and/or the trawl catches. Thus, the distribution of 0-group herring, cod and perhaps sprat could be indicated by the distribution of PFI's in the 3rd quarter. If a good correlation between PFI's and VPA-estimate indicates, that the prey is eaten when encountered, optimal foraging theory predicts, that one prey should show good correspondence (the most profitable), while lower correlation should be found for less profitable prey (Stephens & Krebs, 1986). If the predators behave according to this, herring must be the most profitable prey in the 3rd quarter, while this is only the case in the 1st quarter, if the trawl-catches describe the abundance better than the VPA at this time. Ranking the prey by which prey shows the highest correlation, sandeel is very low on the list. There may be several reasons for this. VPA may not give a realistic index of the abundance experienced by the predators or the availability of sandeel only depends on the abundance to a limited extent due to the behavioral patterns described in section 6.2.4.2. It may also be, that sandeel is in fact only eaten, when not enough of the more profitable prey is present. The last explanation does not seem likely, as sandeel make up a large part of the diet, and thus is not only eaten occasionally.

The low correlation for several of the prey species may be due to the broad diet of the predators. Thus, Lilly et al. and Fahrig et al. found good correlation between the PFI of the cod eating shrimp (Lilly et al., 1998) and capelin (Fahrig et al., 1993, Lilly, 1991). In both investigations, cod fed almost exclusively on the prey examined. Thus, if only the most important prey show good correlation between PFI's and abundance, there should be a tendency for correlation to rise with average PFI. This is however not the case.

The partial fullness index of whiting is likely to describe the abundance experienced by the predators well, as both cod and whiting show the same pattern in PFI's as a function of the trawl index. This may indicate, that the trawl index is not a bad measure for the abundance of whiting in the demersal zone. The lack of coherence of VPA and the trawl index (and also VPA and the index calculated by ICES (ICES, 1996b)) could be due to the 1-group whiting living close to the shore or other places not trawled in the IBTS. This is thought to be the case for young cod (Daan et al., 1990). Consequently, the number of whiting caught in the trawl survey would reflect the number present in that particular area, but not necessarily the abundance of this year class in the whole North Sea. However, as the PFI for whiting eaten by whiting in the 3rd quarter corresponds well with the VPA estimate of 1-year olds in the following year, 0-group whiting would have to be first available and then 6 months later not available.

The correlation for sandeel is, for one reason or the other, too low to be the basis of a reliable index of the abundance of this species. It may however still give an indication of abundance, in lack of a more precise index.

The predictions of sandeel abundance from the model of ratios vary greatly with reference species and length. However, the predictions from the model showing the highest correlation with VPA estimates have a higher correlation than the PFI's, though not dramatically so. The different result of the model predictions for different references could be taken as an indication of lack of fit of the models. This may however also be the result of a low ability of the model to account for size selection of the predators. The other way around, the good fit of the predictions for small references can be seen as an indication of the sufficient ability of the suitability model to describe the observed data.

An index of sandeel abundance can be build from the present model. It should be based on stomach samples from cod and whiting, and should examine only the number of norway pout and sandeel below 150 mm. Stomachs can be pooled within 4-square areas, thus decreasing the time needed to analyze the stomachs. The present data set only allows the correlation with VPA-estimates to be calculated in the 1st quarter, as IBTS-data of norway pout are only available for the remaining quarters in one year. It can thus not be determined, if a reliable index of the number of recruits can be estimated from the stomach content in the 3rd quarter.

To calculate confidence limits from the two models is possible, but in the case of the model of ratios, this becomes rather complicated, as the catch of the reference is not without error. Whether the index derived from the ratios is improved as compared to the partial fullness index to an extent, that makes this analysis preferable to the more simple PFI must be determined. This consideration should take the increased amount of data needed for the ratio model into account.

8. Conclusion

The catch in the IBTS may well be described by a combination of a model of catch or no catch and a model of number caught. This model can be used to calculate the variance of the estimated catch in a particular year. Though trawl catches of small pelagic species are severely influenced by ship effects, it cannot be concluded from the present model, whether this is due to other factors covarying with ship. However, it seems unlikely, that the species other than haddock have the same catchability to the trawl for all ships.

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 will have to 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.

The model suggested by Ursin (1973) to account for predator size preference describes the data adequately. However, the large negative switching introduced in this model affects the predicted particularity in prey choice by predators, and size preference may play a less significant role than previously suggested.

Substantial negative switching by the predators cod and whiting is found. It seems most likely, that this is 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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10. Appendix.

10.1. Including Andersen & Ursin's size preference in the model

10.1.1. Size preference

Andersen & Ursin (1977) suggest, that a predator prefer prey with a certain ratio of prey weight to the predators weight. The preference pattern is log-symmetric, such that a predator has the same preference for a prey of twice the preferred ln(weight-ratio) as half the preferred ln(weight-ratio). The model describing the preferred ratio of prey

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

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

where

pr, i = Predator and prey, respectively

w_i = Weight of i

$g_{pr,i}$ = Size preference constant

η_{pr} = Preferred $\ln\left(\frac{w_{pr}}{w_i} \right)$ of the predator

σ_{pr} = Coefficient describing the particularity of the predator in its choice of prey weight to predator weight is

The size preference coefficient relates to the α introduced in section 3.1

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

where

$l(i)$ = Length of i

$\varphi_{i,pr,l(pr)}$ = Species preference coefficient

$\alpha_{i,l(i)pr,l(pr)}$ = The preference of predator pr at length l for prey i a such that

Thus the suitability model as it is used in this project becomes (allowing b to vary only with predator and predator length as is the case in the suitability model (section 3.4))

$$\ln\left(\frac{F_{i,l(i)}}{F_j}\right) = \ln k_{ij,l(i),pr,l(pr)} + b_{pr,l(pr)} * \ln\left(\frac{T_{i,l(i)}}{T_j}\right)$$

$$k_{ij,l(i),pr,l(pr)} = s_{ij,l(i),pr,l(pr)} * d_{ij,l(i),pr,l(pr)} * q_{ij,l(i)}^{b_{pr,l(pr)}} =$$

$$\alpha_{0,ij,l(i),pr,l(pr)} * v_{0,ij,l(i),pr,l(pr)}^{\beta_{pr,l(pr)}} * d_{ij,l(i),pr,l(pr)} * q_{ij,l(i)}^{b_{pr,l(pr)}}$$

$$\Updownarrow$$

$$\ln k_{ij,l(i),pr,l(p)} = \ln \alpha_{0,ij,l(i),pr,l(pr)} + \beta_{pr,l(pr)} * \ln v_{0,ij,l(i),pr,l(pr)}$$

$$+ \ln d_{ij,l(i)pr,l(pr)} + b_{pr,l(pr)} * \ln q_{ij,l(i)}$$

as

$$\alpha_{0,ij,l(i)pr,l(pr)} = \frac{\alpha_{0,i,l(i),pr,l(pr)}}{\alpha_{0,j,l(j),pr,l(pr)}} = \frac{\varphi_{i,pr,l(pr)} * g_{i,l(i),pr,l(pr)}}{\varphi_{j,pr,l(pr)} * g_{j,l(j)pr,l(pr)}}$$

$$\ln k_{ij,l(i)pr,l(p)} = \ln\left(\frac{g_{i,l(i),pr,l(pr)}}{g_{j,l(j),pr,l(pr)}}\right) + \ln\left(\frac{\varphi_{i,pr,l(pr)}}{\varphi_{j,pr,l(pr)}}\right) + \beta_{pr,l(pr)} * \ln v_{0,ij,l(i),pr,l(pr)}$$

$$+ \ln d_{ij,l(i),pr,l(pr)} + b_{pr,l(pr)} * \ln q_{ij,l(i)}$$

where

i = prey species and lengthgroup

j = reference group

pr = predator species

$l(i)$ = length of i

k = Constant within indices

Remaining notation as in section 3.6

The relative preference of one prey species to another should show some 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 describe the case, where preference for a certain species peaks at a particular predator length.

The model then becomes

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

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

where

$\varphi_{0,i,pr}$ = The theoretical preference for i at predator length 0

$\lambda_{ij,pr}, \Gamma_{ij,pr}$ = Factors describing the dependence of preference on length

$\ln(g_{i,w(i),pr,w(pr)})$ can be rewritten as

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

$$-\frac{\left(\left(\ln(w_{pr})\right)^2+\left(\ln(w_i)\right)^2-2\ln(w_{pr})\ln(w_i)+\eta_{pr}^2-2\eta_{pr}\left(\ln(w_{pr})-\ln(w_i)\right)\right)}{2\sigma_{pr}^2}$$

As the same is true for prey j,

$$\ln g_{i,w(i),pr,w(pr)} - \ln g_{j,w(j),pr,w(pr)} =$$

$$-\frac{\left(\left(\ln(w_{pr})\right)^2+\left(\ln(w_i)\right)^2-2\ln(w_{pr})\ln(w_i)+\eta_{pr}^2-2\eta_{pr}\left(\ln(w_{pr})-\ln(w_i)\right)\right)}{2\sigma_{pr}^2}$$

$$+\frac{\left(\left(\ln(w_{pr})\right)^2+\left(\ln(w_j)\right)^2-2\ln(w_{pr})\ln(w_j)+\eta_{pr}^2-2\eta_{pr}\left(\ln(w_{pr})-\ln(w_j)\right)\right)}{2\sigma_{pr}^2} =$$

$$\frac{\left(-\left(\ln(w_i)\right)^2+\left(\ln(w_j)\right)^2+2\ln(w_{pr})\ln(w_i)-2\ln(w_{pr})\ln(w_j)-2\eta_{pr}\left(\ln(w_i)-\ln(w_j)\right)\right)}{2\sigma_{pr}^2}$$

substituting $w_{pr} = c_{pr} * l_{pr}^{f_{pr}}$ and $w_i = c_i * l_i^{f_i}$

$$\ln g_{i,l(i),pr,l(pr)} - \ln g_{j,l(j),pr,l(pr)} =$$

$$\frac{1}{2\sigma_{pr}^2} * \left(-\left(\ln(c_i)+f_i\ln(l_i)\right)^2+\left(\ln(w_j)\right)^2+2\left(\ln(c_{pr})+f_{pr}\ln(l_{pr})\right)\left(\ln(c_i)+f_i\ln(l_i)\right)\right.$$

$$\left.-2\left(\ln(c_{pr})+f_{pr}\ln(l_{pr})\right)\ln(w_j)-2\eta_{pr}\left(\ln(c_i)+f_i\ln(l_i)-\ln(w_j)\right)\right) =$$

$$\frac{1}{2\sigma_{pr}^2} * \left(\left(\left(\ln(w_j)\right)^2-2\ln(w_j)\left(\ln c_{pr}-\eta_{pr}\right)\right)-\left(\ln(c_i)\right)^2-2\ln(c_i)\left(\eta_{pr}-\ln(c_{pr})\right)\right.$$

$$\left.-f_i^2\left(\ln(l_i)\right)^2+\ln(l_i)\left(2f_i\left(\ln(c_{pr})-\ln(c_i)-\eta_{pr}\right)\right)+\ln(l_{pr})\left(2f_{pr}\left(\ln(c_i)-\ln(w_j)\right)\right)\right)$$

$$+\ln(l_{pr})\ln(l_i)\left(2f_if_{pr}\right)$$

Substituting

$$m_{ijpr} = \frac{\left(\ln(w_j)\right)^2-\left(\ln(c_i)\right)^2+2\left(\ln(c_i)-\ln(w_j)\right)\left(\ln(c_{pr})-\eta_{pr}\right)}{2\sigma_{pr}^2}$$

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

$$p_{ipr} = \frac{f_i\left(\ln(c_{pr})-\ln(c_i)-\eta_{pr}\right)}{\sigma_{pr}^2}$$

$$z_{ijpr} = \frac{f_{pr}\left(\ln(c_i) - \ln(w_j)\right)}{\sigma_{pr}^2}$$

$$u_{ipr} = \frac{f_i f_{pr}}{\sigma_{pr}^2}$$

the expression becomes

$$\ln g_{i,l(i),pr,l(pr)} - \ln g_{j,l(j),pr,l(pr)} = m_{ijpr} + o_{ipr}\left(\ln(l_i)\right)^2 + p_{ipr}\ln(l_i) + t_{ipr}\ln(l_{pr}) + u_{ipr}\ln(l_{pr})\ln(l_i)$$

Thus, a linear dependency on ln(length of predator), ln(length of prey) and ln(length of prey)^2.

10.1.2. Catchability

As it is not possible to examine selection independently of digestion, visibility and catchability, the dependence of these three on predator and prey length must also be modeled. Catchability of fish as a function of fish length appears to be a sigmoid function (Engås & Godø, 1989, Walsh, 1989). However, as the lengths examined here are unlikely to be fully available to the trawl (at least for cod and haddock (Engås & Godø, 1989)), a potency function is thought to be a reasonable relation for the range of lengths examined.

Catchability (q) is thus modeled as a potency function of length:

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

$$\Updownarrow$$

$$\ln q_i = \ln q_{0,i} + r_i * \ln l_i$$

where

$q_{0,i}, r_i$ = Constants.

l = Length of fish i

This gives the following relative catchability

$$\ln\left(\frac{q_{i,l(i)}}{q_{j,l(j)}}\right) = \ln q_{0,i} + r_i * \ln l_i - \ln q_{0,j} - r_j * \ln l_j$$

As the reference is held constant for each analysis, this becomes

$$\ln q_{ij,l(i)} = \ln\left(\frac{q_{i,l(i)}}{q_{j,l(j)}}\right) = \ln q_{0,ij} + r_i * \ln l_i$$

where

$$\ln q_{0,ij} = \ln q_{0,i} - \ln q_{0,j} - r_j * \ln l_j$$

10.1.3. Switching

If switching occurs, the relative catchability should not be used directly. Instead the dependence of ln(ratio in the stomach) on

$b_{ij,pr,l(pr)} * \ln q_{i,j,l(i)}$

catchability should be

The switching coefficient of one predator length should furthermore resemble the switching coefficient of adjacent lengths. It was thus decided to model the dependence of the switching coefficient on

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

where

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

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

predator length as

The total dependency on catchability is then

$$b_{pr,l(pr)} * \ln q_{ij,l(i)} = \left(t_{pr} * \ln(l_{pr}) + b_{0,pr}\right)\left(\ln q_{0,i,j} + r_i * \ln l_i\right) =$$
$$b_{0,pr} \ln\left(q_{0,ij}\right) + t_{pr} \ln q_{0,i,j} \ln\left(l_{pr}\right) + b_{0,pr} r_i \ln\left(l_i\right) + t_{pr} r_i \ln\left(l_{pr}\right) \ln\left(l_i\right)$$

10.1.4. Digestion as a function of prey and predator length

Digestion is likely to render prey unrecognizable, when it has reached a certain percentage, p, of its weight at ingestion, $w_{0,i}$:

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

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

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

where

Λ = Constant

Q_i = Rate of elimination of species i

l_{pd} = Length of predator (in cm)

Describing weight of prey at ingestion as an potency function of length (as above), inserting the two expressions of prey weight in the Jones'

$$\ln(d_i) = K_i + \Lambda f_i \ln(l_i) - 1.4 \ln(l_{pd})$$

where

$$K_i = \ln(1 - p_i^B) + \ln(175) + \Lambda \ln(c_i) - \ln(\Lambda Q_i)$$

formula and rearranging

The expression, that should be included in the model of ratios is then

As length of j is constant within analyses,

$$\ln(d_i) - \ln(d_j) = K_{ij} + \Lambda f_i \ln(l_i) - \Lambda f_j \ln(l_j)$$

where

$$K_{ij} (= K_i - K_j) \ln(d_{ij,l(i),pr,l(pr)}) = \ln(d_i) - \ln(d_j) = K_{2,ij} + \Lambda f_i \ln(l_i)$$

where

$$K_{2,ij} = K_{ij} - \Lambda f_j \ln(l_j)$$

10.1.5. Visibility

Modeling visibility is less straight forward, as this factor includes several rather subtle variables. It 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 change its spatial distribution, both on local and North Sea scale (as is the case for herring, see section 6.2.3). The same may be said for the predators, so the dependencies on the lengths are difficult to assess. However, if the

prey and predator are randomly distributed, the encounter-rate can be described as

$$n_{i,l(i),pr,l(pr)} = \frac{\pi * R_{pr,l(pr)}{}^2 * N_{i,l(i)}}{3}\left(\frac{\overline{u_i}^2 + 3v_{pr}^2}{v_{pr}^2}\right)$$

where

n = Encounterate of predator pr with i

R = Visual radius of the predator

N = Abundance of i

$\overline{u_i}$ = Mean velocity of i

v = velocity of pr

(Gerritsen & Strickler, 1977).
Comparing two prey, the relative encounter rate becomes

$$\frac{n_{i,l(i),pr,l(pr)}}{n_{j,l(j),pr,l(pr)}} = \frac{N_{i,l(i)}}{N_{j,l(j)}}\left(\frac{\overline{u_i}^2 + 3v_{pr}^2}{\overline{u_j}^2 + 3v_{pr}^2}\right)$$

Kaiser (1992 in Kaiser & Hughes, 1993) found average velocity to be a linear function of fish length and the expression of fish velocity is then

$$\overline{u_i}^2 = \left(u_{0,i} + u_{1,i} * l_i\right)^2$$

The same is true for the predator. Thus, as a predator is larger than its prey, and as prey length generally does not vary too much within a predator length group, the expression of the ratio of velocities approach 1.

However, fish are not randomly distributed, and prey and predators may change behavior as they grow. As an approximation, visibility was thus assumed to rise or fall with lengths, not allowing for peak visibility at intermediate lengths. It does seem reasonable, that prey visibility should change gradually if at all. The expression included for visibility was thus

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

$$\Downarrow$$

$$\ln\left(v_{i,l(i),j,pr,l(pr)}\right) = \ln\left(v_{i,l(i),pr,l(pr)}\right) - \ln\left(v_{j,l(j),pr,l(pr)}\right) =$$

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

where

V_0, v_1, v_2 = Visibility - constants (within indices)

As j is constant within analyses, this becomes

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

where

$$V_{0,ij,pr}=V_{0,i,pr}-V_{0,j,pr}-v_{2,j,pr}\ln\left(l_j\right)$$

$$v_{1,ij,pr}=v_{1,i,pr}-v_{1,j,pr}$$

10.1.6. Predator choice switching

As was the case for catchability, the expression for visibility has to be corrected by an exponent before the dependency can be included in the model. The exponent to be used here is the actual predator choice component of the switching coefficient, β (see section 3.4). Describing the dependence of β on predator length in a similar way as the

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

where

$\beta_{0,pr}$ = The theoretical β of a predator of length 1

B_{pr} = Factor describing dependence of β on length

dependency of b on length, β is

As β relates to b as described in section 3.4, γ is simultaneously defined as:

$$\gamma_{pr,l(pr)}=\frac{t_{pr}*\ln(l_{pr})+b_{0,pr}-1}{\mathrm{B}*\ln\left(l_{pr}\right)+\beta_{0,pr}}$$

This term can not vary between prey species, due to the bond put on b restrcting it to vary only with predator species and length.

10.1.7. Combination of the models

Now, including all these separate expressions in the model for ratios it becomes

$$\ln\left(\frac{F_{i,l(i)}}{F_j}\right) = \ln k_{ij,l(i),pr,l(pr)} + b_{pr,l(pr)} * \ln\left(\frac{T_{i,l(i)}}{T_j}\right) =$$

$$\ln \alpha_{0,ij,l(i),pr,l(pr)} + \beta_{pr,l(pr)} * \ln v_{0,ij,l(i),pr,l(pr)} + \ln d_{ij,l(i),pr,l(pr)} + b_{ij,pr,l(pr)} * \ln q_{ij,l(i)}$$

$$+ b_{pr,l(pr)} * \ln\left(\frac{T_{i,l(i)}}{T_j}\right) =$$

$$\ln\left(\frac{\varphi_{0,i,pr}}{\varphi_{0,j,pr}}\right) + \lambda_{ij,pr} * \ln(l_{pr}) + \Gamma_{ij,pr} * \left(\ln(l_{pr})\right)^2 + m_{ijpr} + o_{ipr}\left(\ln(l_i)\right)^2 + p_{ipr}\ln(l_i) + z_{ijpr}\ln(l_{pr})$$

$$+ u_{ipr}\ln(l_{pr})\ln(l_i) + \left(\mathrm{B}_{pr} * \ln(l_{pr}) + \beta_{0,pr}\right)\left(V_{0,ij,pr} + v_{1,ij,pr}\ln(l_{pr}) + v_{2,i,pr}\ln(l_i)\right)$$

$$+ K_{2,ij} + \Lambda f_i \ln(l_i) + b_{0,pr}\ln(q_{0,ij}) + t_{pr}\ln q_{0,i,j}\ln(l_{pr}) + b_{0,pr}r_i\ln(l_i) + t_{pr}r_i\ln(l_{pr})\ln(l_i)$$

$$+ \left(t_{pr} * \ln(l_{pr}) + b_{0,pr}\right) * \ln\left(\frac{T_{i,l(i)}}{T_j}\right)$$

Introducing

$$C_{ij,pr} = \ln\left(\frac{\varphi_{0,i,pr}}{\varphi_{0,j,pr}}\right) + m_{ijpr} + \beta_{0,pr}V_{0,ij,pr} + K_{2,ij} + b_{0,pr}\ln(q_{0,ij})$$

$$E_{ij,pr} = \lambda_{ij,pr} + z_{ijpr} + \mathrm{B}_{pr}V_{0,ij,pr} + t_{pr}\ln q_{0,i,j} + \beta_{0,pr}v_{1,ij,pr}$$

$$G_{ij,pr} = \Gamma_{ij,pr} + \mathrm{B}_{pr} * v_{1,ij,pr}$$

$$H_{i,pr} = p_{ipr} + \beta_{0,pr}v_{2,i,pr} + \Lambda f_i + b_{0,pr}r_i$$

$$M_{i,pr} = u_{ik} + \mathrm{B}_{pr}v_{2,i,pr} + t_{pr}r_i$$

the model becomes

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

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

Table 5.1.1.1

Number of ships participating in the IBTS		
year	quarter	No. Of ships
1981	1	4
1985	1	9
1986	1	9
1987	1	9
1991	1	8
1991	2	7
1991	3	5
1991	4	5
all years and quarters		15

Table 5.1.2.1

Length groups for which the IBTS-model was build	
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

Table 5.2.1.1

Desired number of predators sampled			
	Desired no.		
Length(cm)	Cod	Haddock	Whiting
5-5,9	5	5	5
6-6,9	5	5	5
7-7,9	5	5	5
8-9,9	5	5	5
10-11,9	5	5	5
12-14,9	5	5	5
15-19,9	10	5	10
20-24,9	10	5	10
25-29,9	10	5	10
30-39,9	10	5	10
40-49,9	10	5	10
50-59,9	10	5	10
60-69,9	25	5	10
70-79,9	25	5	
80-99,9	25		
100-119,9	25		
>120	25		

From: ICES, 1991

Table 5.2.5.1

Predator length groups included in analyses of ratios	
Predator	Length groups
Cod	350, 450, 600, 850
Whiting	250, 350

Table 6.1.1.1

Summary of 0-1 model of IBTS catches. Model including ship effect.
Empty cells denotes parameter effects not significantly different from zero.

		Proportion of total deviance explained							
species	length in mm	model	area	year	area*year	quarter	quarter*area	ship	ship*year
Cod	125	0,442	0,104	0,112		0,052		0,053	0,121
Cod	175	0,400	0,182	0,100		0,032		0,038	0,048
Cod	225	0,438	0,158	0,022	0,192	0,028		0,038	
Cod	275	0,420	0,149	0,062	0,158	0,03		0,021	
Cod	350	0,337	0,217	0,049				0,026	0,045
Haddock	125	0,371	0,228	0,027		0,116			
Haddock	175	0,473	0,413	0,017				0,043	
Haddock	225	0,490	0,437	0,031		0,022			
Haddock	275	0,570	0,48	0,037		0,015		0,038	
Haddock	350	0,593	0,347	0,097	0,12			0,029	
Herring	125	0,576	0,296	0,081		0,03	0,074	0,041	0,054
Herring	175	0,466	0,188	0,041	0,134	0,03		0,073	
Herring	225	0,463	0,161	0,036	0,154	0,011		0,071	0,03
Herring	275	0,414	0,314	0,037				0,063	
Herring	350	0,527	0,159	0,046		0,043	0,146	0,062	0,071
Norway pout	75	0,588	0,207	0,051	0,146	0,059		0,055	0,07
Norway pout	125	0,443	0,371	0,008		0,012		0,052	
Norway pout	175	0,486	0,378	0,014		0,003		0,045	0,046
Sprat	75	0,547	0,155	0,025		0,061	0,083	0,101	0,122
Sprat	125	0,497	0,267	0,015		0,013		0,125	0,077
Whiting	75	0,590	0,13	0,072	0,124	0,077		0,13	0,057
Whiting	125	0,473	0,119	0,049		0,059	0,105	0,106	0,035
Whiting	175	0,333	0,202	0,022		0,033		0,076	
Whiting	225	0,477	0,173	0,026	0,149	0,004		0,077	0,048
Whiting	275	0,410	0,196	0,094		0,001		0,076	0,043
Whiting	350	0,388	0,246	0,039				0,055	0,048

Table 6.1.1.2

Test for significance of crossed effects with ship in the 0-1 model of IBTS catches
p=probability of no effect
r^2=proportion of total deviance explained
Empty cells denotes parameter effects not significantly different from zero.

		Ship*area		ship*quarter	
species	length in mm	p	r^2	p	r^2
Cod	125	0.041	0.269	0.028	0.024
Cod	175	0.039	0.268	0.029	0.019
Cod	225	0.048	0.259	0.004	0.024
Cod	275	0.001	0.288	0.009	0.021
Cod	350	0.750	0.240	0.000	0.041
Haddock	125	0.000	0.329	0.036	0.033
Haddock	175	1.000	0.208	0.158	0.016
Haddock	225	0.000	0.262	0.096	0.016
Haddock	275	0.012	0.214	0.094	0.015
Haddock	350	0.000	0.248	0.000	0.031
Herring	125	0.009	0.216	0.211	0.011
Herring	175	0.379	0.280	0.350	0.011
Herring	225	0.007	0.264	0.013	0.019
Herring	275	0.229	0.843	0.023	0.018
Herring	350	0.004	0.298	0.152	0.023
Norway pou	75	0.055	0.252	0.045	0.022
Norway pou	125	0.041	0.241	0.033	0.018
Norway pou	175	0.830	0.235	0.263	0.012
Sprat	75	0.001	0.233	0.569	0.008
Sprat	125	0.000	0.219	0.083	0.015
Whiting	75	0.000	0.257	0.076	0.015
Whiting	125	0.004	0.299	0.074	0.019
Whiting	175	0.000	0.351	0.026	0.028
Whiting	225	0.000	0.361	0.255	0.016
Whiting	275	0.014	0.275	0.284	0.014
Whiting	350	0.000	0.817	0.016	0.019

Table 6.1.1.3

Summary of 0-1 model of IBTS catches. Model excluding ship effect. Empty cells denotes parameter effects not significantly different from zero.							
		Proportion of total deviance explained					
species	length in mm	model	area	year	area*year	quarter	quarter*area
Cod	125	0.268	0.104	0.112		0.052	
Cod	175	0.314	0.182	0.100		0.032	
Cod	225	0.401	0.158	0.022	0.192	0.028	
Cod	275	0.399	0.149	0.062	0.158	0.03	
Cod	350	0.266	0.217	0.049			
Haddock	125	0.371	0.228	0.027		0.116	
Haddock	175	0.430	0.413	0.017			
Haddock	225	0.490	0.437	0.031		0.022	
Haddock	275	0.532	0.48	0.037		0.015	
Haddock	350	0.564	0.347	0.097	0.12		
Herring	125	0.407	0.296	0.081		0.03	
Herring	175	0.258	0.188	0.041		0.03	
Herring	225	0.363	0.161	0.036	0.154	0.011	
Herring	275	0.449	0.314	0.037		0.006	0.093
Herring	350	0.383	0.159	0.046		0.043	0.146
Norway pout	75	0.318	0.207	0.051		0.059	
Norway pout	125	0.392	0.371	0.008		0.012	
Norway pout	175	0.392	0.378	0.014			
Sprat	75	0.323	0.155	0.025		0.061	0.083
Sprat	125	0.285	0.267	0.015		0.013	
Whiting	75	0.279	0.13	0.072		0.077	
Whiting	125	0.228	0.119	0.049		0.059	
Whiting	175	0.257	0.202	0.022		0.033	
Whiting	225	0.198	0.173	0.026			
Whiting	275	0.290	0.196	0.094			
Whiting	350	0.284	0.246	0.039			

Table 6.1.1.4

Comparison between 0-1 model with and without ship-effect							
		Model r^2			Dispersion		
species	length in mm	with ship	without ship	% decrease	with ship	without ship	% increase
Cod	125	0.442	0.268	39.4	1.061	1.118	5.3
Cod	175	0.400	0.314	21.5	1.062	1.085	2.1
Cod	225	0.438	0.401	8.4	1.093	1.110	1.5
Cod	275	0.420	0.399	5.0	1.056	1.060	0.3
Cod	350	0.337	0.266	21.1	1.023	1.041	1.7
Haddock	125	0.371	0.371	0.0	1.102	1.102	0.0
Haddock	175	0.473	0.430	9.1	1.063	1.070	0.6
Haddock	225	0.490	0.490	0.0	1.025	1.025	0.0
Haddock	275	0.570	0.532	6.7	1.037	1.032	-0.5
Haddock	350	0.593	0.564	4.9	1.029	1.046	1.6
Herring	125	0.576	0.407	29.3	1.096	1.137	3.7
Herring	175	0.465	0.258	44.5	1.133	1.174	3.6
Herring	225	0.465	0.363	21.9	1.114	1.165	4.6
Herring	275	0.413	0.449	-8.7	1.065	1.099	3.1
Herring	350	0.528	0.383	27.5	0.993	1.031	3.8
Norway pout	75	0.590	0.318	46.1	1.060	1.078	1.7
Norway pout	125	0.444	0.392	11.7	1.041	1.074	3.2
Norway pout	175	0.486	0.392	19.3	1.018	1.017	-0.1
Sprat	75	0.546	0.323	40.8	1.126	1.256	11.6
Sprat	125	0.497	0.285	42.7	1.083	1.205	11.3
Whiting	75	0.589	0.279	52.6	1.078	1.188	10.2
Whiting	125	0.475	0.228	52.0	1.097	1.153	5.1
Whiting	175	0.332	0.257	22.6	1.067	1.082	1.4
Whiting	225	0.476	0.198	58.4	1.042	1.081	3.7
Whiting	275	0.411	0.290	29.4	1.013	1.043	2.9
Whiting	350	0.387	0.284	26.6	1.013	1.054	4.0

Table 6.1.2.1

Summary of model of number caught in the IBTS. Model including ship effect.
Empty cells denotes parameter effects not significantly different from zero.

		Proportion of total variance explained (r^2) by each significant factor							
species	length in mm	model	area	year	area*year	quarter	quarter*area	ship	ship*year
Cod	125	0.603	0.283	0.073		0.034	0.099	0.025	0.04
Cod	175	0.484	0.234	0.045		0.019	0.093	0.018	0.075
Cod	225	0.392	0.154	0.013	0.166	0.013		0.0494	
Cod	275	0.491	0.192	0.083	0.139	0.011		0.048	0.018
Cod	350	0.447	0.195	0.065	0.125			0.048	0.014
Haddock	125	0.666	0.288	0.048	0.116	0.122	0.077	0.014	
Haddock	175	0.544	0.215	0.04	0.099	0.079	0.099	0.012	
Haddock	225	0.538	0.292	0.018	0.116	0.056	0.057		
Haddock	275	0.545	0.379	0.029	0.094	0.025		0.018	
Haddock	350	0.563	0.313	0.054	0.101	0.022	0.049	0.018	0.006
Herring	125	0.536	0.180	0.07	0.138	0.009	0.046	0.062	0.031
Herring	175	0.461	0.199	0.025	0.144	0.007	0.053	0.033	
Herring	225	0.477	0.203	0.025	0.144	0.016	0.077	0.013	
Herring	275	0.513	0.178	0.016	0.129	0.016	0.137	0.02	0.017
Herring	350	0.453	0.174	0.01	0.1914			0.04	0.037
Norway pout	75	0.652	0.186	0.081	0.117	0.107	0.108	0.053	
Norway pout	125	0.554	0.228	0.022	0.107	0.063	0.094	0.028	0.012
Norway pout	175	0.446	0.240	0.046		0.007	0.132	0.021	
Sprat	75	0.526	0.195	0.034	0.15	0.002	0.045	0.073	0.028
Sprat	125	0.511	0.200	0.02	0.142	0.01	0.065	0.028	0.077
Whiting	75	0.571	0.176	0.094		0.099	0.146	0.027	0.03
Whiting	125	0.549	0.195	0.07	0.133	0.018	0.109	0.006	0.017
Whiting	175	0.541	0.226	0.041	0.14	0.037	0.078	0.007	0.012
Whiting	225	0.515	0.191	0.041	0.153	0.013	0.105	0.013	
Whiting	275	0.500	0.211	0.077	0.1	0.009	0.074	0.018	0.011
Whiting	350	0.454	0.195	0.027	0.109	0.011	0.072	0.04	

Table 6.1.2.2

Comparison of residuals of model of number caught with and without ship-effect									
		Standard deviation			Skewness			p(normal distributed residuals)	
species	length in mm	with ship	without ship	% increase	with ship	without ship	increase	with ship	without ship
Cod	125	0.9477	1.021	7.7	0.0846	0.1469	0.06	0.227	0.4747
Cod	175	0.9452	0.924	-2.2	0.4403	0.3833	-0.06	0.0001	0.0001
Cod	225	0.9296	0.964	3.7	0.64	0.6558	0.02	0.0001	0.0001
Cod	275	0.9038	0.96	6.2	0.5352	0.5738	0.04	0.0032	0.0001
Cod	350	0.9452	0.943	-0.2	0.4333	0.4693	0.04	0.028	0.0159
Haddock	125	1.2078	1.234	2.2	-0.2958	-0.2618	0.03	0.1388	0.3865
Haddock	175	1.3653	1.384	1.4	-0.3167	-0.3037	0.01	0.0002	0.0001
Haddock	225	1.3651	1.365	0.0	-0.2641	-0.264	0.00	0.0014	0.0014
Haddock	275	1.3328	1.359	2.0	-0.2116	-0.173	0.04	0.0342	0.0248
Haddock	350	1.1649	1.197	2.8	-0.0787	-0.083	0.00	0.1761	0.227
Herring	125	1.7682	1.936	9.5	-0.1099	-0.091	0.02	0.2596	0.0425
Herring	175	1.8602	1.916	3.0	-0.0164	0.00831	0.02	0.2081	0.2136
Herring	225	1.8033	1.825	1.2	0.4121	0.399	-0.01	0.0001	0.0001
Herring	275	1.6256	1.687	3.8	0.2912	0.396	0.10	0.0001	0.0001
Herring	350	1.2412	1.326	6.8	0.4246	0.497	0.07	0.1306	0.016
Norway pout	75	1.4758	1.584	7.3	-0.3251	-0.247	0.08	0.003	0.0032
Norway pout	125	1.7154	1.792	4.5	-0.3874	-0.3026	0.08	0.0002	0.0223
Norway pout	175	1.7217	1.7543	1.9	-0.1182	-0.1015	0.02	0.5253	0.8013
Sprat	75	1.6583	1.896	14.3	0.0519	0.1183	0.07	0.8541	0.2631
Sprat	125	1.6786	1.8	7.2	0.0492	0.0537	0.00	0.905	0.8678
Whiting	75	1.1033	1.173	6.3	-0.0536	-0.0074	0.05	0.9182	0.9479
Whiting	125	1.3128	1.346	2.5	-0.2861	-0.2512	0.03	<0,01	<0,01
Whiting	175	1.3836	1.4129	2.1	-0.0538	-0.03577	0.02	<0,01	<0,01
Whiting	225	1.4918	1.5117	1.3	0.1157	0.1436	0.03	<0,01	<0,01
Whiting	275	1.4607	1.503	2.9	0.0462	0.0945	0.05	0.0103	0.0255
Whiting	350	1.2608	1.3061	3.6	0.2798	0.282	0.00	0.0119	0.0037

Table 6.1.2.3

Test for significance of crossed effects with ship in the model of number caught
p=probability of no effect
r^2=proportion of total variance explained
Empty cells denotes parameter effects not significantly different from zero.

		Ship*area		ship*quarter	
species	length in mm	p	r2	p	r2
Cod	125	0.891	0.060	0.152	0.007
Cod	175	0.845	0.072	0.549	0.004
Cod	225	0.943	0.084	0.374	0.007
Cod	275	0.983	0.075	0.745	0.004
Cod	350	0.998	0.071	0.690	0.003
Haddock	125	0.751	0.053	0.020	0.006
Haddock	175	0.605	0.068	0.001	0.009
Haddock	225	0.524	0.071	0.015	0.006
Haddock	275	0.716	0.064	0.211	0.003
Haddock	350	0.889	0.064	0.150	0.004
Herring	125	0.005	0.071	0.004	0.009
Herring	175	0.111	0.076	<0,001	0.011
Herring	225	0.017	0.103	0.778	0.006
Herring	275	0.150	0.101	0.076	0.008
Herring	350	0.123	0.146	0.193	0.015
Norway pout	75	0.129	0.085	<0,0001	0.019
Norway pout	125	0.279	0.076	0.068	0.005
Norway pout	175	0.328	0.091	0.308	0.005
Sprat	75	0.692	0.064	0.057	0.008
Sprat	125	0.572	0.062	0.595	0.003
Whiting	75	0.006	0.091	0.017	0.007
Whiting	125	0.020	0.073	0.040	0.005
Whiting	175	0.328	0.060	0.367	0.002
Whiting	225	0.137	0.066	0.095	0.004
Whiting	275	0.128	0.076	0.128	0.004
Whiting	350	0.147	0.095	0.449	0.003

Table 6.1.2.4

Summary of model of number caught in the IBTS. Model excluding ship effect. Empty cells denotes parameter effects not significantly different from zero.							
		Proportion of total deviance explained					
species	length in mm	model	area	year	area*year	quarter	quarter*area
Cod	125	0.539	0.283	0.073		0.084	0.099
Cod	175	0.507	0.234	0.045	0.142	0.019	0.067
Cod	225	0.347	0.154	0.013	0.166	0.013	
Cod	275	0.425	0.192	0.083	0.139	0.011	
Cod	350	0.450	0.195	0.065	0.123	0.003	0.064
Haddock	125	0.651	0.288	0.048	0.116	0.122	0.077
Haddock	175	0.532	0.215	0.04	0.099	0.079	0.099
Haddock	225	0.538	0.291	0.018	0.116	0.056	0.057
Haddock	275	0.527	0.379	0.029	0.094	0.025	
Haddock	350	0.539	0.313	0.054	0.101	0.022	0.049
Herring	125	0.443	0.18	0.07	0.138	0.009	0.046
Herring	175	0.428	0.199	0.025	0.144	0.007	0.053
Herring	225	0.464	0.203	0.025	0.144	0.016	0.077
Herring	275	0.476	0.178	0.016	0.129	0.016	0.137
Herring	350	0.375	0.174	0.01	0.191		
Norway pout	75	0.599	0.186	0.081	0.117	0.107	0.108
Norway pout	125	0.514	0.228	0.022	0.107	0.063	0.094
Norway pout	175	0.425	0.24	0.046		0.007	0.132
Sprat	75	0.380	0.195	0.034	0.151		
Sprat	125	0.438	0.2	0.02	0.142	0.01	0.065
Whiting	75	0.515	0.176	0.094		0.099	0.146
Whiting	125	0.526	0.195	0.07	0.133	0.018	0.109
Whiting	175	0.521	0.226	0.041	0.14	0.037	0.078
Whiting	225	0.502	0.191	0.041	0.153	0.013	0.105
Whiting	275	0.470	0.21	0.077	0.100	0.009	0.074
Whiting	350	0.414	0.195	0.027	0.109	0.011	0.072

Table 6.1.2.5

Comparison between model of number caught with and without ship-effect				
		Model r^2		
species	length in mm	with ship	without ship	% decrease
Cod	125	0.603	0.539	10.6
Cod	175	0.484	0.507	-4.8
Cod	225	0.392	0.347	11.6
Cod	275	0.491	0.425	13.4
Cod	350	0.447	0.450	-0.7
Haddock	125	0.666	0.651	2.3
Haddock	175	0.544	0.532	2.2
Haddock	225	0.538	0.538	0.0
Haddock	275	0.545	0.527	3.3
Haddock	350	0.563	0.539	4.3
Herring	125	0.536	0.443	17.4
Herring	175	0.461	0.428	7.2
Herring	225	0.477	0.464	2.7
Herring	275	0.513	0.476	7.2
Herring	350	0.453	0.375	17.2
Norway pout	75	0.652	0.599	8.1
Norway pout	125	0.554	0.514	7.2
Norway pout	175	0.446	0.425	4.7
Sprat	75	0.526	0.380	27.8
Sprat	125	0.511	0.438	14.3
Whiting	75	0.571	0.515	9.8
Whiting	125	0.549	0.526	4.2
Whiting	175	0.541	0.521	3.7
Whiting	225	0.515	0.502	2.5
Whiting	275	0.500	0.470	6.0
Whiting	350	0.454	0.414	8.8

Table 6.1.4.1

Correlation VPA, ICES estimate and predicted catch			
Correlation between			
	VPA	VPA	Predicted
	Predicted	ICES	ICES
prey			
cod	0.8616501	0.9206219	0.98707
haddock	0.8372021	0.9294276	0.9684958
herring	0.8454682	0.9823279	0.8839711
norway pou	0.32545	0.8548802	-0.061003
sprat			0.4502539
whiting	0.0781597		

Table 6.2.4.1

Correaltion between PFI, VPA and predicted catch
3rd quarter vaules compared to VPA or ICES estimate as described in section 5.2.4

	1st quarter Correlation with VPA		catch in IBTS		Correlation between PFI's	3rd quarter		
Predator / prey	cod	whiting	cod	whiting	cod and whiting	cod	whiting	Prey length less than
cod	0.9567694	0.8036783	0.8418071	0.4015247	0.790481618	0.734868	0.1668365	200
haddock	0.4014474	0.6369268	0.1409084	0.2359685	0.154406682	0.4239961	0.7999963	150
herring	0.4413169	0.6785667	0.7711042	0.7612939	0.88144103	0.9200137	0.9246368	100
norway pout	0.3959258	0.622694	-0.733836	0.0175725	0.4795948	0.336929	0.6723382	100
sandeel	0.5626818	0.5068819			0.061467462	0.2347951	-0.019263	100
sprat			0.5076947	0.9363225	0.741877053	0.5417122	0.8413911	150
whiting	-0.189704	0.2885651	0.9080004	0.7270517	0.810513911	0.4651292	0.8323776	100

Table 6.3.1.1

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 6.3.1.2

Summary of fit of basic model of ratios
Proportion of total variance explained (r^2) by each significant factor
Empty cells denotes parameter effects not significantly different from zero.

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	0.1241	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 6.3.1.3

The proportion of the total variance (r2) explained of factors and their crossed effects in the basic model
Empty cells denotes parameter effects not significantly different from zero.

Reference		Factor				
species	length in mm	ln(ibts)	prey	prey length	predator	predator length
Pout	75	0.25379	0.10166	0.025	0.1234	0.07975
Pout	125	0.24445	0.0764	0.13965	0.0345	0.0528
Pout	175	0.2179	0.117	0.10849	0.0273	0.09459
Sprat	75	0.2543	0.0699	0.1108		0.0971
Sprat	125	0.1915		0.1862	0.0203	
Whiting	75	0.18286	0.37399	0.17448	0.12366	0.1745
Whiting	125	0.1981	0.1004	0.0487	0.01213	0.0864
Whiting	175	0.1926		0.0877	0.00308	0.02
Whiting	225	0.1931	0.1026	0.0772		0.02
Whiting	275	0.232	0.09443	0.08413		0.0219

Table 6.3.2.1

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

Table 6.3.2.2

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 parameter effects not significantly different from zero.										
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)	0.169	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	
no. 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)*no. 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*no. sample									0.047	
prey length* no. sample	0.011	0.011			0.037					
predator* no. sample		0.001								
predator length* no. sample	0.024		0.039	0.033			0.016		0.016	
ln(ibts)*pred. length* no. samp.		0.025								
ln(ibts)*prey*predator						0.037				
ln(ibts)*prey*predator length						0.067				

Table 6.3.2.3

Summary of fit of model of ratios including ln(number of stomachs) as a factor
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
Pout	75	610	0.447	38	1.073	0.616
Pout	125	904	0.421	54	1.047	0.430
Pout	175	341	0.363	19	0.965	0.198
Sprat	75	381	0.327	28	1.153	0.752
Sprat	125	320	0.381	19	1.220	0.114
Whiting	75	184	0.591	56	0.776	0.538
Whiting	125	529	0.287	16	1.002	0.628
Whiting	175	461	0.238	12	1.070	0.739
Whiting	225	436	0.252	14	1.037	0.161
Whiting	275	281	0.163	2	1.124	0.002

Table 6.3.2.4

Comparison of fit of model including number of stomachs and model including ln(number of stomachs) as a factor.
Increase when going from number to ln(number)

Reference		Model		
species	length in mm	r^2	dimension	std
pout	75	-0.0595	4	0.061
pout	125	-0.098	-11	0.077
pout	175	-0.097	9	0.085
sprat	75	0.021	15	0.007
sprat	125	-0.119	-12	0.086
whiting	75	-0.067	4	0.075
whiting	125	-0.044	21	0.053
whiting	175	-0.0509	-2	0.033
whiting	225	-0.067	11	0.06
whiting	275	0.05	22	0.012

Table 6.3.3.1

Summary of fit of model of ratios build on IBTS predictions ignoring ship effect
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	715	0.488	53	4.62	0.760	0.074
Pout	125	947	0.470	39	4.15	0.432	0.041
Pout	175	355	0.436	25	3.81	0.766	0.070
Sprat	75	382	0.409	43	6.64	0.600	0.113
Sprat	125	320	0.413	12	7.06	0.523	0.038
Whiting	75	184	0.633	46	4.09	0.207	0.250
Whiting	125	532	0.420	56	4.53	0.905	0.105
Whiting	175	466	0.323	10	5.52	0.657	0.021
Whiting	225	445	0.392	39	5.25	0.345	0.088
Whiting	275	283	0.363	24	5.41	0.099	0.085

Table 6.3.3.2

Summary of fit of model of ratios build on IBTS predictions ignoring ship effect
Proportion of total variance explained (r^2) by each significant factor
Empty cells denotes parameter effects not significantly different from zero.

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)	0.238	0.187	0.214	0.193	0.202	0.072	0.202	0.223	0.155	0.236
prey	0.041	0.070	0.094	0.045		0.133	0.054		0.080	0.023
preylength	0.016	0.128	0.047	0.015	0.167	0.131	0.023	0.079	0.030	0.016
predator	0.076	0.010	0.000		0.021	0.026		0.003		
predator length	0.046	0.011	0.019	0.055		0.040	0.042	0.017	0.020	0.024
ln(ibts)*prey	0.015								0.018	
ln(ibts)*prey length		0.009	0.011	0.015	0.023	0.027	0.003			
ln(ibts)*predator			0.020			0.000				
ln(ibts)* predator length	0.002					0.041	0.024			
prey* prey length				0.036					0.047	0.064
prey*predator		0.033	0.031							
prey*predator length						0.136	0.040		0.043	
predator*prey length						0.001				
prey length*predator length	0.029	0.021		0.050						
ln(ibts)*prey*predator length	0.024									
ln(ibts)*prey length*predator length							0.033			
ln(ibts)*prey length*predator						0.028				

Table 6.3.3.3

Comparison of basic model and model without ship effect
Change when going from basic model to model ignoring ship effect on catches

Reference		Change in model		
species	length in mm	r2	std	dimension
Pout	75	-0.011	0.20	-11
Pout	125	0.004	-0.09	4
Pout	175	-0.053	0.18	3
Sprat	75	-0.045	0.16	0
Sprat	125	0.015	-0.03	-5
Whiting	75	-0.146	0.11	14
Whiting	125	0.007	-0.10	-19
Whiting	175	0.007	-0.01	0
Whiting	225	0.010	-0.06	-14
Whiting	275	0.002	0.00	0

Table 6.3.4.1

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	0.27784	0.08576	<0.0001	<0.0001
Whiting	125	0.212	0.27256	0.15104	<0.0001	<0.0001
Whiting	175	0.169	0.26092	0.07668	<0.0001	<0.0001
Whiting	225	0.154	0.23858	0.07002	<0.0001	<0.0001
Whiting	275	0.142	0.26518	0.01822	<0.0001	<0.0001

Table 6.3.4.2

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 parameter effects not significantly different from zero.					
Reference species length in mm Factor	Pout 75	Pout 125	Pout 175	Sprat 75	Sprat 125
ln(ibts)	0.2356	0.2058	0.2179	0.2429	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 6.3.4.2 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 parameter effects not significantly different from zero.					
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 6.3.4.3

Comparison of basic model and model build on IBTS predictions ignoring ship effect Change when going from basic model to model ignoring ship effect on catches				
Reference		Change in model		
species	length in mm	r2	std	dimension
Pout	75	0.29855	-1.23	165
Pout	125	0.28725	-0.9	218
Pout	175	0.31071	-0.78	98
Sprat	75	0.3303	-1.79	72
Sprat	125	0.446	-2.53	117
Whiting	75	0.09895	-0.36	22
Whiting	125	0.35487	-0.86	169
Whiting	175	0.57562	-2.3	220
Whiting	225	0.4728	-1.74	161
Whiting	275	0.48977	-1.91	116

Table 6.3.5.1

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 6.3.5.2

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 parameter effects not significantly different from zero.

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	0.1242	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 6.3.5.3

Comparison of basic model and model including lengths as polynomial
Change when going from basic model to polynomial model

Reference		Change in model		
species	length in mm	r2	std	dimension
Pout	75	-0.03795	0.0208145	-21
Pout	125	-0.02975	0.0143868	-23
Pout	175	-0.05739	0.0239669	-17
Sprat	75	-0.1109	0.045679	-32
Sprat	125	0.0625	-0.03653	11
Whiting	75	-0.10455	0.0394472	-29
Whiting	125	-0.03443	0.0111447	-16
Whiting	175	-0.01298	0.0034358	-5
Whiting	225	-0.0498	0.0174011	-16
Whiting	275	-0.09493	0.0310906	-5

Table 6.3.5.4

Parameter values of "o" in the model describing lengths as polynomial
up95=Upper 95% confidence limit
lo95=Lower 95% confidence limit

Reference		"o"			Particularity		
species	length in mm	Estimate	lo95%	up95%	Estimate	lo95%	up95%
Pout	75	0					
Pout	125	0					
Pout	175	-1.800	-2.634	-0.965	5.001	3.417	9.322
Sprat	75	0					
Sprat	125	0					
Whiting	75	0					
Whiting	125	0					
Whiting	175	-0.081	-0.110	-0.052			
Whiting	225	-0.846	-1.473	-0.219	10.638	6.112	41.023
Whiting	275	-0.056	-0.094	-0.017			

Table 6.3.5.5

Parameter values of "H" in the model describing dependence on lengths as polynomial

Reference		"H" for predator	
species	length in mm	Cod	Whiting
Pout	75	-0.40819	-1.512
Pout	125	-0.9177	-1.8646
Pout	175	17.7932	14.712
Sprat	75	-0.7678	-0.7678
Sprat	125	-1.0298	0.4743
Whiting	75	-2.1718	-2.1718
Whiting	125	-0.6428	-0.6428
Whiting	175	0	0
Whiting	225	8.156	8.156
Whiting	275	0	0

Table 6.3.6.1

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)	r^2	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 6.3.6.2

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 parameter effects not significantly different from zero.

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)	0.3829	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 6.3.6.3

Comparison of basic model and model build on roundfish areas
Change when going from basic model to model build on roundfish areas

Reference		Change in model		
species	length in mm	r2	dimension	%dimension
Pout	75	-0.090	21	0.034
Pout	125	-0.183	-16	-0.023
Pout	175	-0.229	-23	-0.025
Sprat	75	-0.164	-14	-0.007
Sprat	125	-0.256	-45	-0.096
Whiting	75	0.071	9	0.171
Whiting	125	-0.245	-35	-0.026
Whiting	175	-0.256	-58	-0.078
Whiting	225	-0.236	-36	-0.052
Whiting	275	-0.110	-4	0.020

Table 6.3.6.4

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)	r^2	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 6.3.6.5

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 parameter effects not significantly different from zero.

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)	0.2594	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		

Table 6.3.6.6

Comparison of basic model and model build on North Sea scale
Change when going from basic model to model build on roundfish areas

Reference		Change in model		
species	length in mm	r2	dimension	%dimension
Pout	75	0.178	-21	-0.034
Pout	125	0.219	16	0.023
Pout	175	0.183	23	0.025
Sprat	75	0.271	14	0.007
Sprat	125	0.185	45	0.096
Whiting	75	-0.018	-9	-0.171
Whiting	125	0.292	35	0.026
Whiting	175	0.493	58	0.078
Whiting	225	0.224	36	0.052
Whiting	275	0.130	4	-0.020

Table 6.3.7.1

Correlation between sandeel abundance predicted by model of ratios and VPA estimates of 1-year olds in the 1st quarter

Reference species	length	Correlation
Pout	75	0.6173
Pout	125	0.6277
Pout	175	0.1387
Sprat	125	-0.1349
Whiting	75	0.299
Whiting	125	0.1853
Whiting	175	-0.0607
Whiting	225	-0.0304

Table 6.4.1.1

Summary of fit of model of maximum weight of stomach content
p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

	Model				
n(obs)	r2	dimension	std	p	% dimension
10	0.9884	1	0.219	0.41	0.111

Parameter estimates	
Parameter	Estimate
ln(predator length)	2.824
Intercept	-5.205
exp(intercept)	0.00548905

Table 6.4.2.1

Summary of fit of model of maximum prey weight in the stomachs
p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

	Model				
n(obs)	r^2	dimension	std	p	% dimension
126	0.9612	22	0.2248	0.0295	0.176

Table 6.4.2.2

Model of maximum weight of prey in the stomachs
Estimates of slope and intercept for the relationship w=a+b*ln(l)
Standardized to a predator in lengthgroup 350

Predator	Prey	Slope	Intercept	exp(intercept)
Cod	Cod	2.829	-3.568	0.0282
Cod	Haddock	2.255	-0.571	0.5651
Cod	Herring	2.370	-1.213	0.2974
Cod	Norway pout	2.375	-1.052	0.3491
Cod	Sandeel	1.692	1.285	3.6130
Cod	Sprat	2.162	-0.309	0.7341
Cod	Whiting	2.473	-1.751	0.1735
Whiting	Cod	1.956	0.644	1.9046
Whiting	Haddock	1.381	3.454	31.6251
Whiting	Herring	1.496	3.127	22.8043
Whiting	Norway pout	1.501	2.970	19.4968
Whiting	Sandeel	0.819	5.771	320.8424
Whiting	Sprat	1.288	3.912	49.9963
Whiting	Whiting	1.599	2.307	10.0437

Table 6.4.3.1

Summary of fit of model of maximum ratio as a function of available space
Weight of reference excluded
p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

	Model				
n(obs)	r^2	dimension	std	p	% dimension
1001	0.724	41	0.8187	0.0006	0.041

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

Factor	r^2
ln(avai(w))	0.186735088
ln(length)	0.205780049
prey species	0.087147335
predator length	0.184021128
prey*ln(length)	0.006670675
prey*predator length	0.010672908

Parameter estimate of dependence on ln(avai(w))

Estimate	lo95%	up95%
1.172	1.1097	1.2343

Table 6.4.3.2

Summary of fit of model of maximum ratio as a function of available space
Weight of reference included
p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

	Model				
n(obs)	r^2	dimension	std	p	% dimension
1001	0.7388	62	0.8053	0.1243	0.062

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

Factor	r^2
ln(avai(w))	0.22321467
ln(length)	0.20943015
prey species	0.08777429
predator length	0.19105939
prey*ln(length)	0.00654442
ln(length)*predator length	0.00349551
prey*predator length	0.00902692
prey*predator length*ln(length)	0.00817624

Parameter estimate of dependence on ln(avai(w))

Estimate	lo95%	up95%
1.227	1.162	1.293

Table 6.4.3.3

Summary of fit of model of minimum ratio as a function of available space
Weight of prey excluded
p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

	Model				
n(obs)	r^2	dimension	std	p	% dimension
814	0.7036	8	0.7755	0.0004	0.010

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

Factor	r^2
ln(avai(w))	0.3454334
ln(length)	0.1388345
reference species	0.0141161
predator length	0.2052277

Parameter estimate of dependence on ln(avai(w))

Estimate	lo95%	up95%
-1.137	-1.197	-1.076

Table 6.4.3.4

Summary of fit of model of minimum ratio as a function of available space
Weight of prey excluded
p=Probability of normal distribution of residuals
% dimension= Model dimension in percent of the full model

	Model				
n(obs)	r^2	dimension	std	p	% dimension
814	0.7066	8	0.7716	0.0014	0.010

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

Factor	r^2
ln(avai(w))	0.340040402
ln(length)	0.141827865
reference species	0.013516161
predator length	0.21123286

Parameter estimate of dependence on ln(avai(w))

Estimate	lo95%	up95%
-1.191	-1.254	-1.128

Table 6.4.4.1

Summary of fit of the logit 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	0.355507	33	0.22	0.855	0.0541
Pout	125	904	0.240361	34	0.24	0.000	0.0376
Pout	175	341	0.152419	11	0.25	0.009	0.0323
Sprat	75	381	0.226293	11	0.19	0.191	0.0289
Sprat	125	320	0.26503	26	0.21	0.038	0.0813
Whiting	75	184	0.21423	11	0.19	0.290	0.0598
Whiting	125	529	0.178969	11	0.24	0.026	0.0208
Whiting	175	461	0.108811	6	0.25	0.088	0.0130
Whiting	225	436	0.071479	2	0.25	0.012	0.0046
Whiting	275	281	0.064254	2	0.26	0.008	0.0071

Table 6.4.4.2

Summary of fit of logit model of ratios Proportion of total variance explained (r^2) by each significant factor Empty cells denotes parameter effects not significantly different from zero.										
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)	0.1354643	0.1014763	0.097621	0.1190733	0.0581162	0.0220709	0.1455989	0.0751091	0.071373	0.064254
predator	0.0887081							0.0081299		
predator length	0.035399	0.0227892	0.0056452	0.0258621	0.0384569	0.0984479	0.0152089	0.0255718		
prey	0.0290777		0.0491532	0.0813578	0.0847896	0.0937226	0.0181616			
prey length		0.0514548								
ln(ibts)*prey length		0.0321485								
ln(ibts)* predator length		0.019163								
prey*predator	32.84									
prey*predator length	30.59				0.083517					
predator length*prey length		0.0361187								

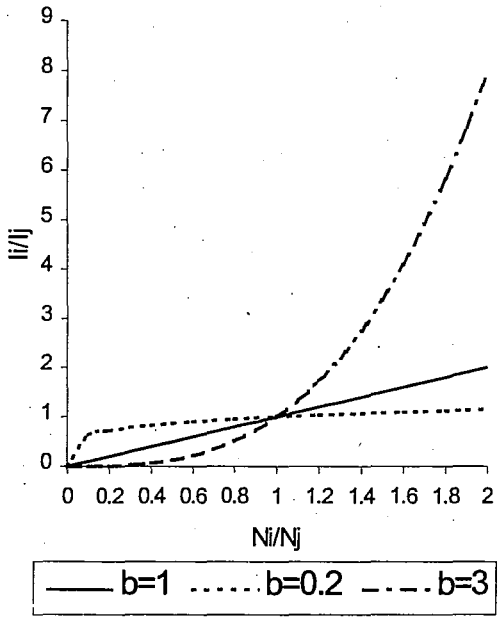


Fig. 3.4.1. Examples of the relation between the ratio ingested and the ratio available when the predator exhibits no switching (b=1), negative switching (b=0.2) and positive switching (b=3).

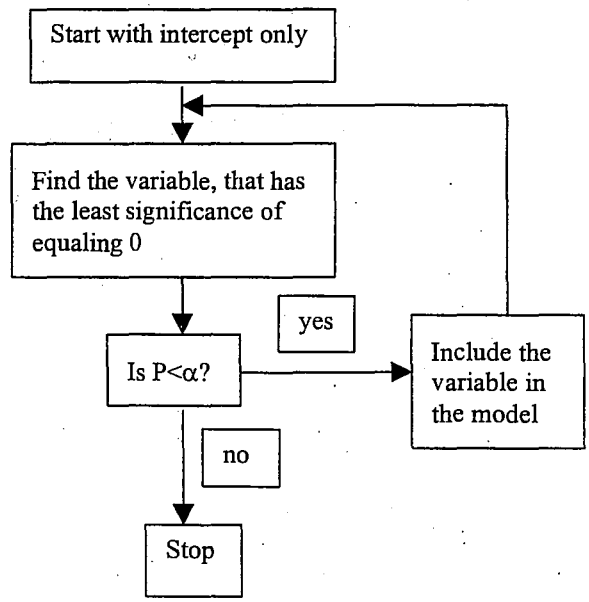


Fig. 4.5.1 Forward selection. From Conradsen (1984).

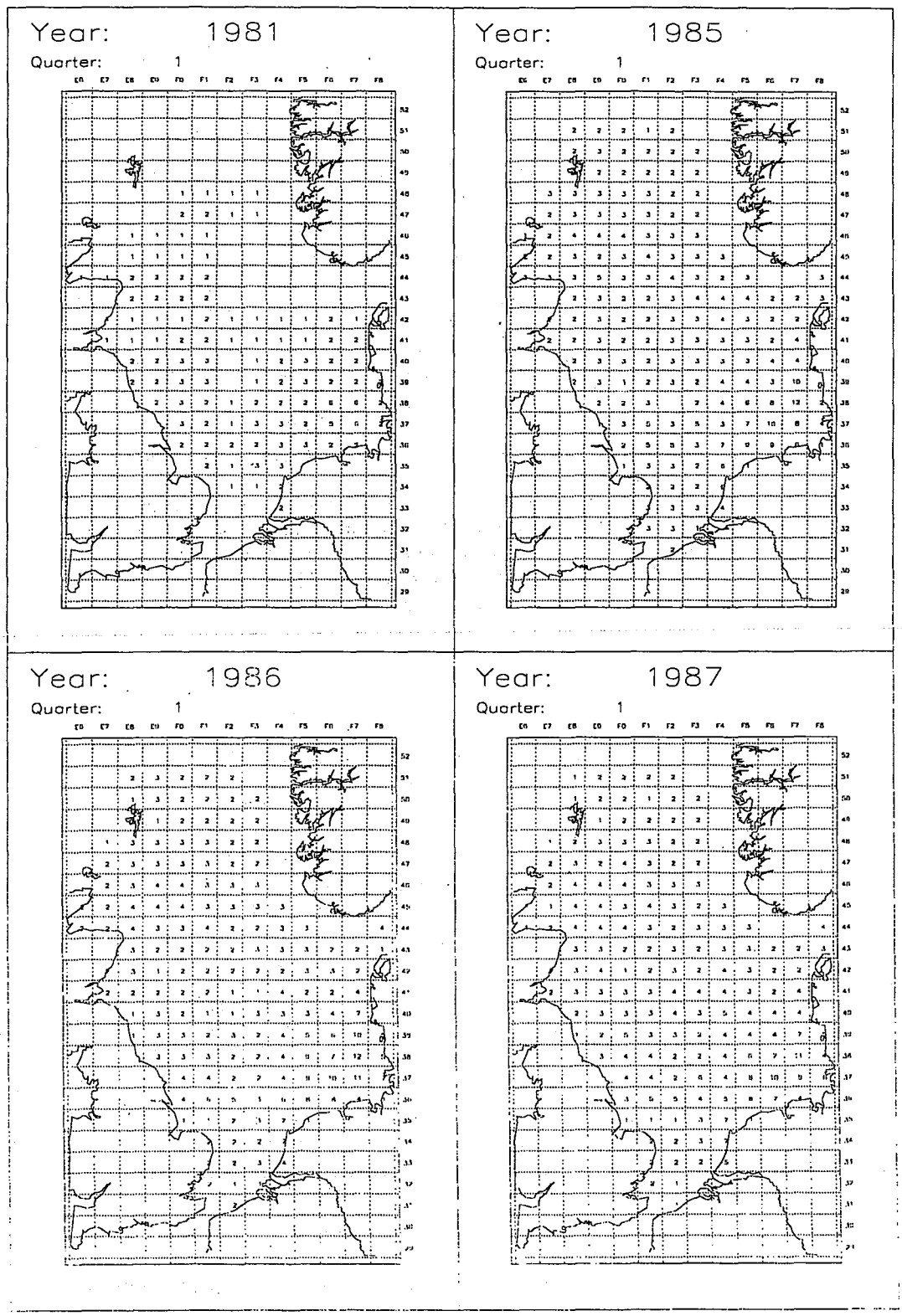


Fig. 5.1.1.1. The number hauls taken in each ICES/square in the IBTS.

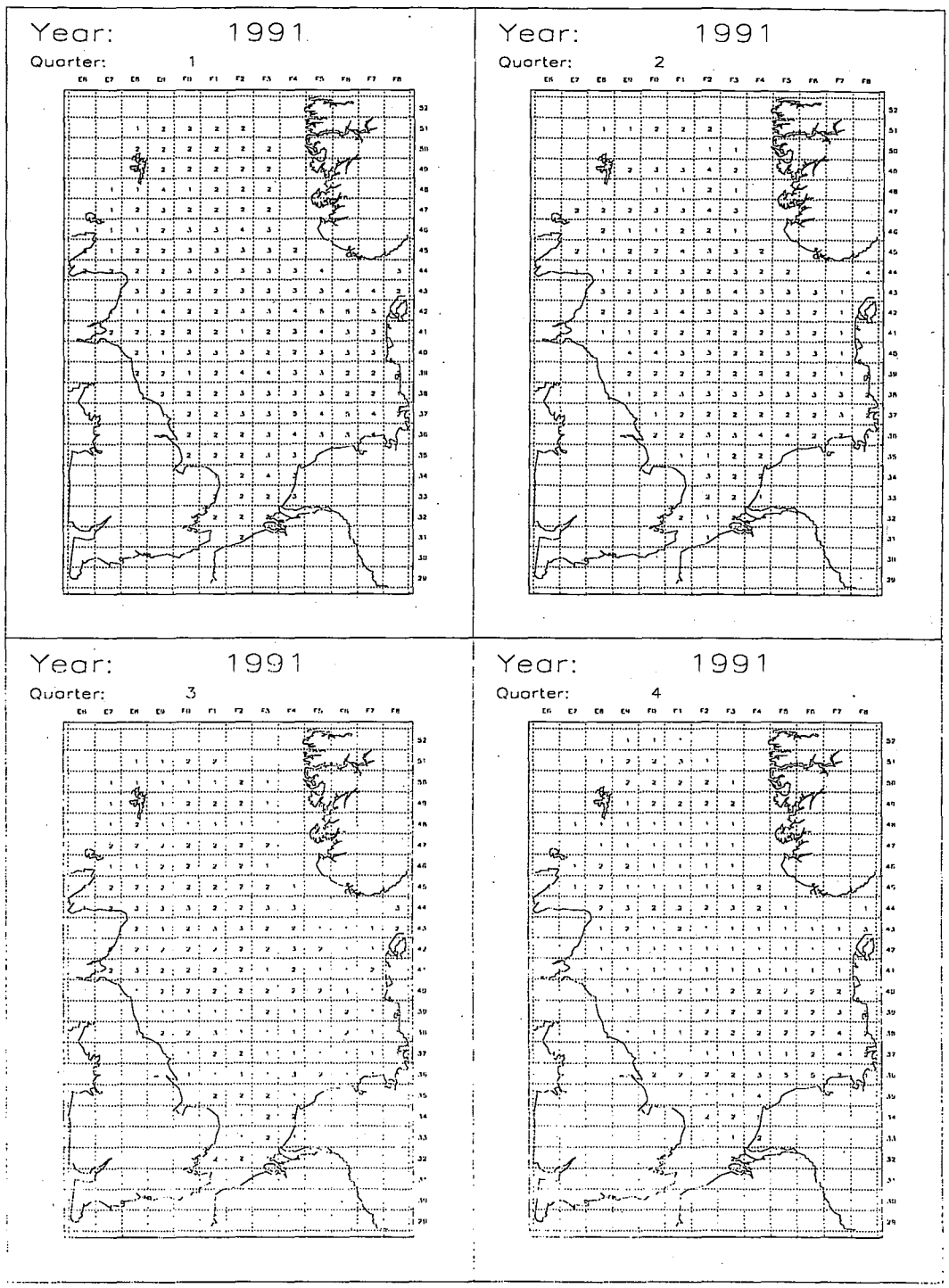


Fig. 5.1.1.1 continued. The number hauls taken in each ICES/square in the IBTS.

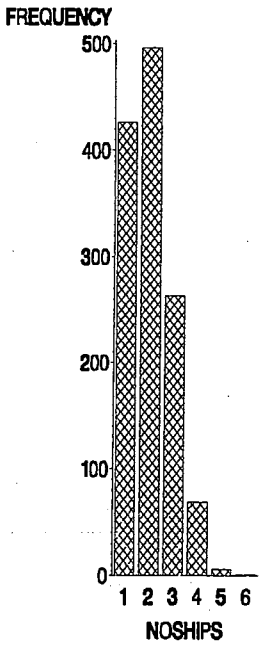


Fig. 5.1.1.2. Ship overlap in time and space. The number of squares trawled by 1, 2, 3.... ships at a particular time.

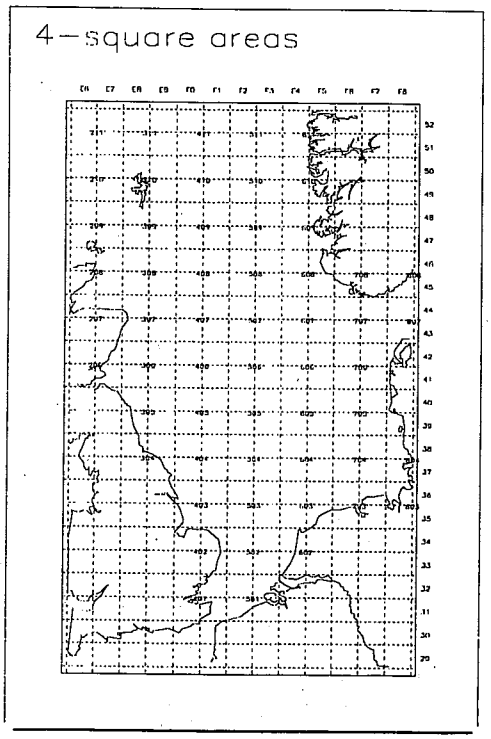


Fig. 5.1.2.1. Definition of the 4-square-areas used.

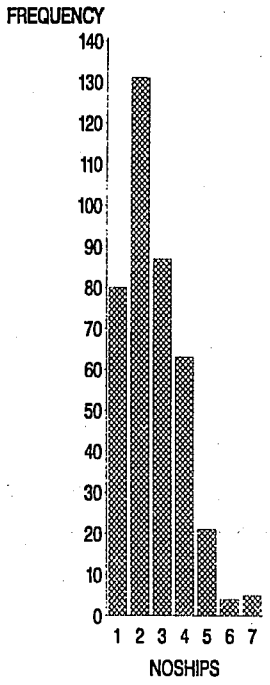


Fig. 5.1.2.2. Ship overlap in time and space. The number of 4-square areas trawled by 1, 2, 3.... ships at a particular time.

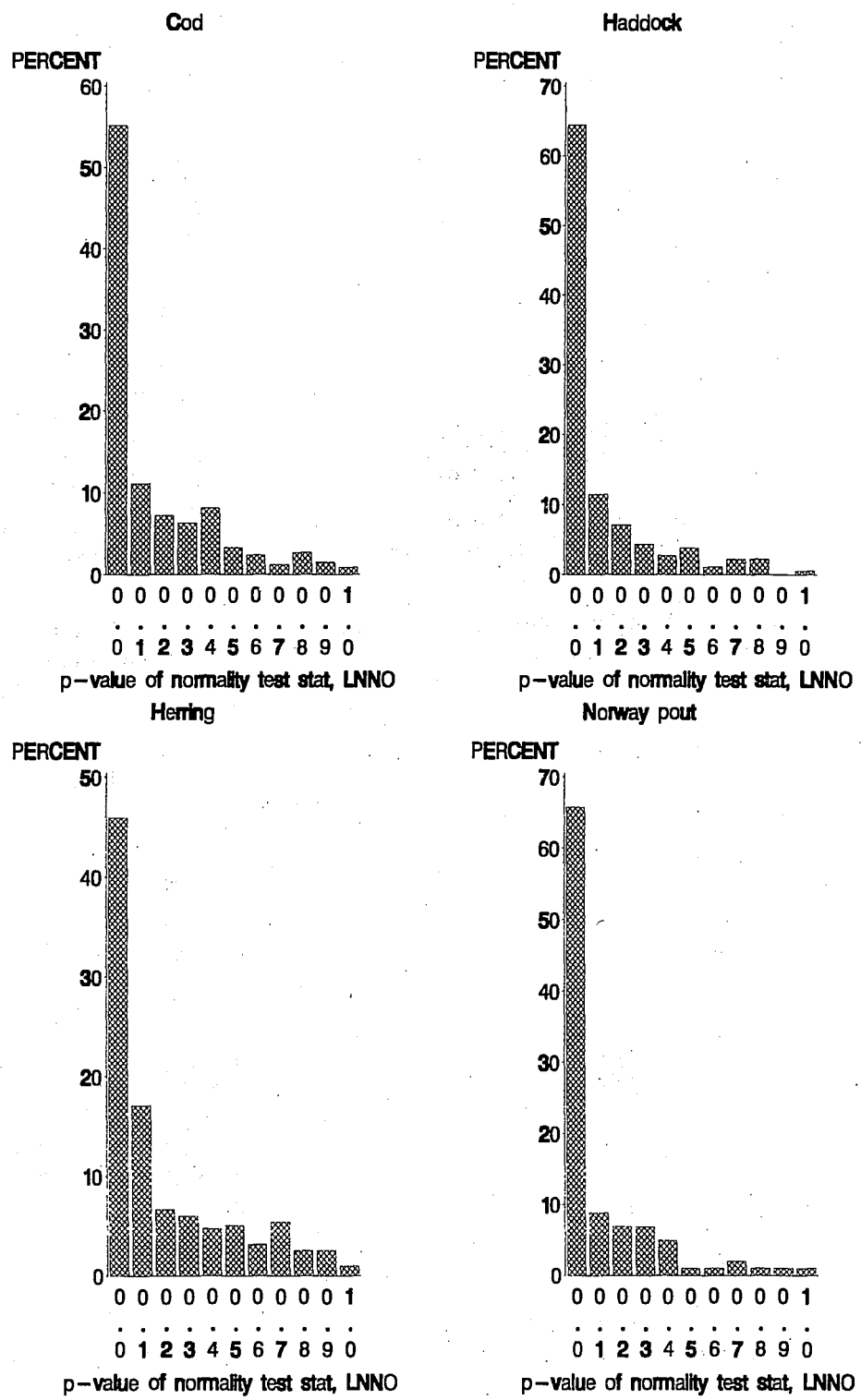


Fig. 5.1.2.3. Probability of normal distribution of ln(number caught+1) within a 4-square area at a given time by a given ship. Only cells with more than 5 observations tested.

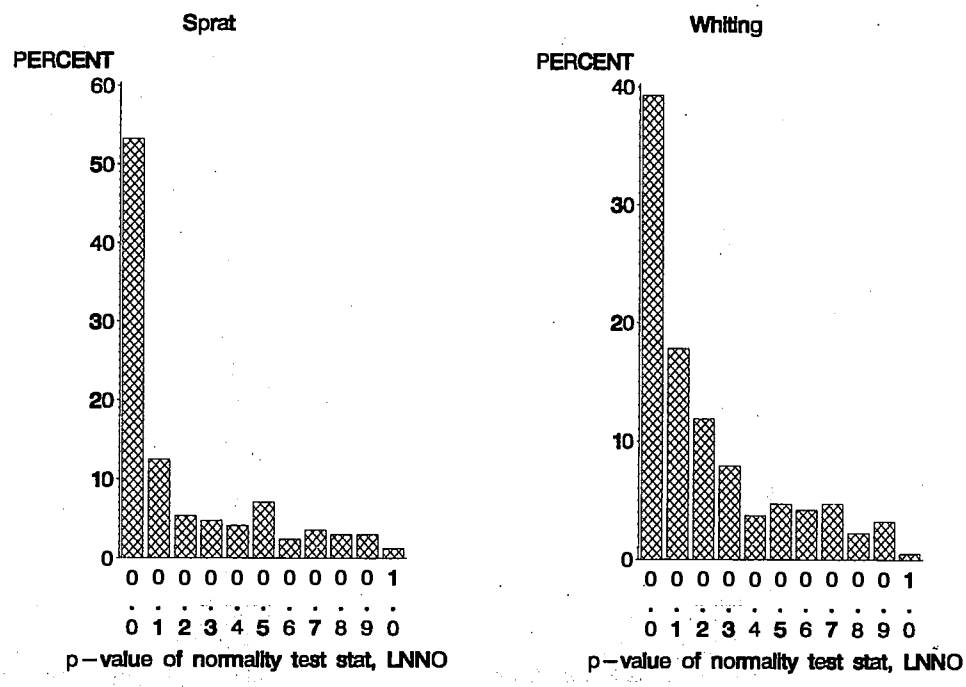


Fig. 5.1.2.3 continued. Probability of normal distribution of ln(number caught+1) within a 4-square area at a given time by a given ship. Only cells with more than 5 observations tested.

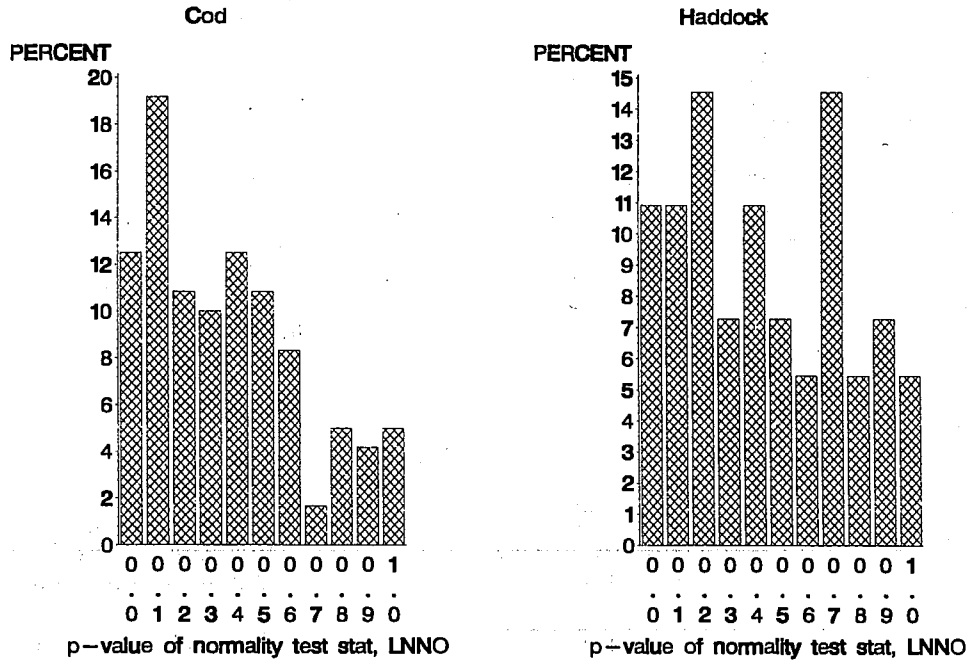


Fig. 5.1.2.4. Probability of normal distribution of ln(number caught given number not equal to 0) within a 4-square area at a given time by a given ship. Only cells with more than 5 observations tested.

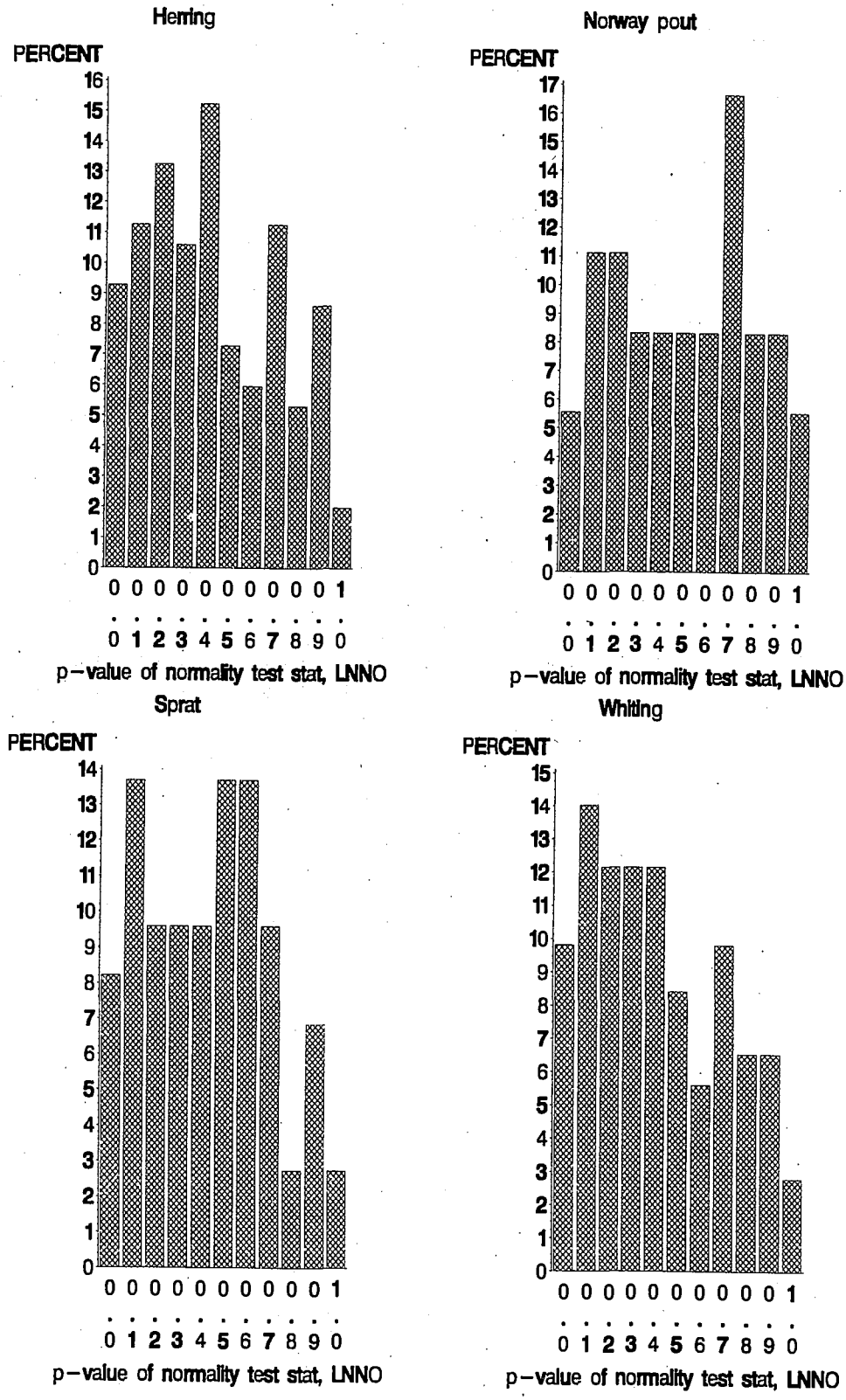


Fig. 5.1.2.4 continued. Probability of normal distribution of ln(number caught given number not equal to 0) within a 4-square area at a given time by a given ship. Only cells with more than 5 observations tested.

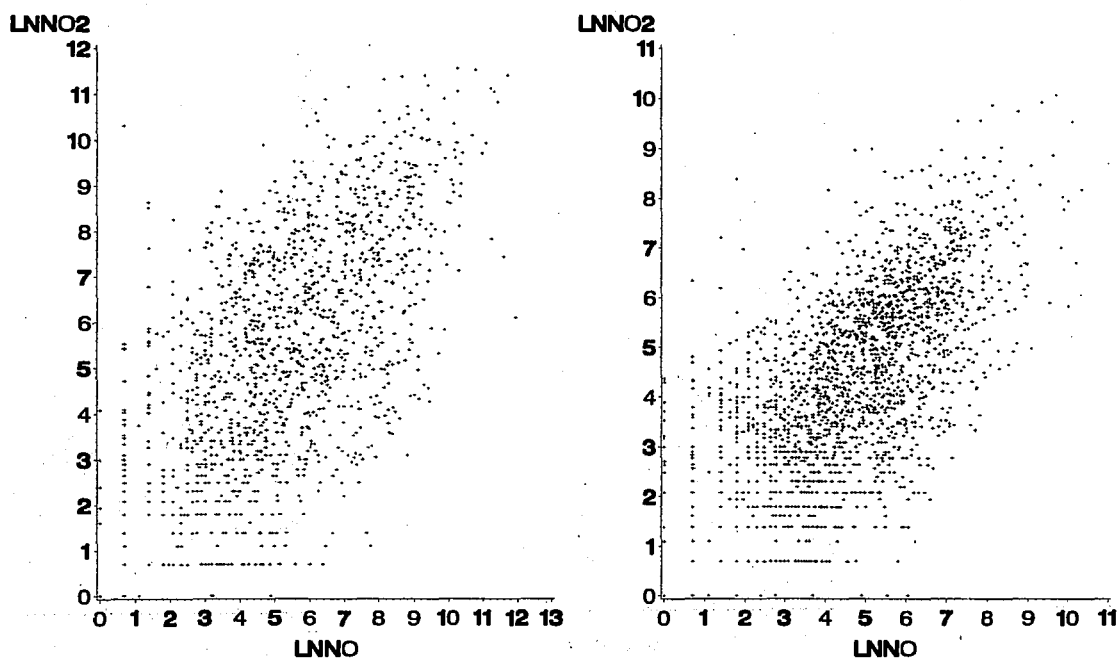


Fig. 5.1.2.5. Left: Catch of herring at 225 mm as a function of catch of herring at 175 mm. Right: Catch of whiting at 225 mm as a function of catch of whiting at 175 mm. Units: ln(number caught given number bot equal to 0).

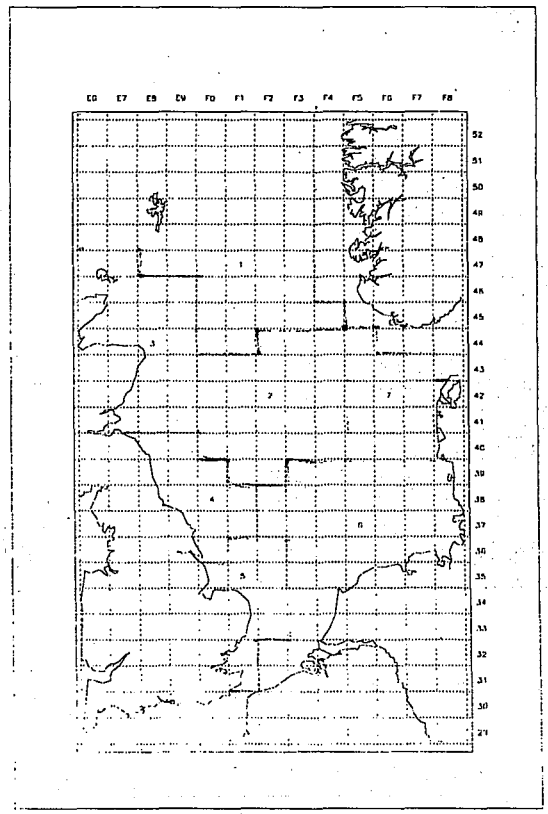


Fig. 5.1.2.6. ICES roundfish areas.

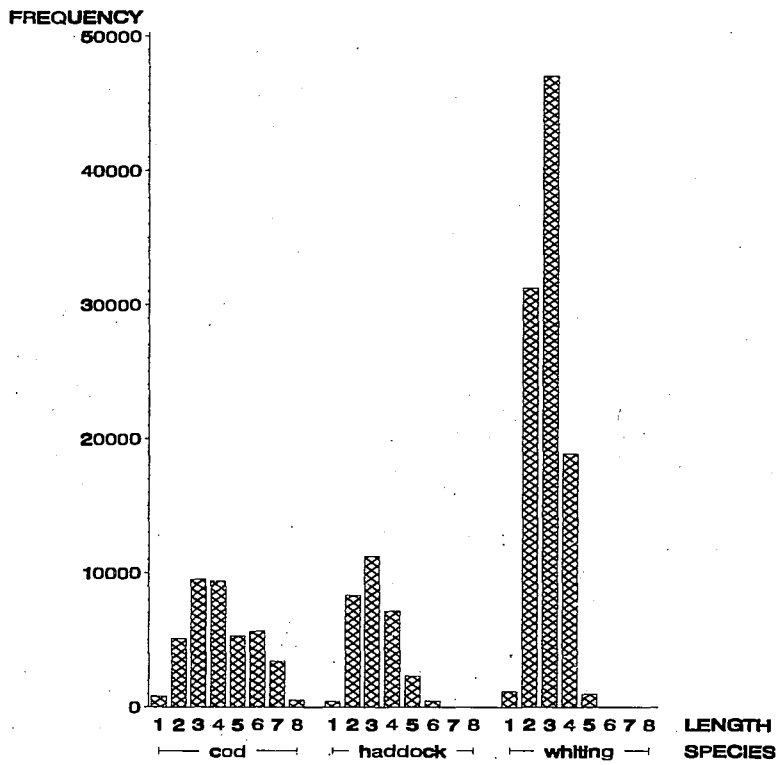


Fig. 5.2.1.2. Number of stomachs sampled in all years and quarters as distributed on lengths of predators.

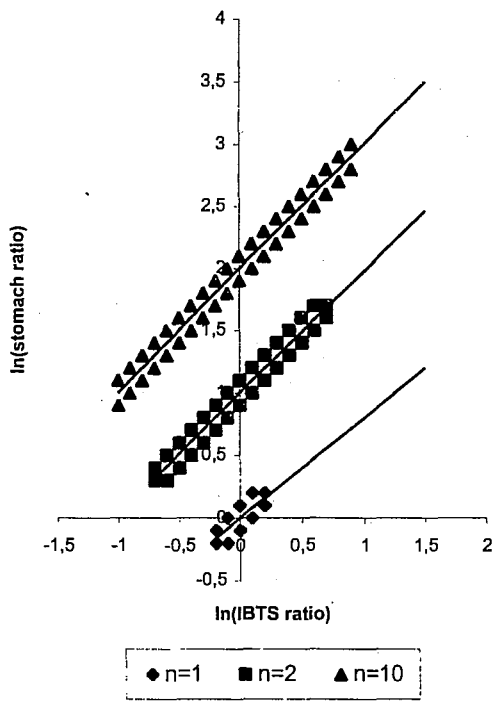


Fig. 5.5.1.1. The effect of limited stomach size on the slope of the dependency. n= number of stomachs in the sample. Maximum ratio in one stomach is set to 0.2. A constant has been added to the lines of n=2 and n=10 to clarify the picture.

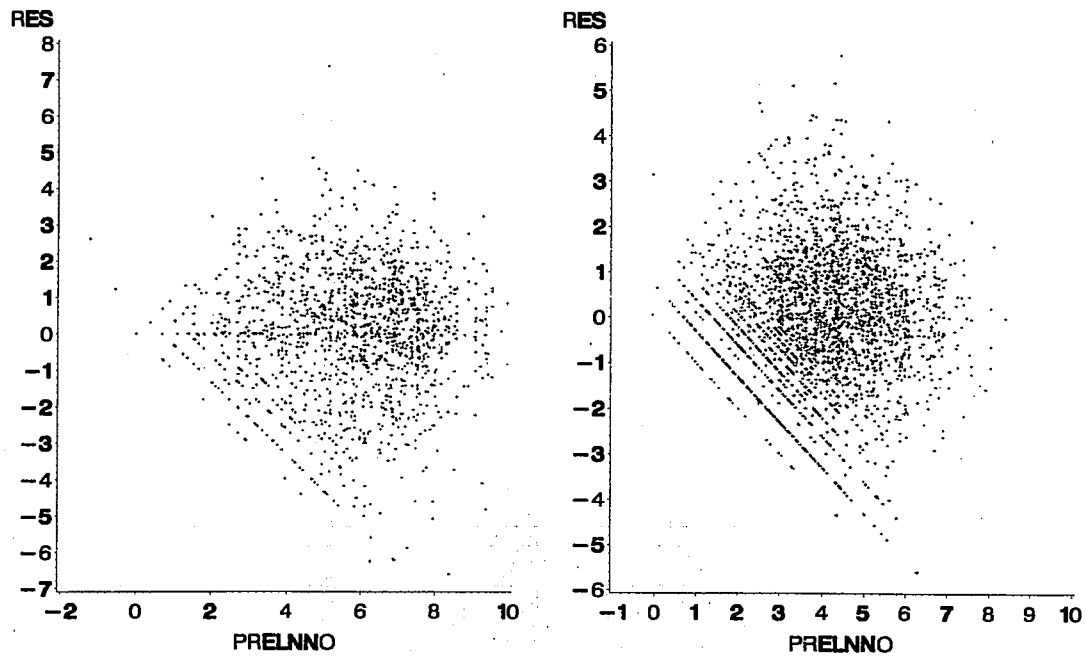


Fig. 6.1.2.2. Examples of plots of residuals from general linear model of ln(number caught given number not equal to 0). Residuals as a function of predicted value. Left: Norway pout at 125 mm. Right: Whiting at 275 mm.

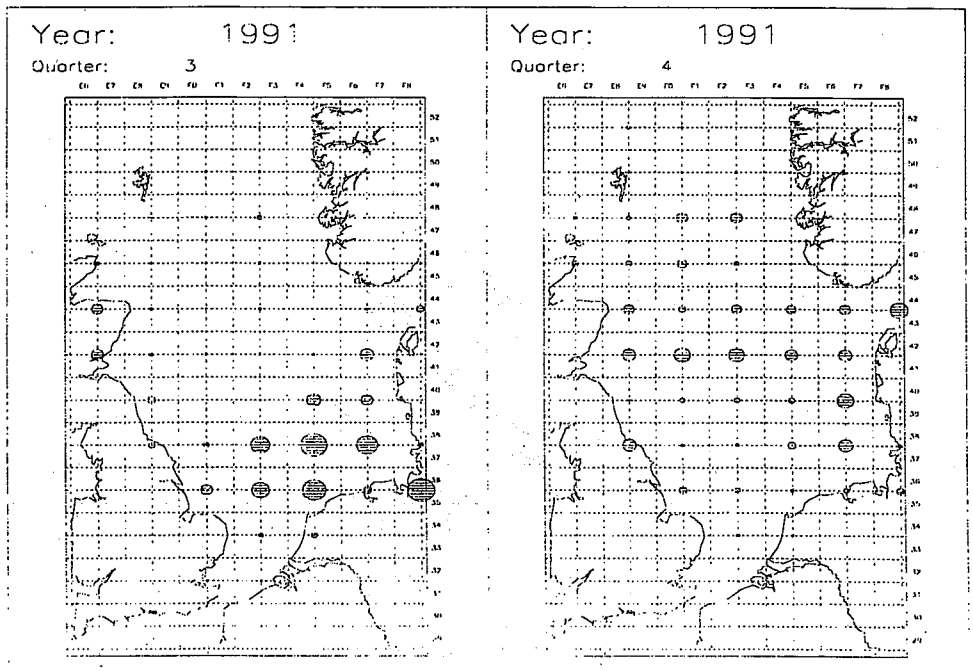


Fig. 6.1.3.1. Predicted catch of whiting at 175 mm in one haul in 1991. The pies are at the same scale.

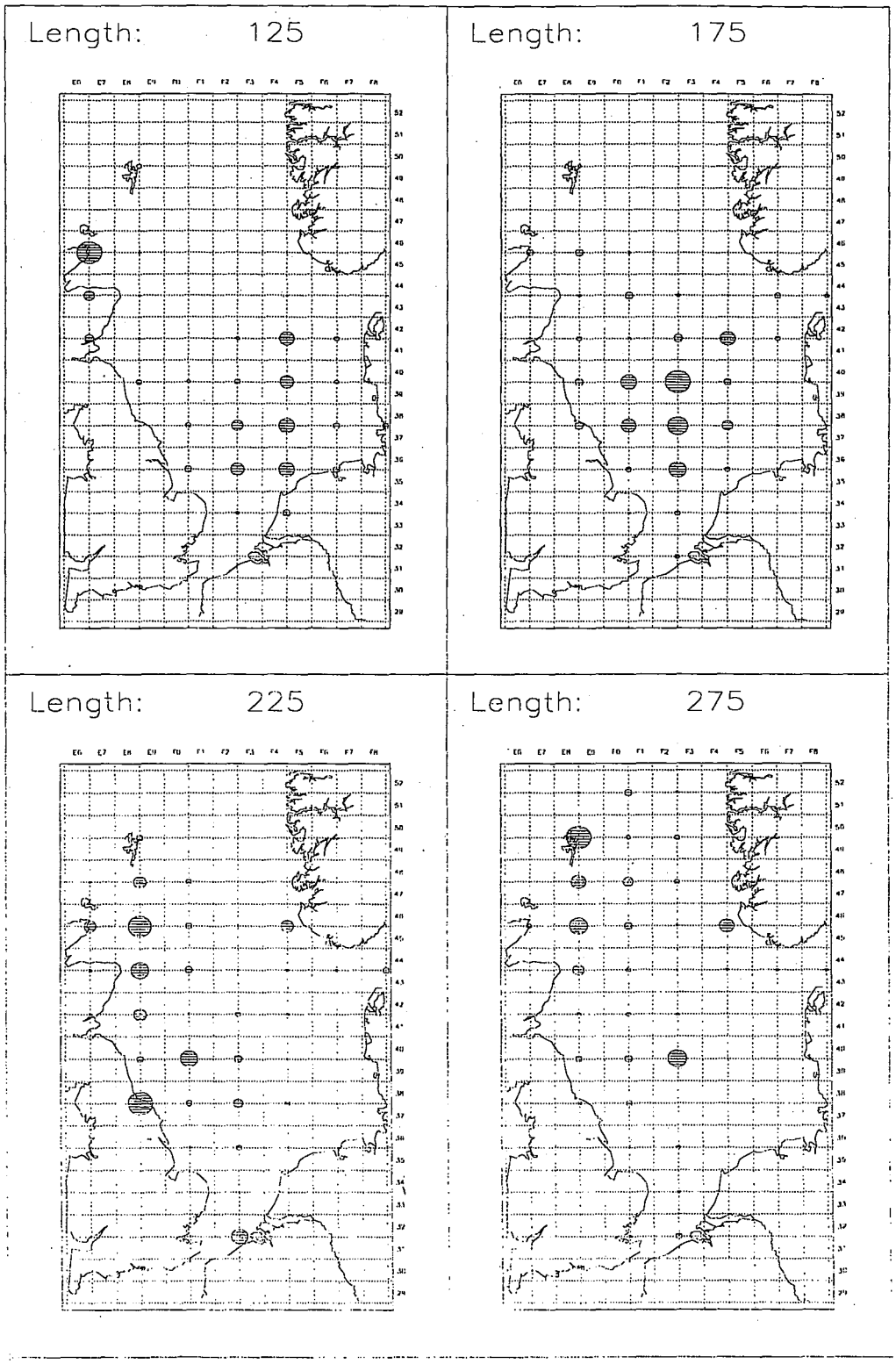


Fig.6.1.3.2 Predicted catch of herring at different lengths in the 1st quarter of 1987. Maps are to the same scale. Area of pie denotes predicted number caught.

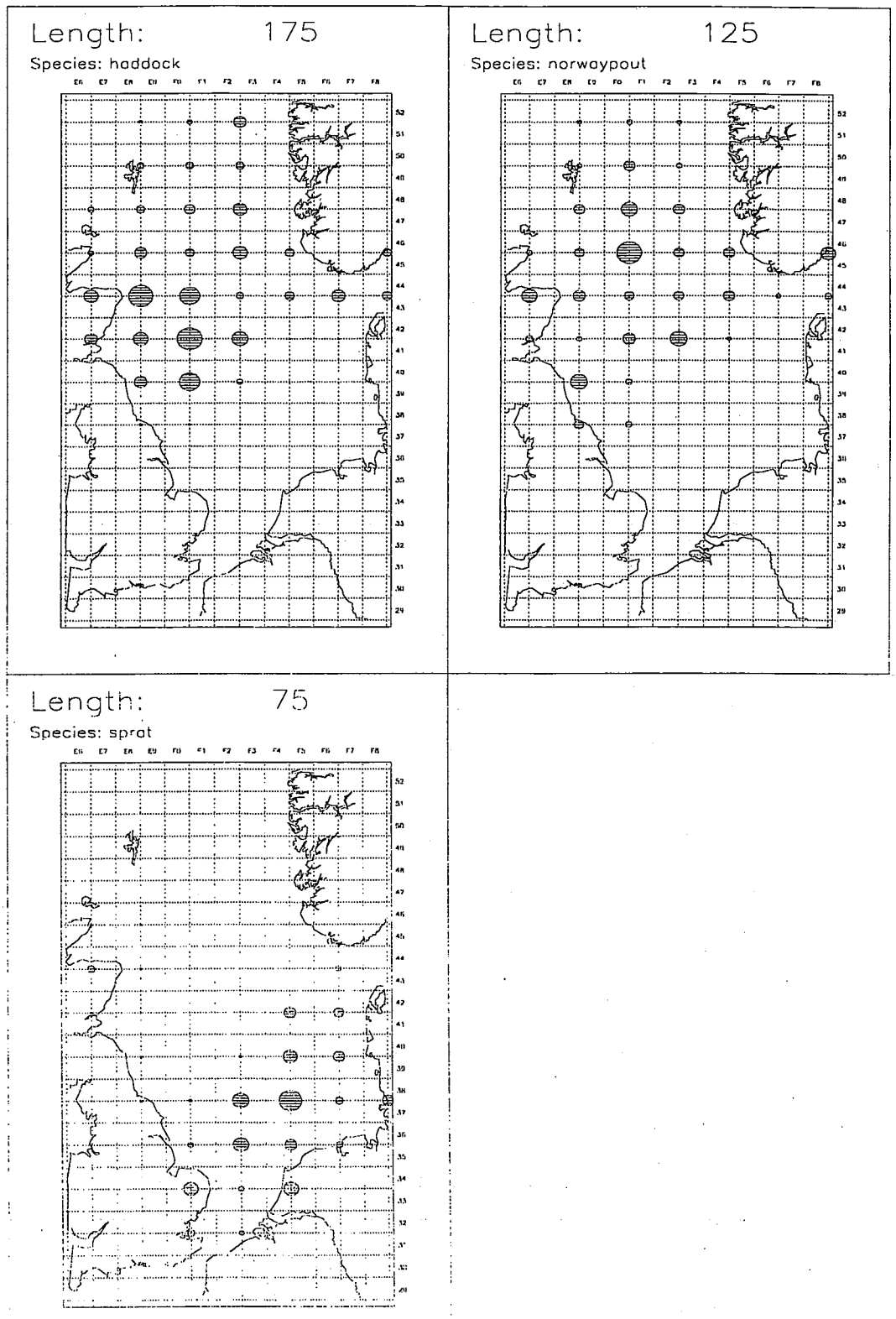


Fig. 6.1.3.3. Predicted catch of haddock at 175 mm, norway pout at 125 mm and sprat at 75 mm in the 1st quarter of 1991. Area of pie denotes predicted number. Pies are not drawn to scale betwen maps.

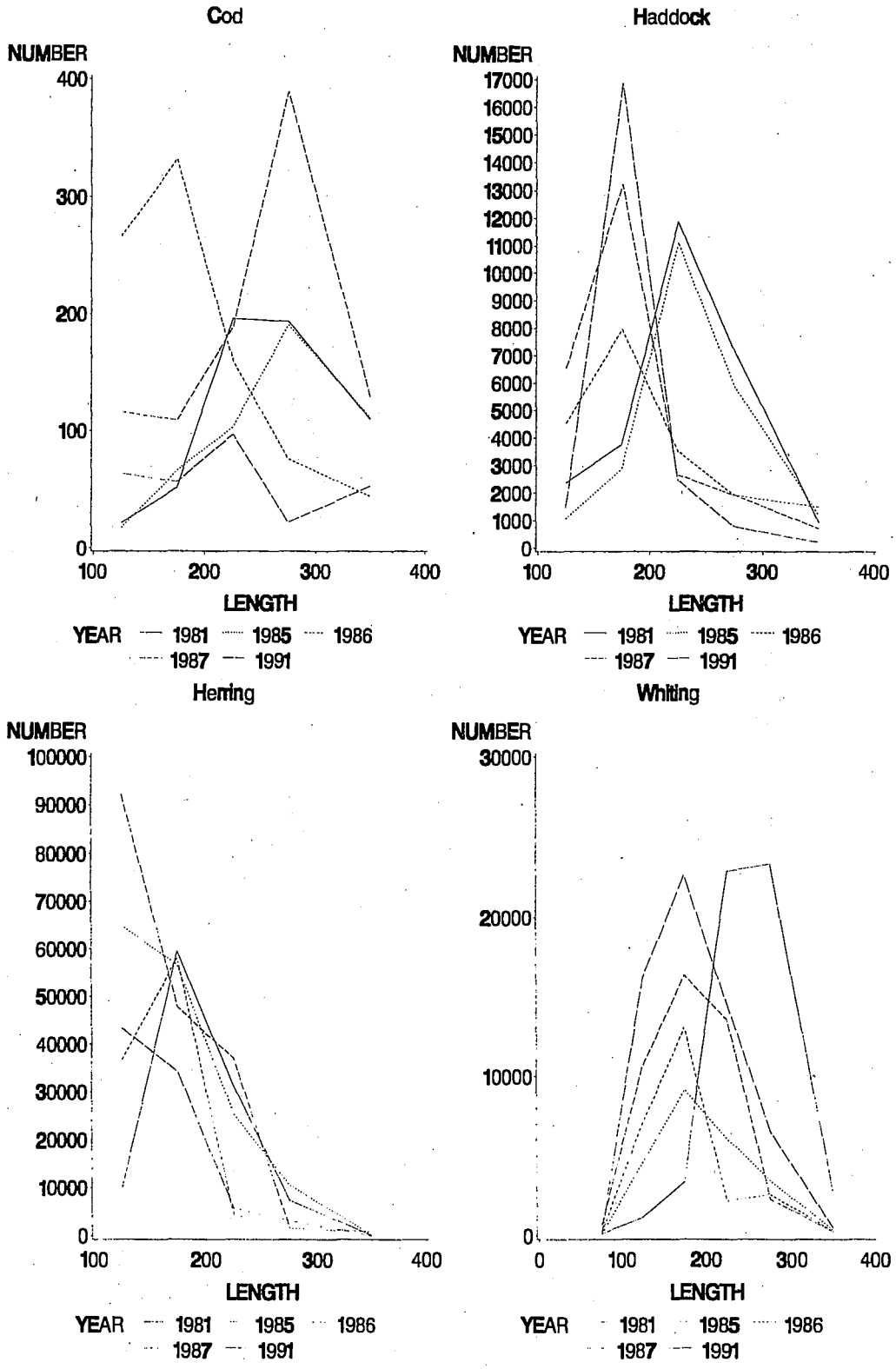


Fig. 6.1.4.1. Total catch predicted if Cirolana trawled once in ech 4-square area. 1st quarter

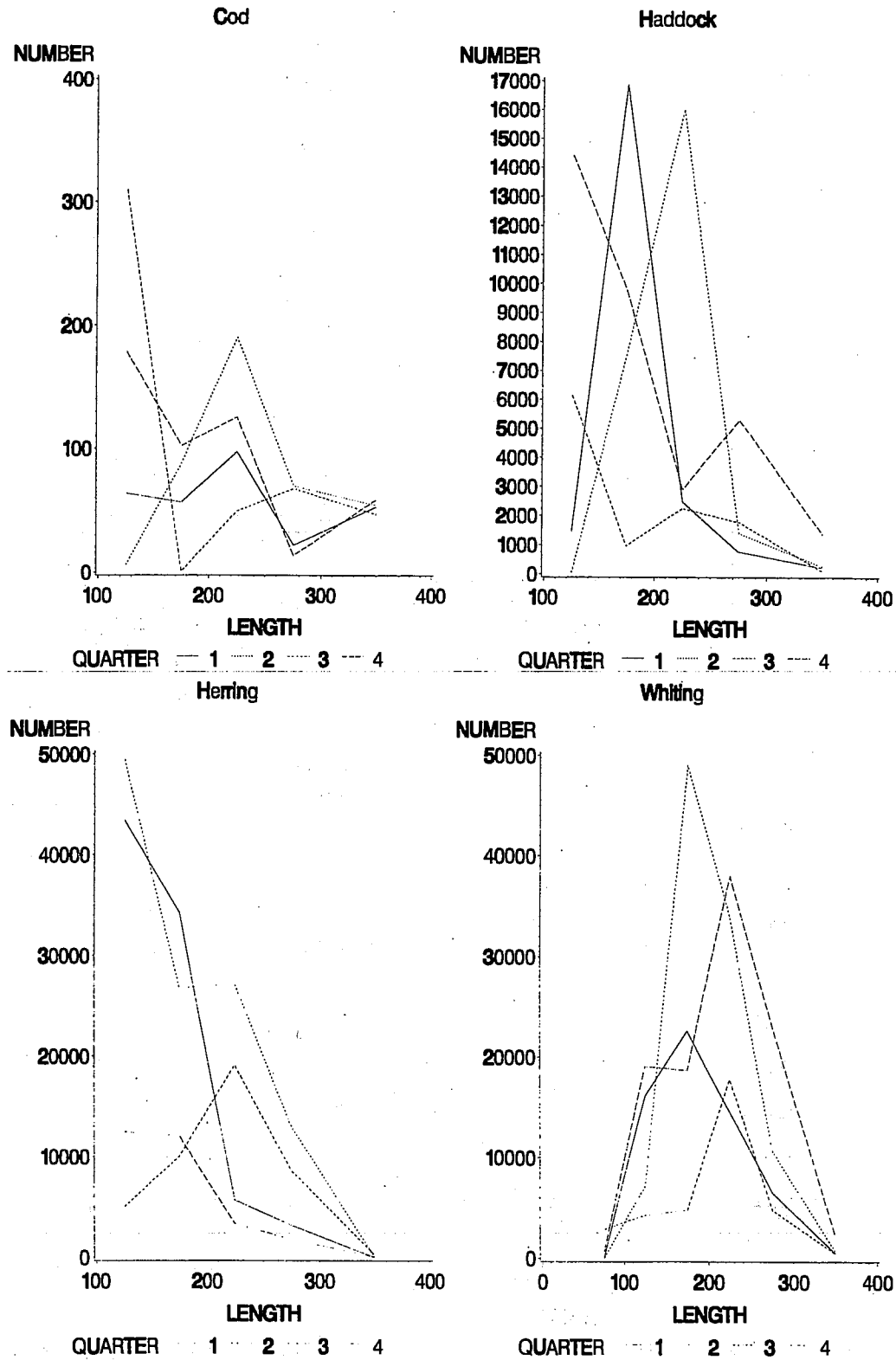


Fig. 6.1.4.2. Total catch predicted if Cirolana trawled once in ech 4-square are in each quarter of 1991.

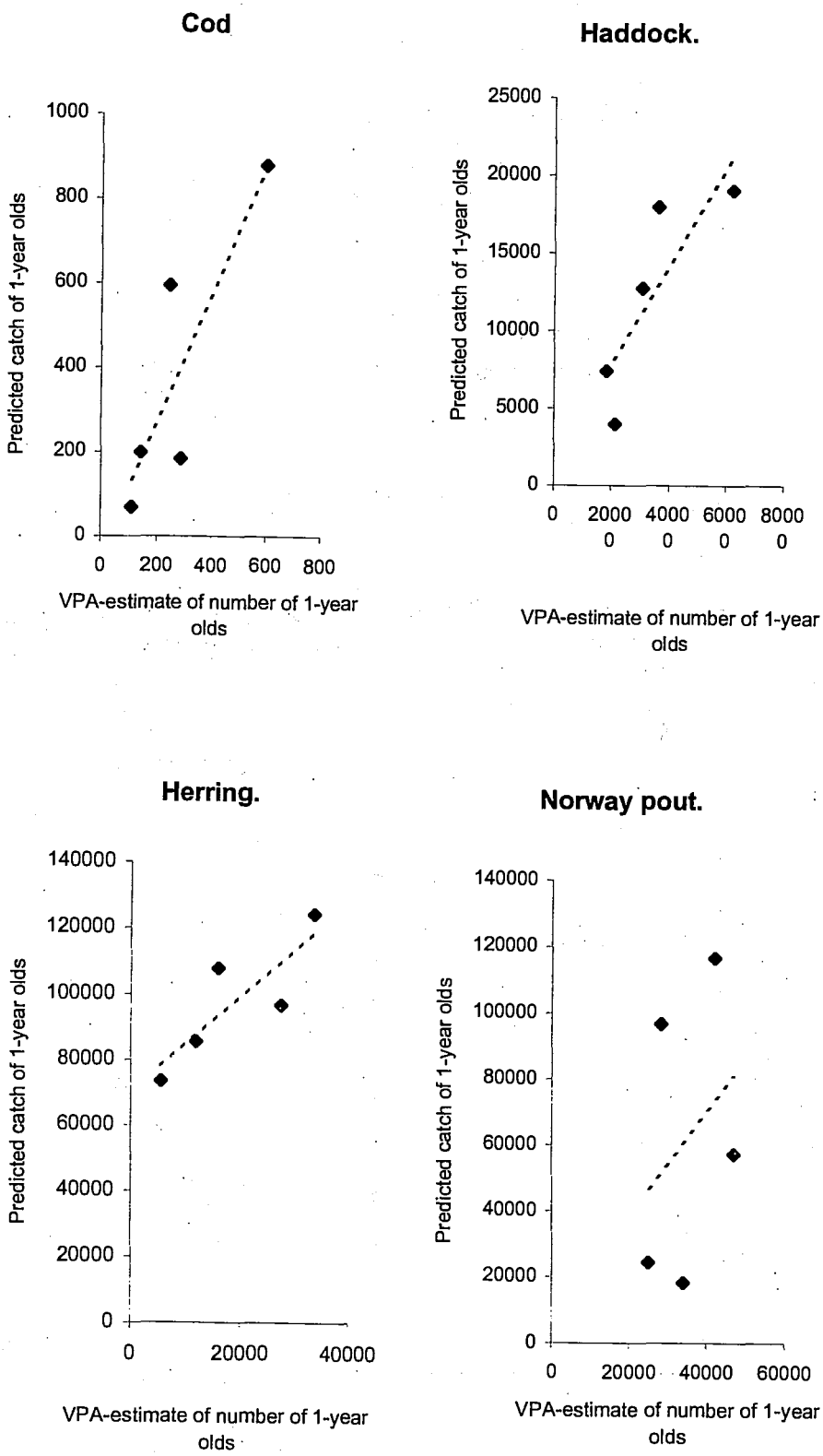


Fig. 6.1.4.3. Predicted catch of 1-year olds in the 1st quarter as a function of VPA estimate of number of 1-year olds.

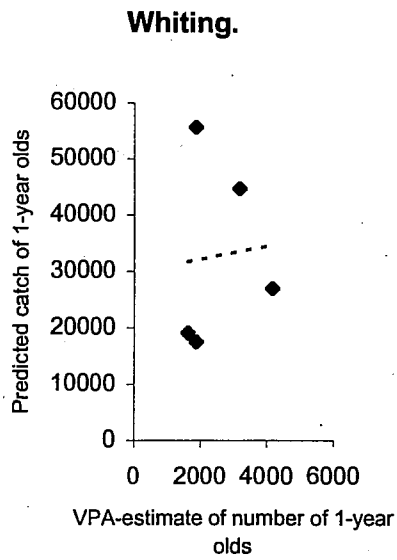


Fig. 6.1.4.3 continued. Predicted catch of 1-year olds in the 1st quarter as a function of VPA estimate of number of 1-year olds.

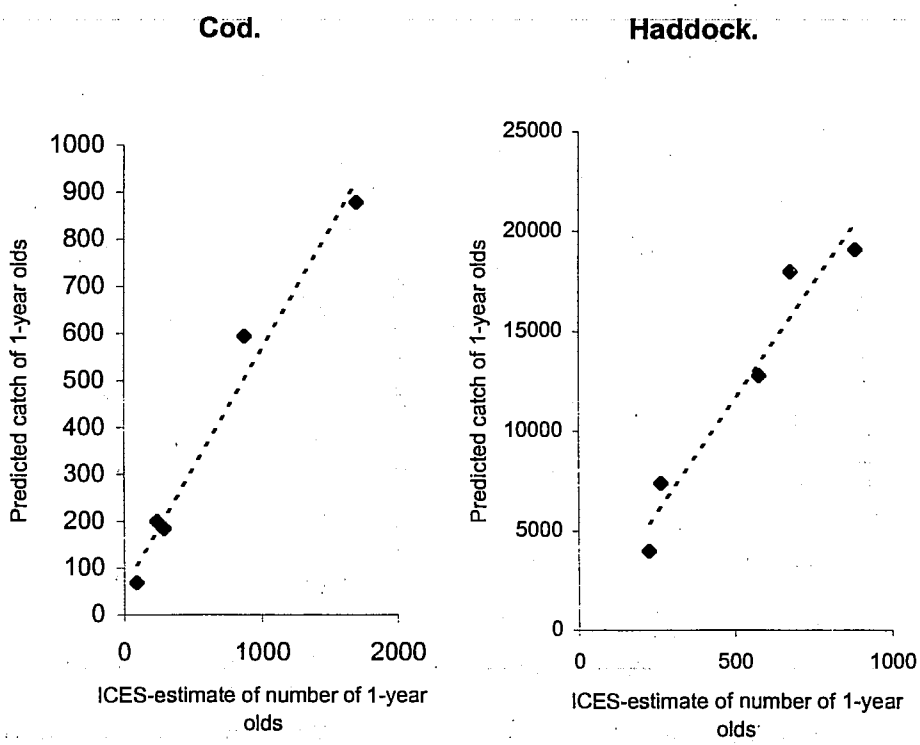


Fig. 6.1.4.4. Predicted catch of 1-year olds in the 1st quarter as a function of ICES index of number of 1-year olds.

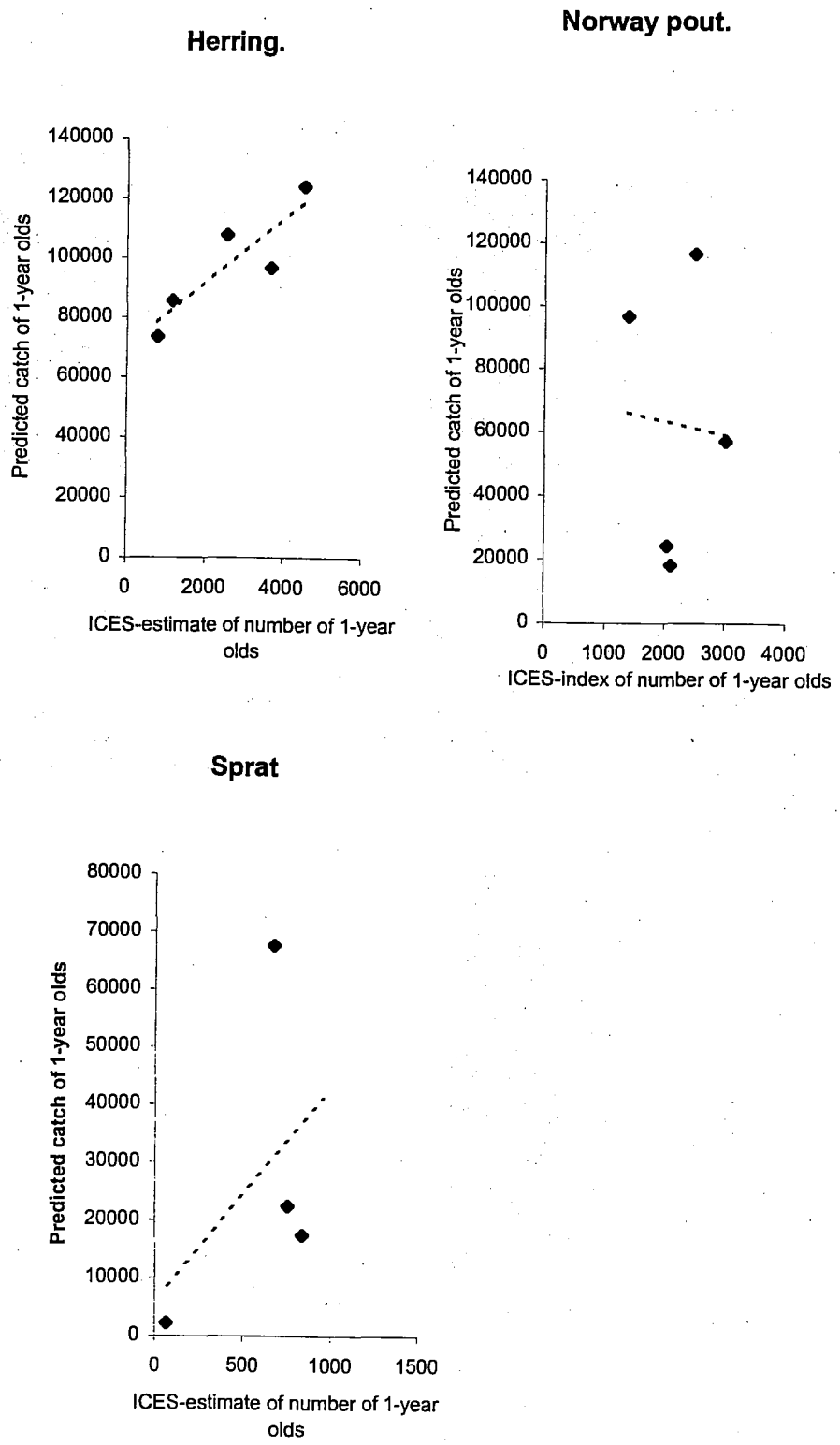


Fig. 6.1.4.4 continued. Predicted catch of 1-year olds in the 1st quarter as a function of ICES index of number of 1-year olds.

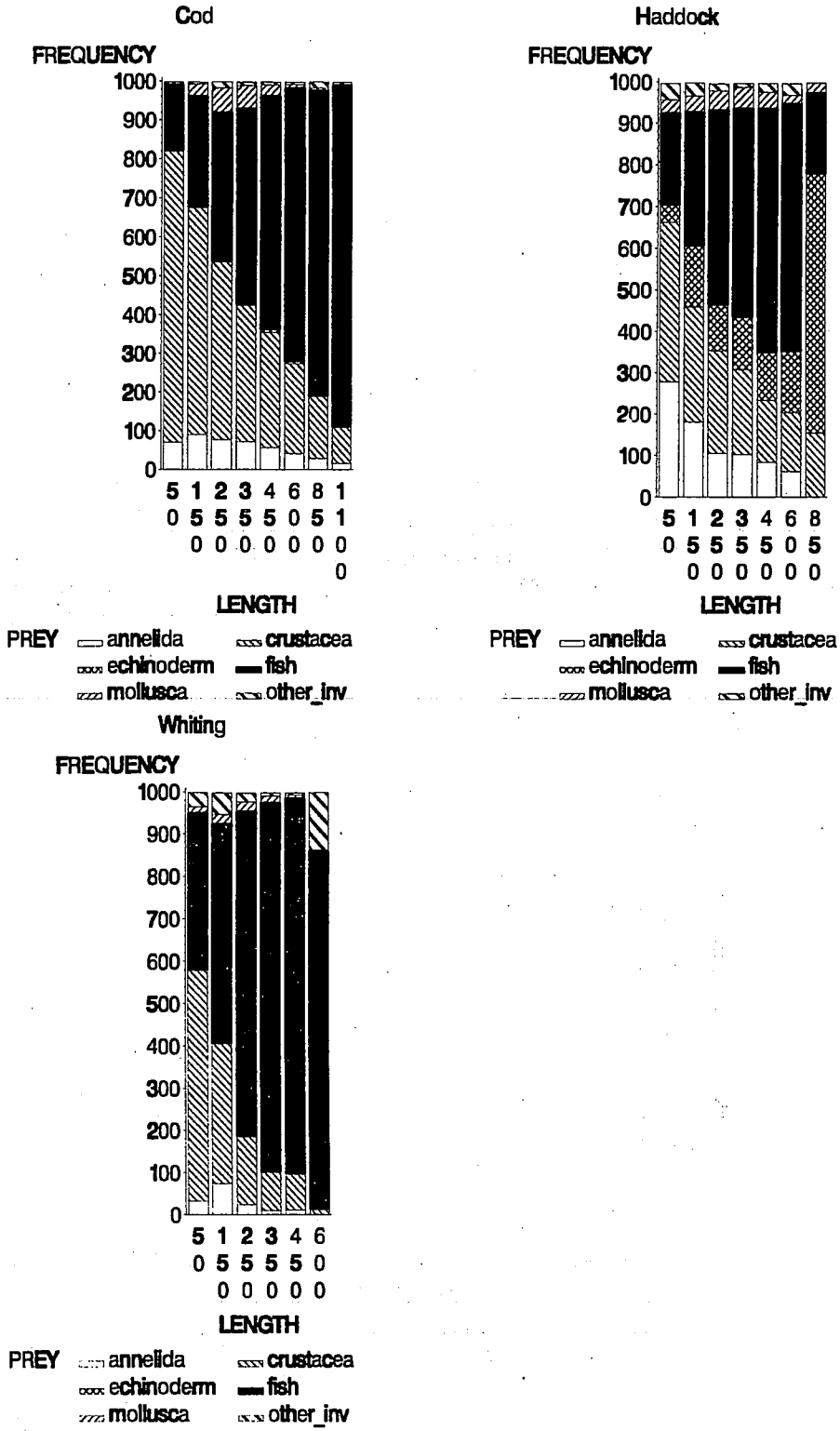


Fig. 6.2.1.1. Weight composition of food in the stomachs of predators at different lengths. Units: grams pr. thousand grams. Due to rounding errors, not all bars sum up to 1000.

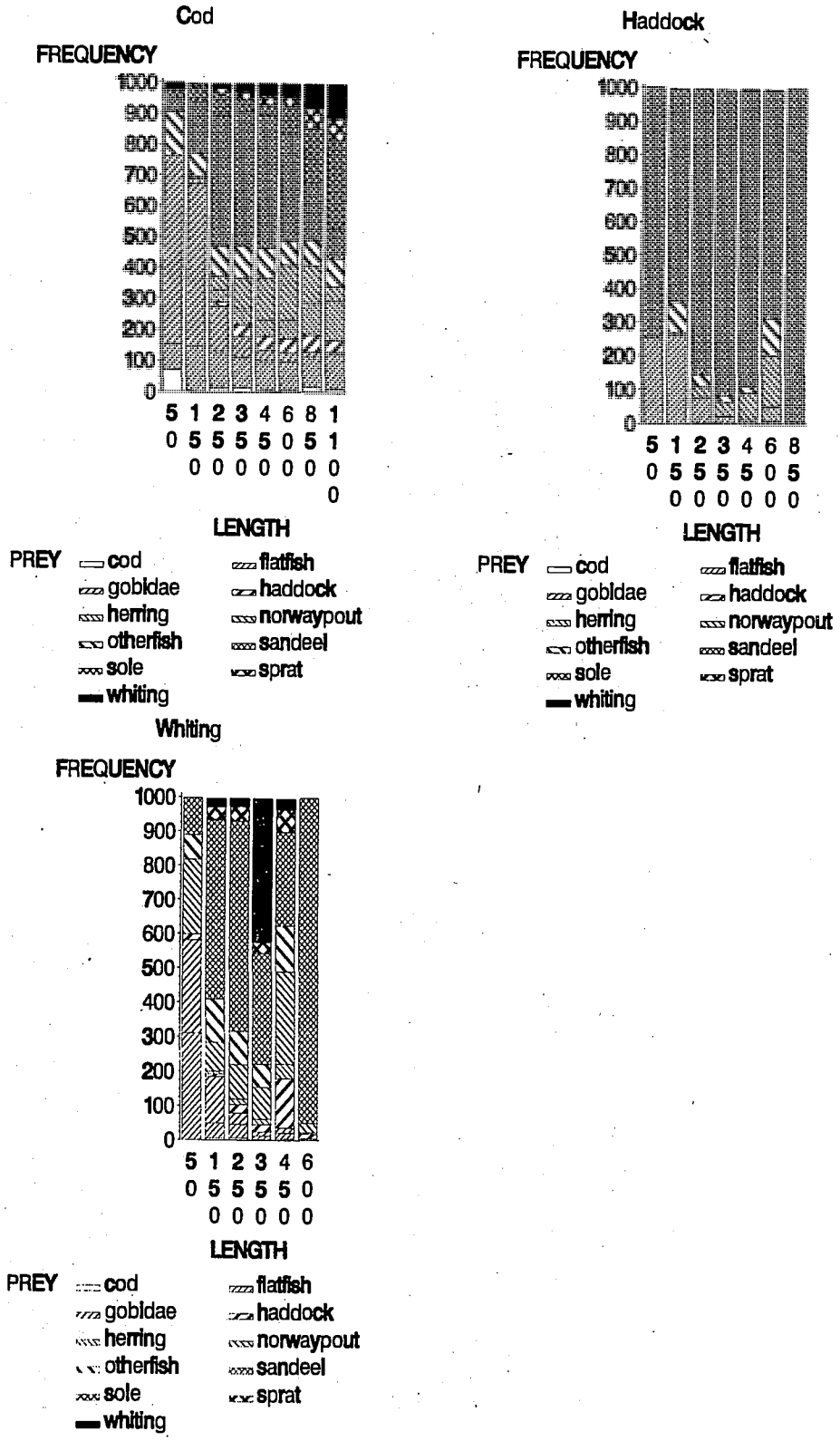


Fig. 6.2.2.1. Species composition of fish found in the stomachs of predators at different lengths. Units: numbers pr. thousand. Due to rounding errors, not all bars sum up to 1000.

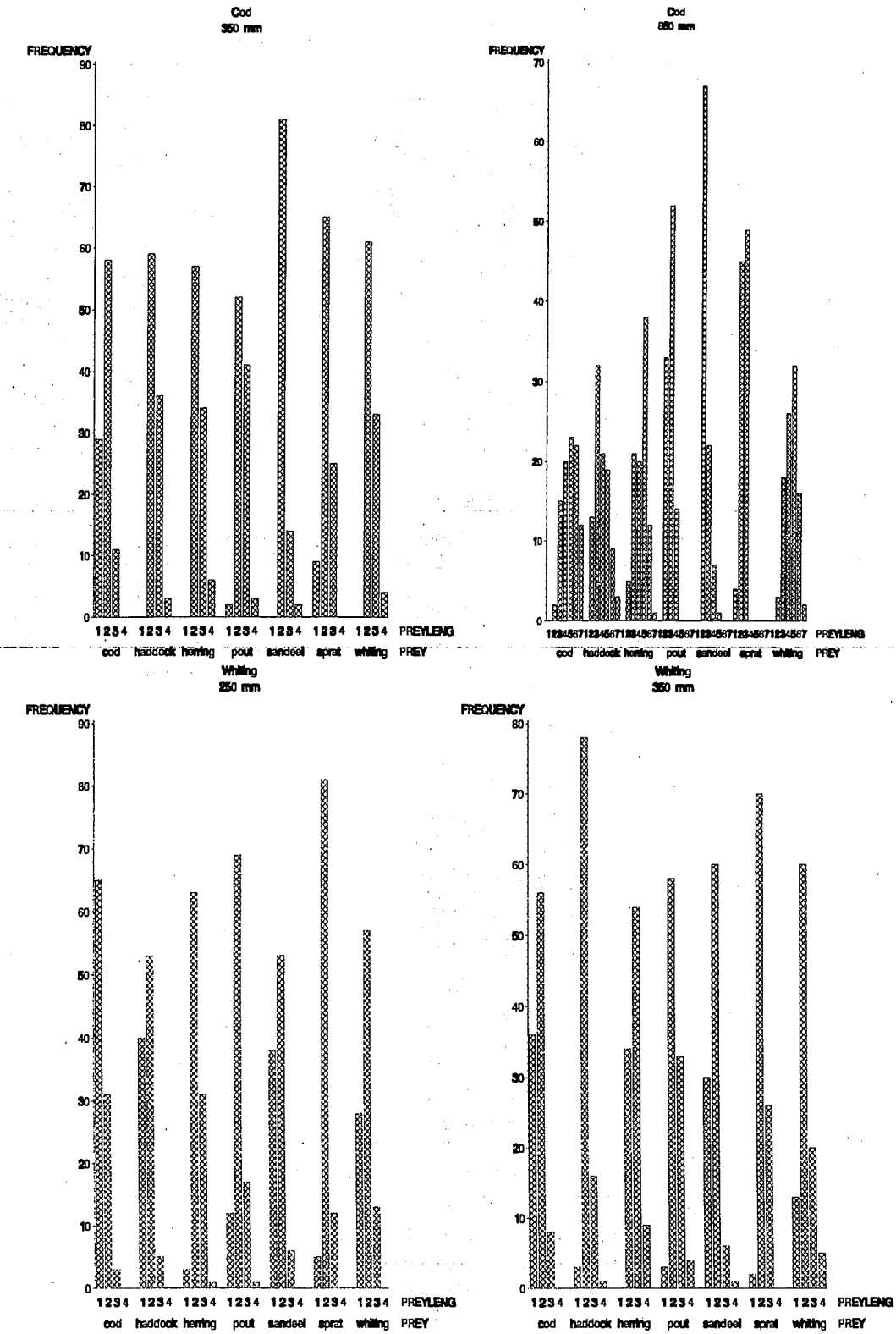


Fig. 6.2.3.1. Length distribution of fish prey of cod at 350 mm and 850 mm and whiting at 250 mm and 350 mm. Lengthgroups: 1=25 mm, 2=75 mm, 3=125 mm, 4=175mm, 5=225 mm, 6=275 mm, 7=350 mm.

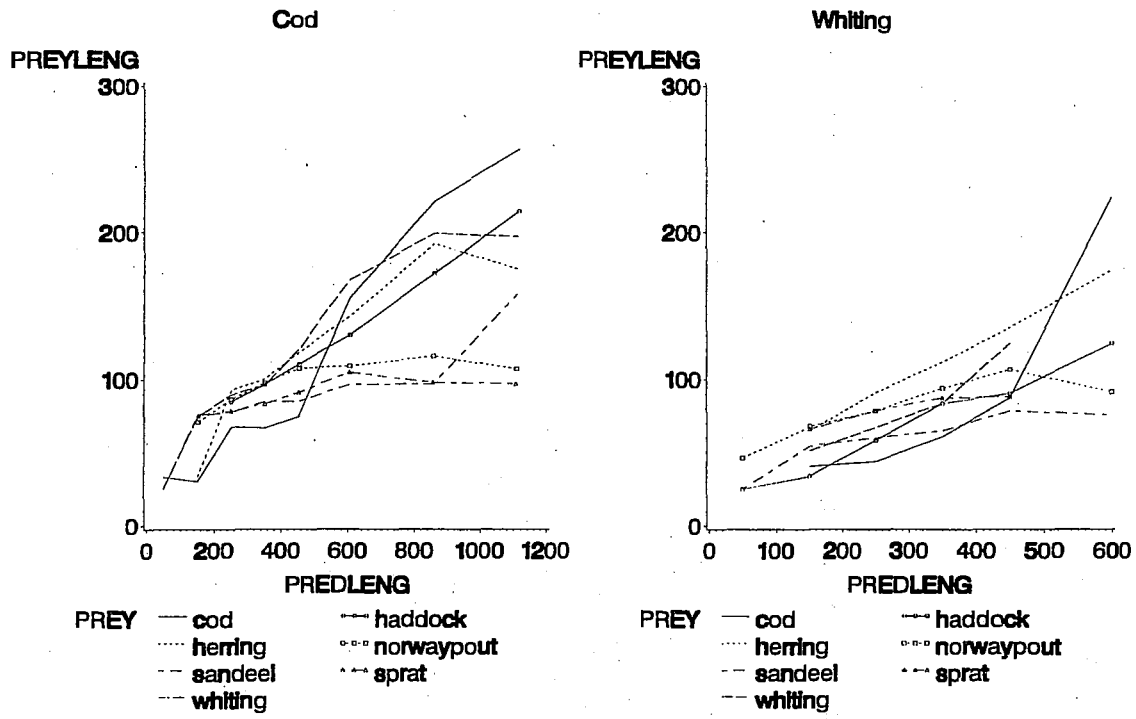


Fig. 6.2.3.2. Mean length of fish prey as a function of predator length for the predators cod and whiting. Units= mm.

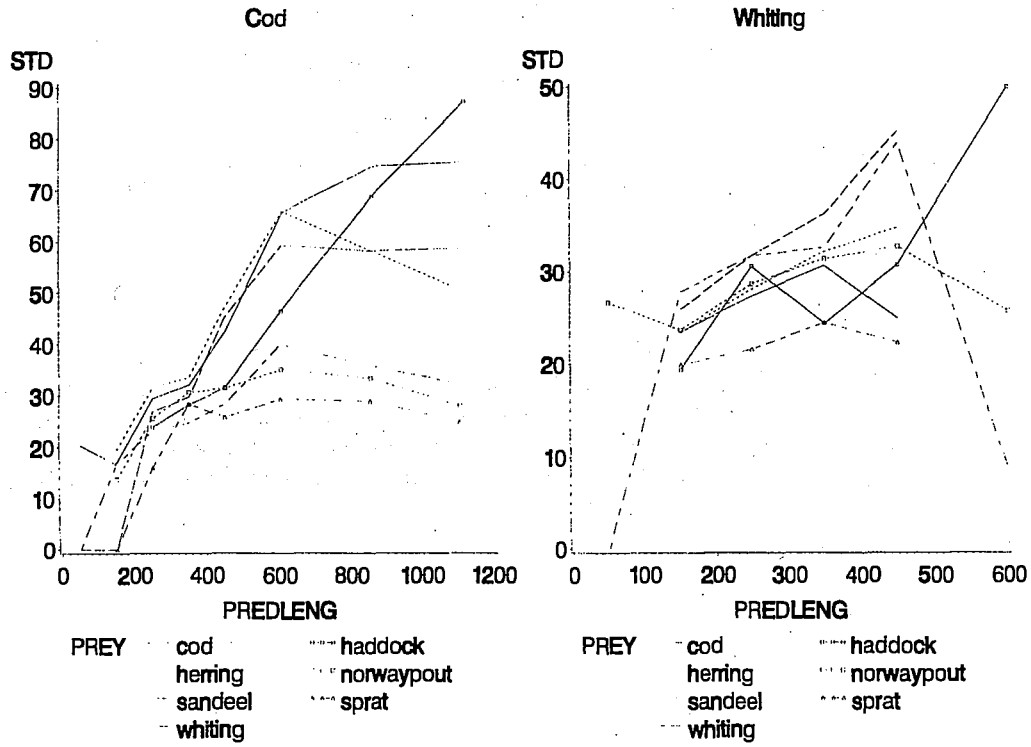


Fig. 6.2.3.3. Standard deviation of length distribution of fish prey as a function of predator length for the predators cod and whiting. Length units= mm.

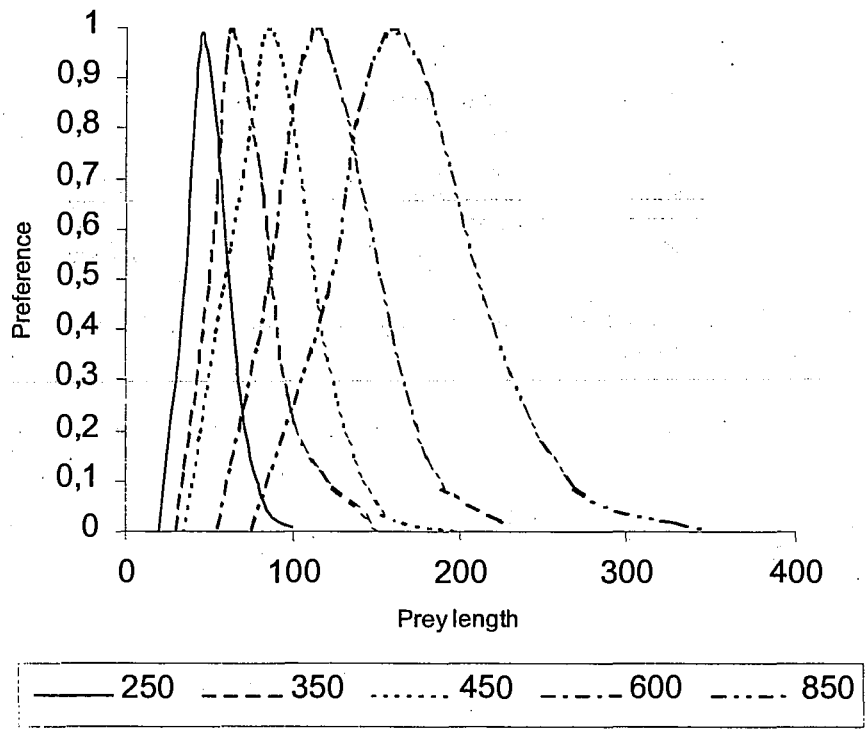


Fig. 6.2.3.4. Theoretical length ditribution of prey eaten by different sized predators with a prefered (weight of predator/weight of prey) of 5 and a particularity of 2 (these values are close to the values given by Ursin (1973) for cod). Legend: Predator length. Units: Length: mm. Preference scaled to one for the preferred sizeratio.

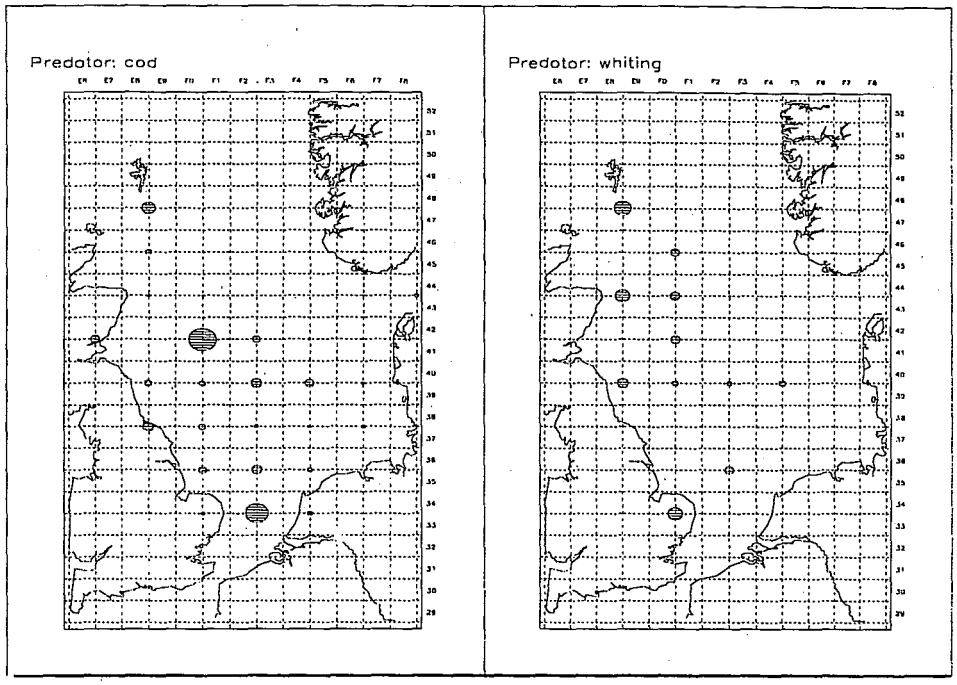


Fig. 6.2.4.1. Partial fullness index of herring at 125 mm eaten by cod and whiting in the 1st quarter of 1987. Area of pie denotes PFI. Pies are not to the same sclae..

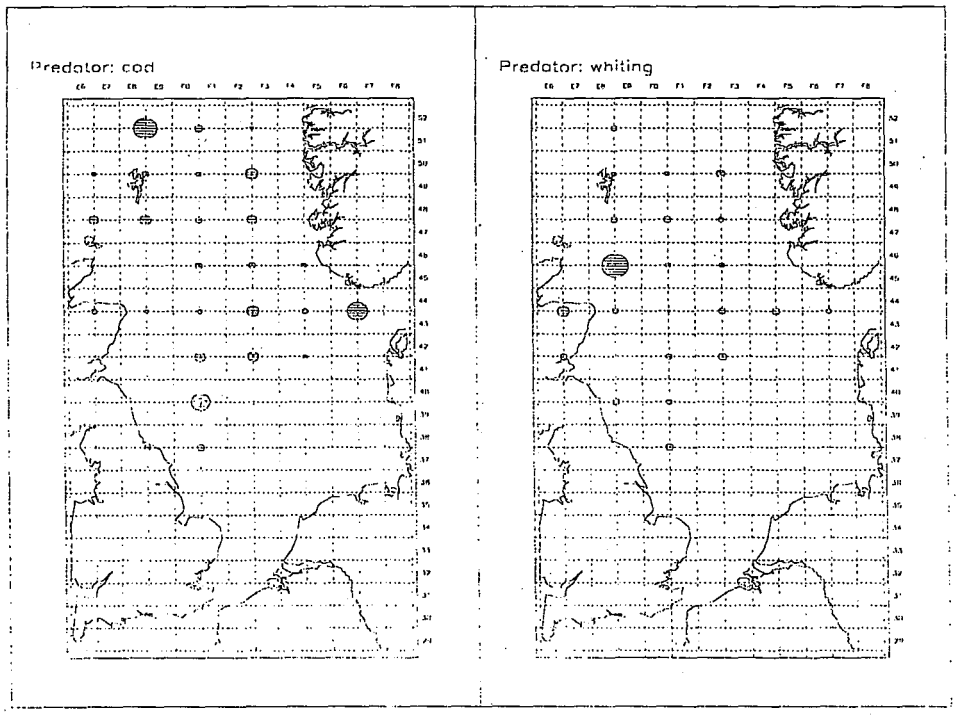


Fig. 6.2.4.1 continued. Partial fullness index of norway pout at 125 mm eaten by cod and whiting in the 1st quarter of 1991. Area of pie denotes PFI. Pies are not to the same sclae..

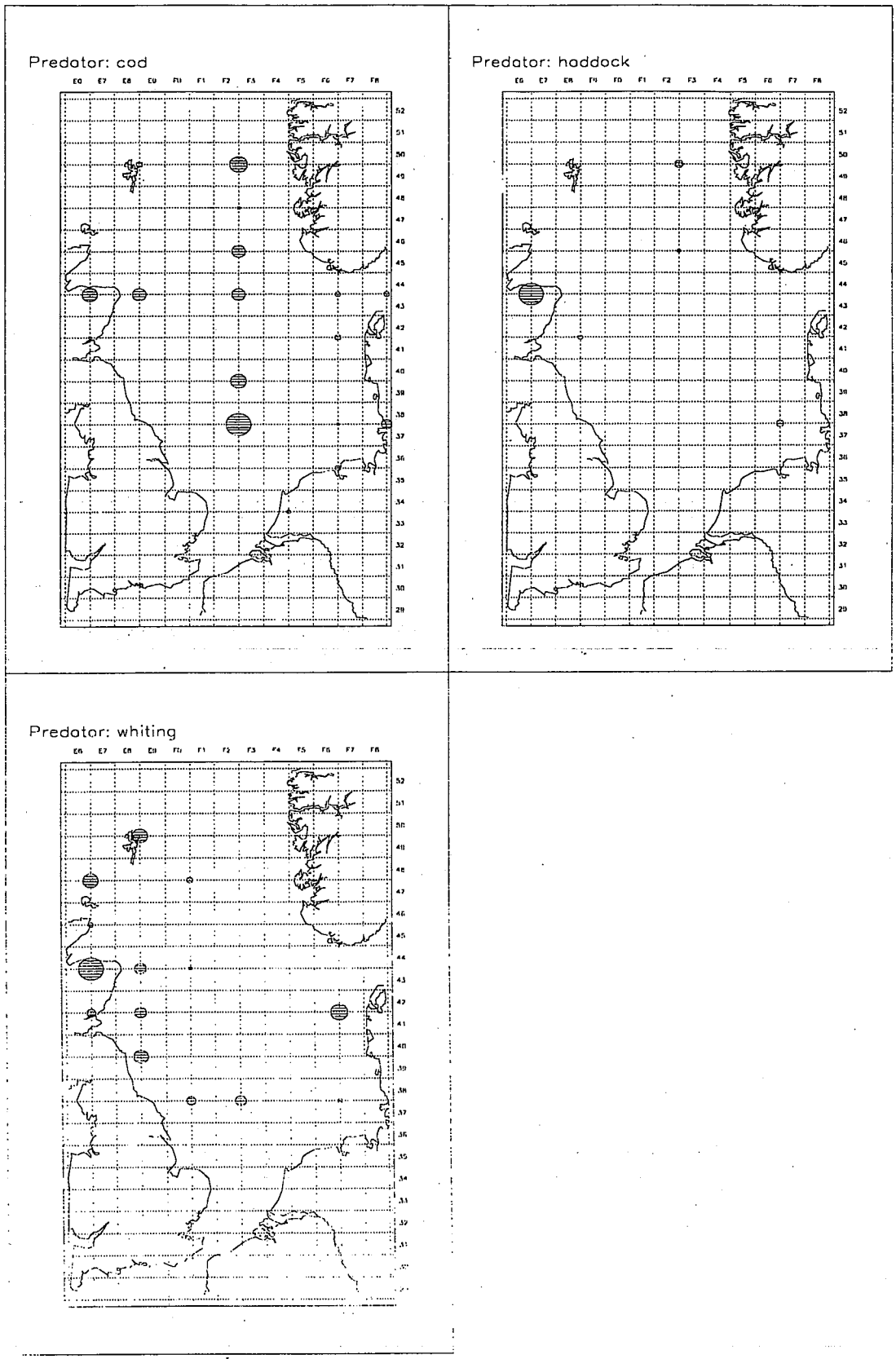


Fig. 6.2.4.2. Partial fullness index of sandeel at 75 mm eaten by cod and whiting in the 1st quarter of 1981. Area of pie denotes PFI. Pies are not to the same scale.

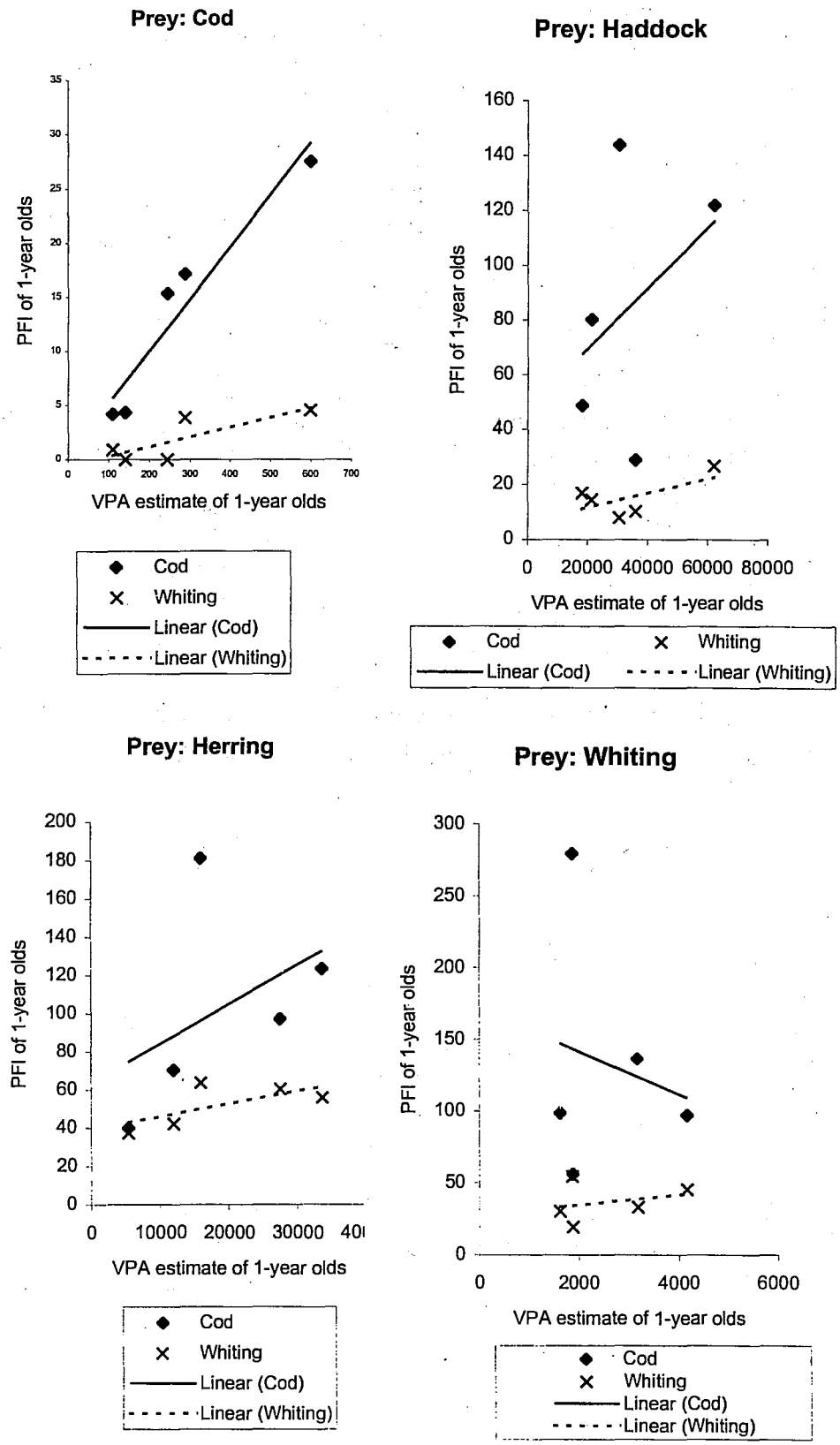


Fig. 6.2.4.3. Patrial fullness index of 1-year olds eaten by different predators in the 1st quarter as a function of VPA estimate of abundance.

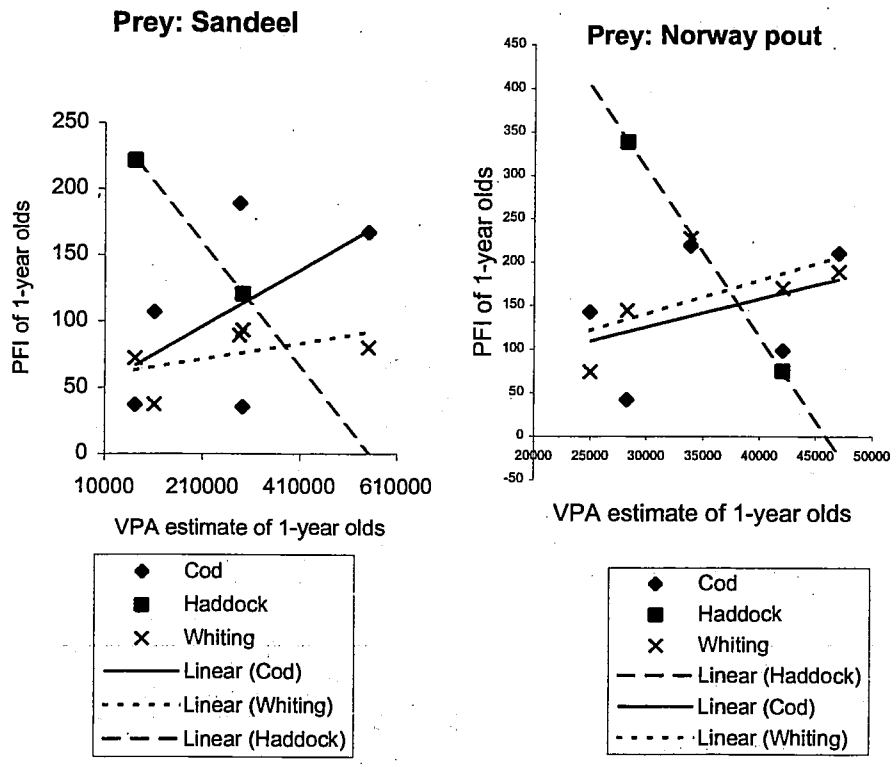


Fig. 6.2.4.3 continued. Patrial fullness index of 1-year olds eaten by different predators in the 1st quarter as a function of VPA estimate of abundance.

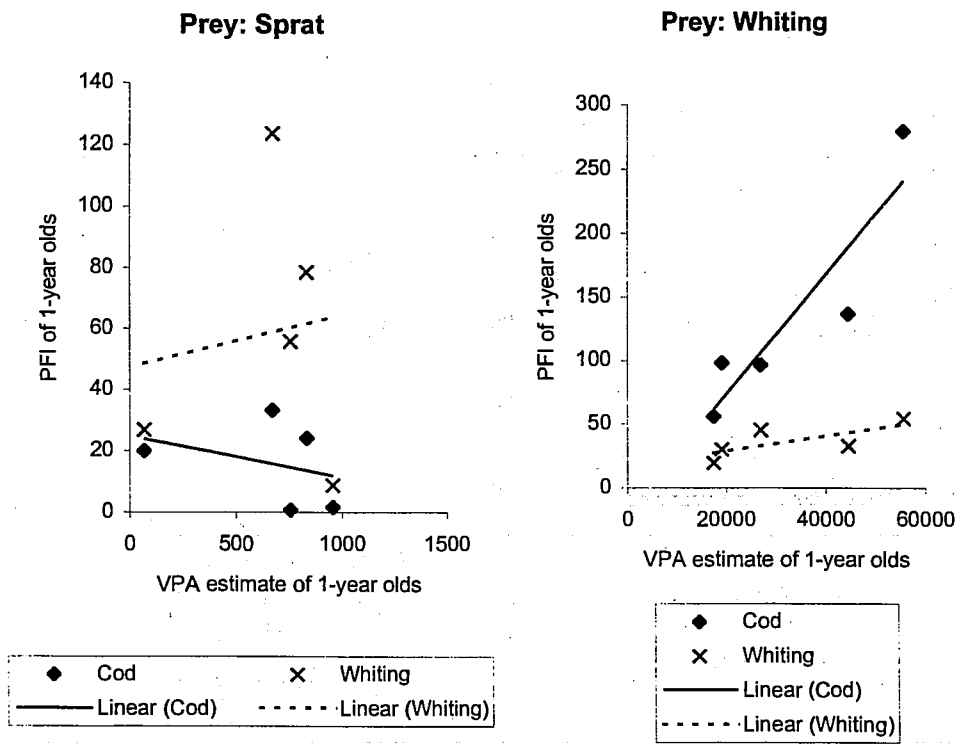


Fig. 6.2.4.4. Patrial fullness index of 1-year olds eaten by different predators in the 1st quarter as a function of predicted catch in the IBTS.

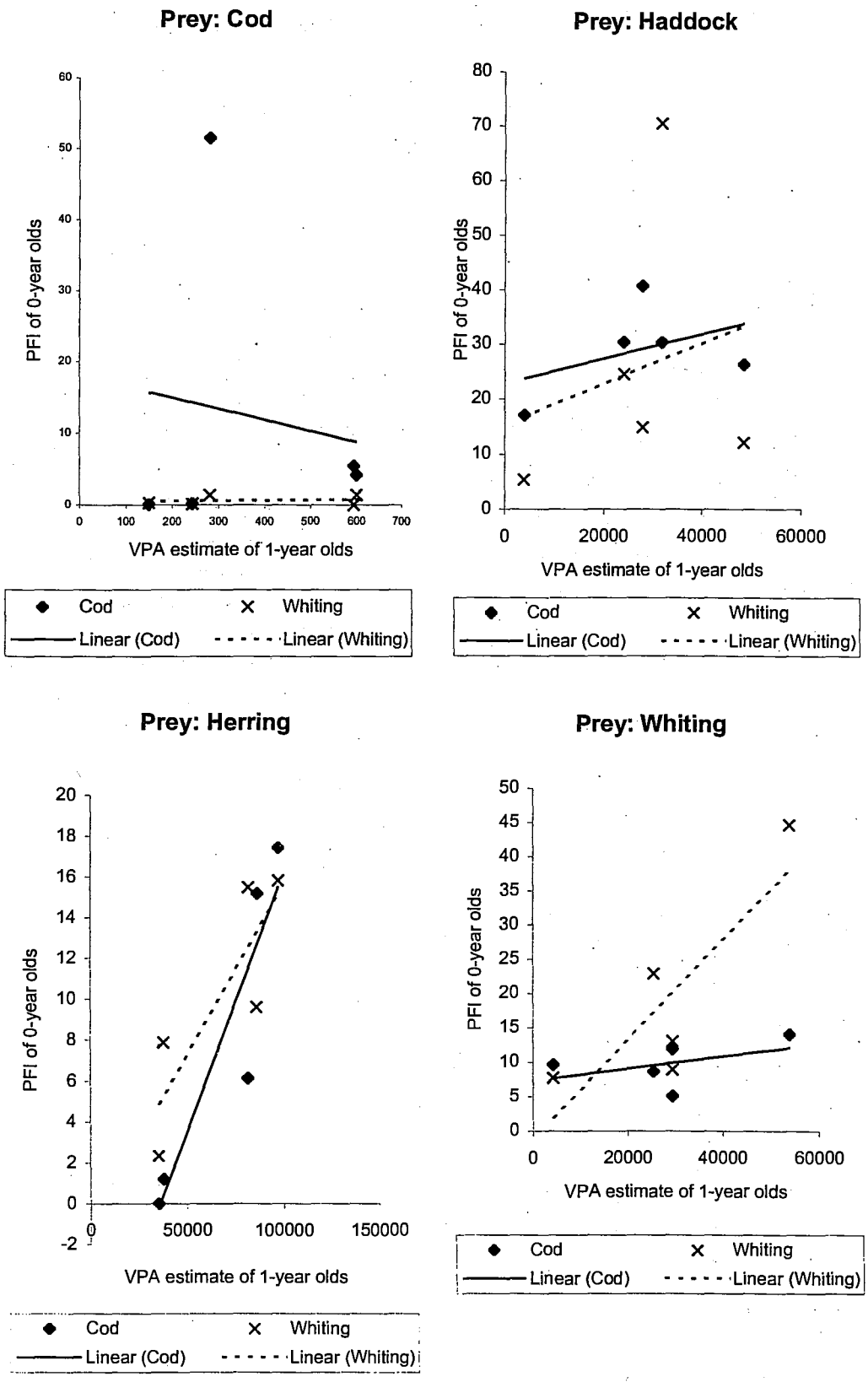
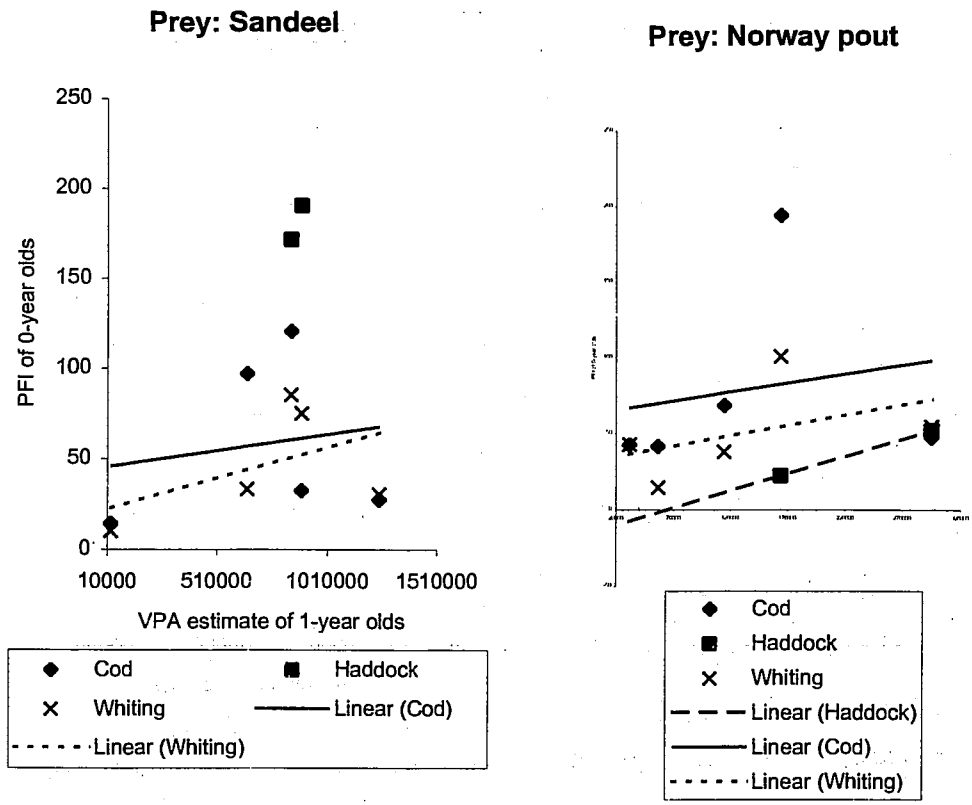


Fig. 6.2.4.5. Patrial fullness index of 0-year olds eaten by different predators in the 3rd quarter as a function of VPA estimate of abundance of 1-year olds in the following year.



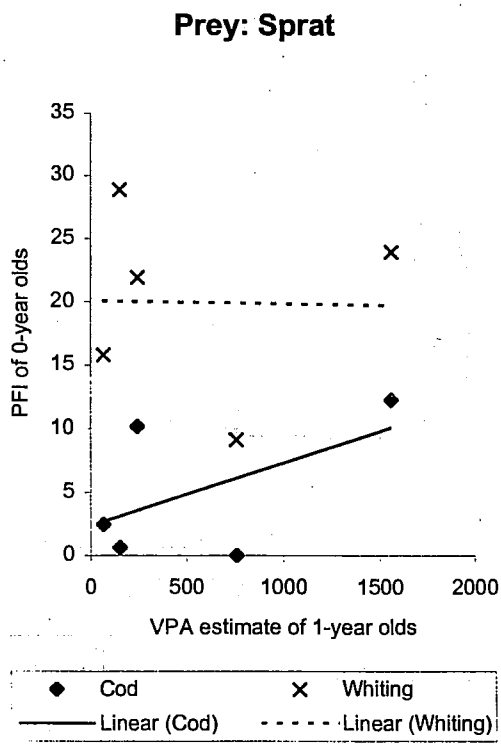


Fig. 6.2.4.5 continued. Patrial fullness index of 0-year olds eaten by different predators in the 3rd quarter as a function of VPA estimate of abundance of 0-year olds in the same quarter for sandeel and norway pout and as a function of IBTS estimate of 1-year olds in the following year.

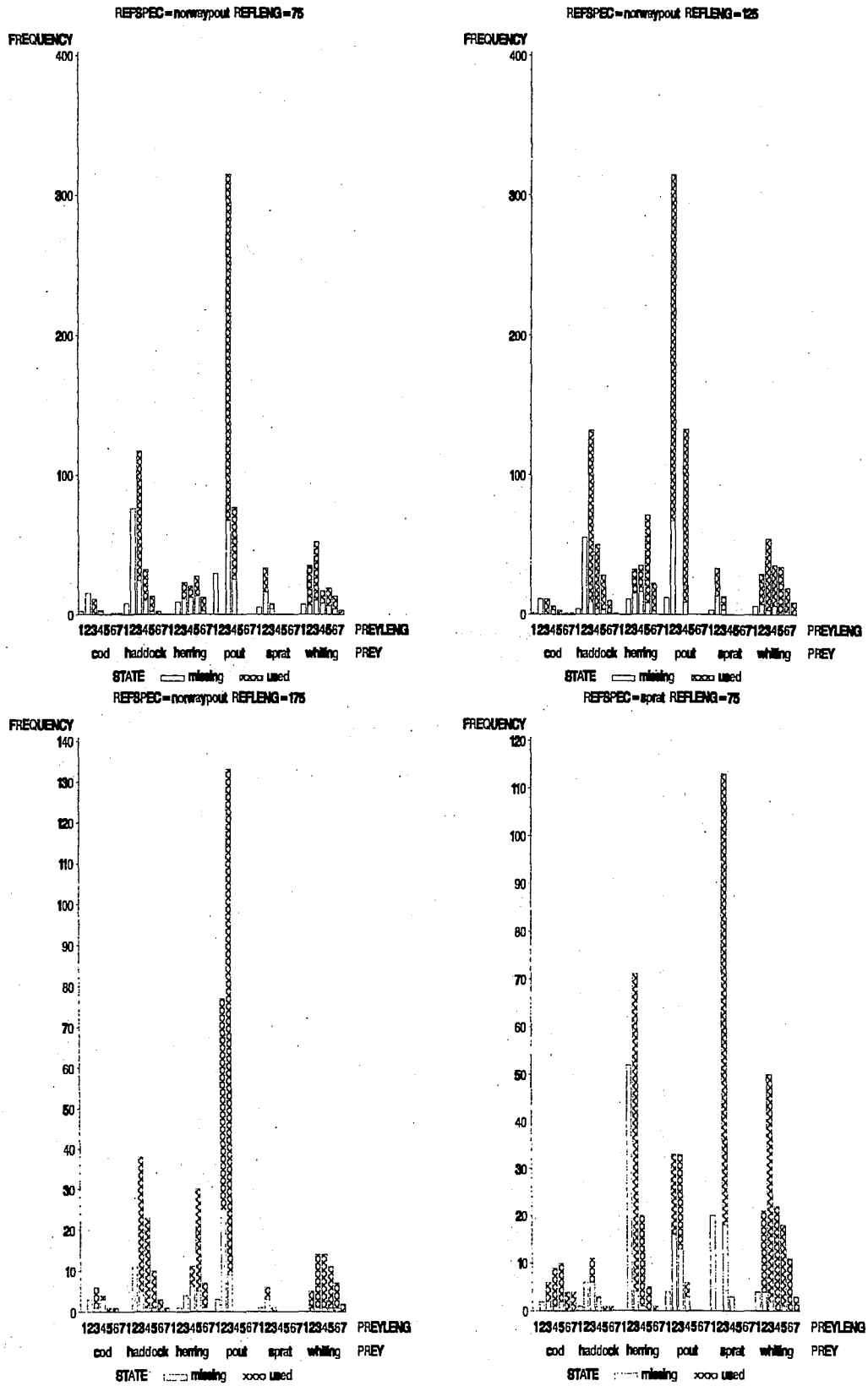


Fig. 6.2.5.1. The number of ratios used in analyses and the number excluded due to one or both of the species not caught or not modelled.

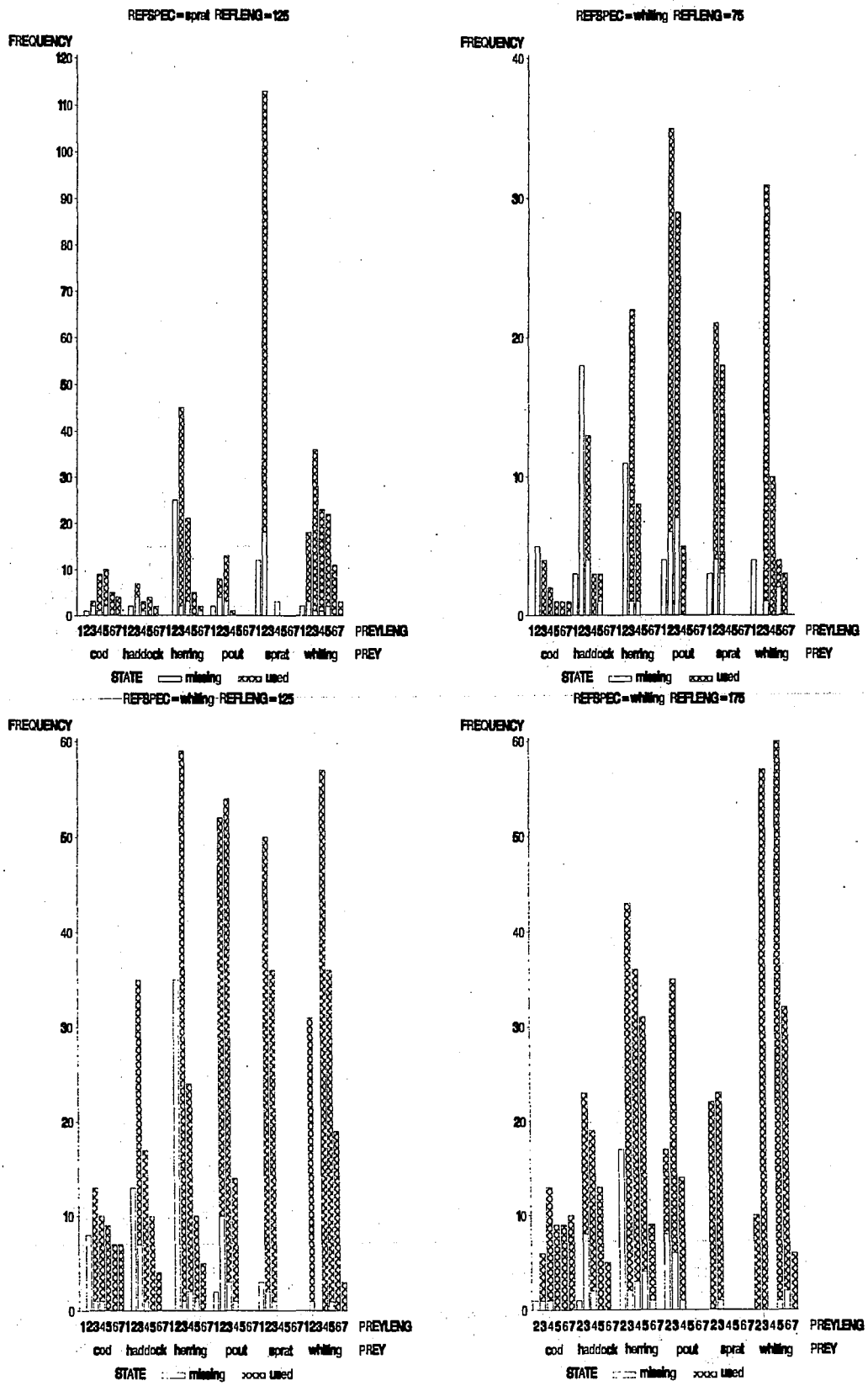


Fig. 6.2.5.1 continued. The number of ratios used in analyses and the number excluded due to one or both of the species not caught or not modelled.

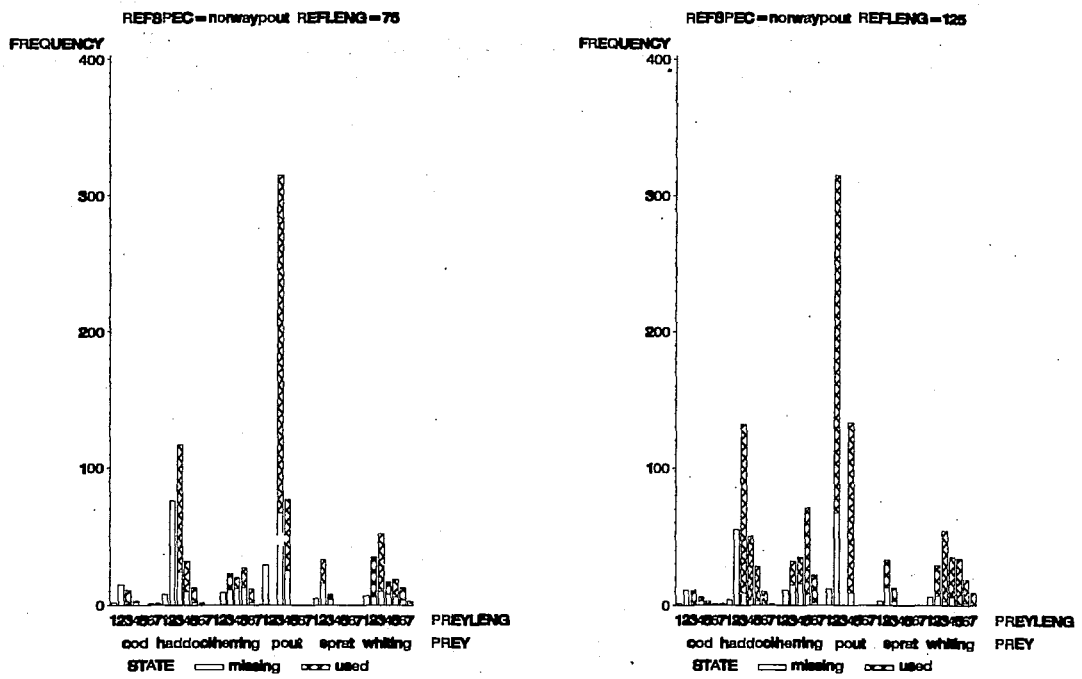


Fig. 6.2.5.1 continued. The number of ratios used in analyses and the number excluded due to one or both of the species not caught or not modelled.

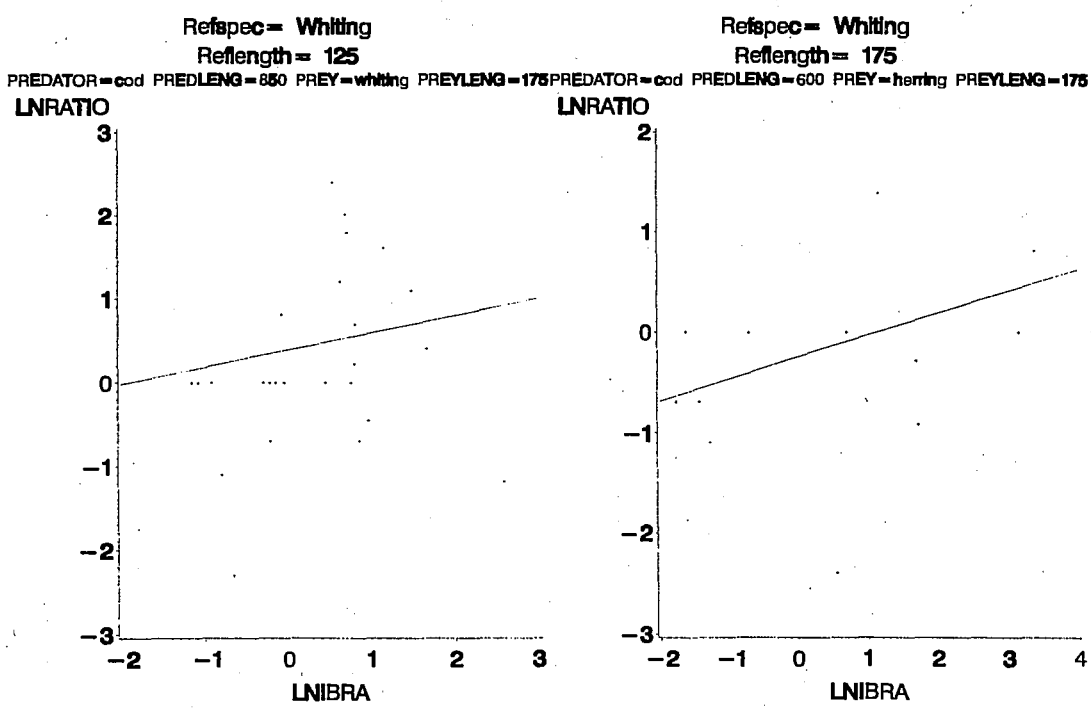


Fig. 6.3.1.1. Examples of observed values (+) and predicted values (line) of ln(stomach ratio) as a function of ln(ibts ratio). Ratio=number of prey/number of reference. Reference= refspec at length reflength.

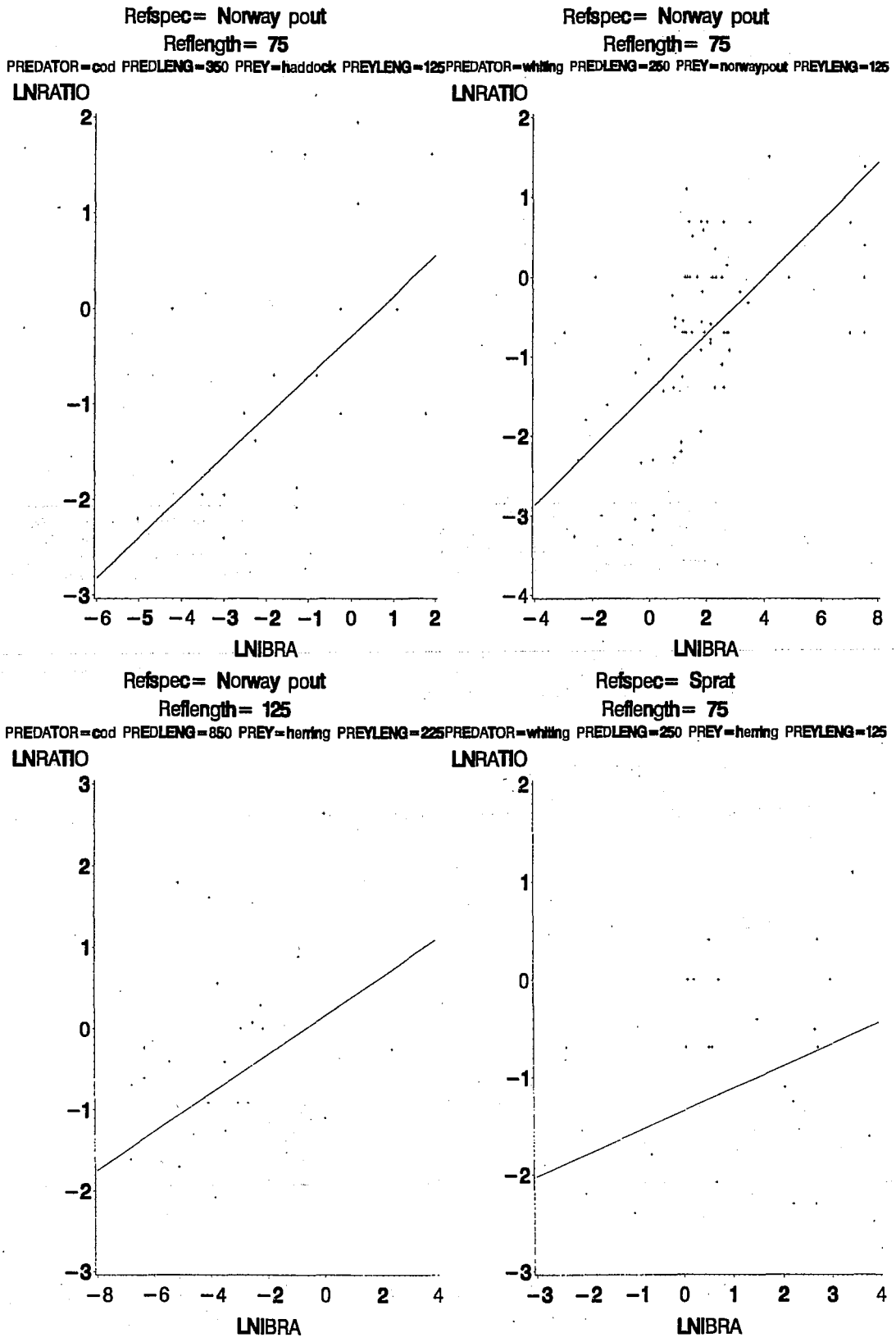


Fig. 6.3.1.1 continued. Examples of observed values (+) and predicted values (line) of ln(stomach ratio) as a function of ln(ibts ratio). Ratio=number of prey/number of reference. Reference= refspec at length reflength.

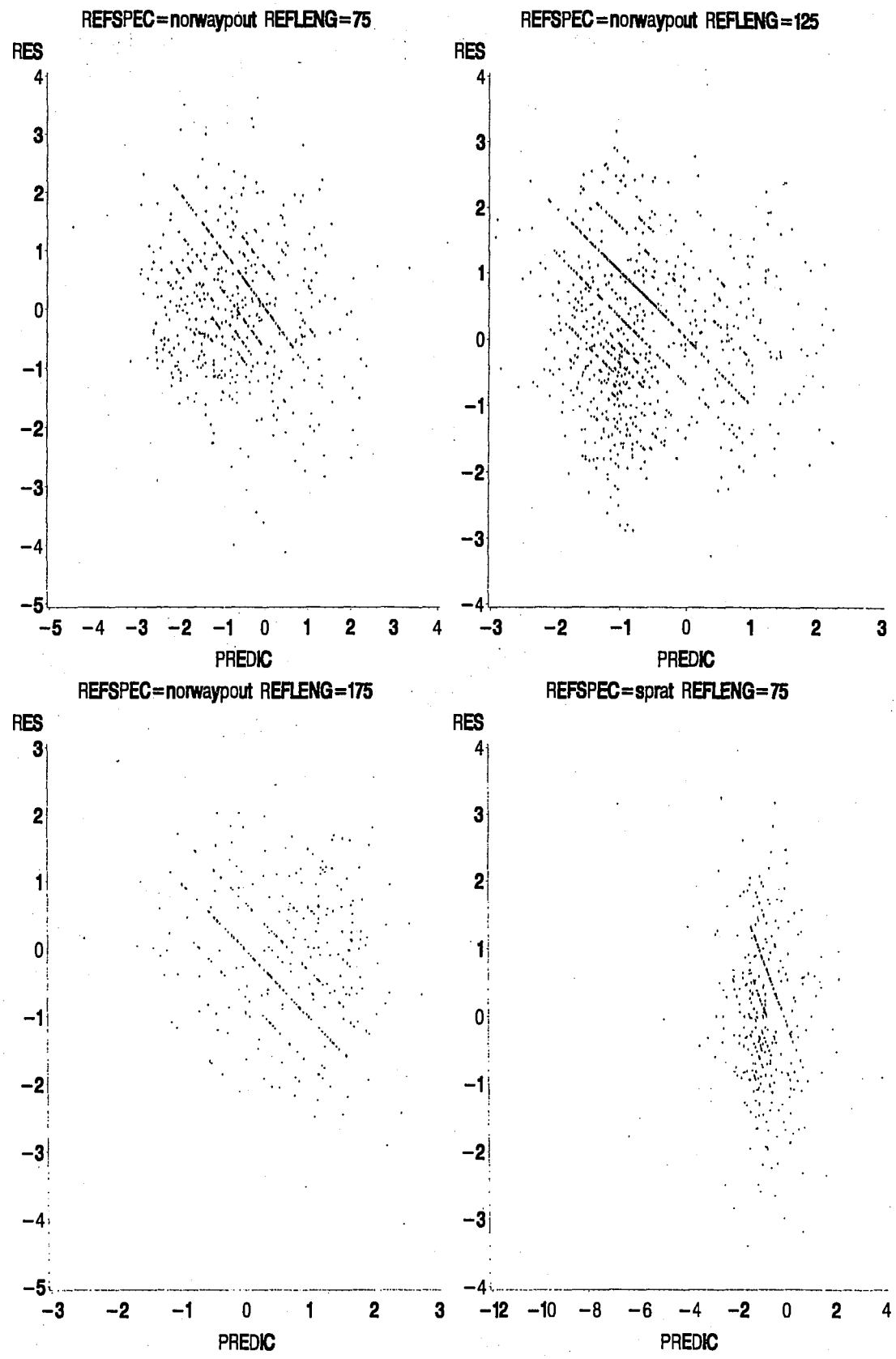


Fig. 6.3.1.2. Residuals as a function of predicted value in the basic model for ratios.

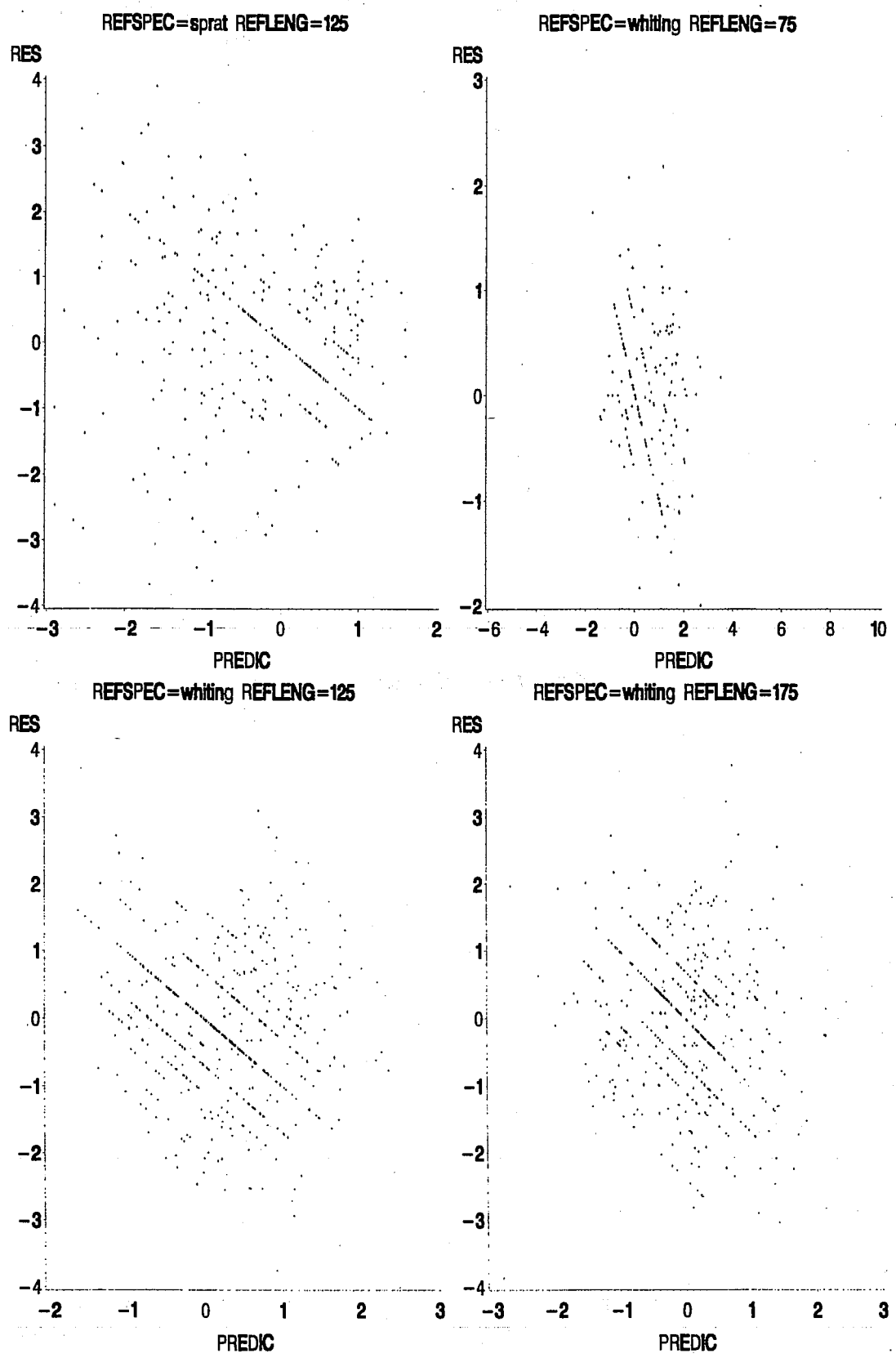


Fig. 6.3.1.2 continued. Residuals as a function of predicted value in the basic model for

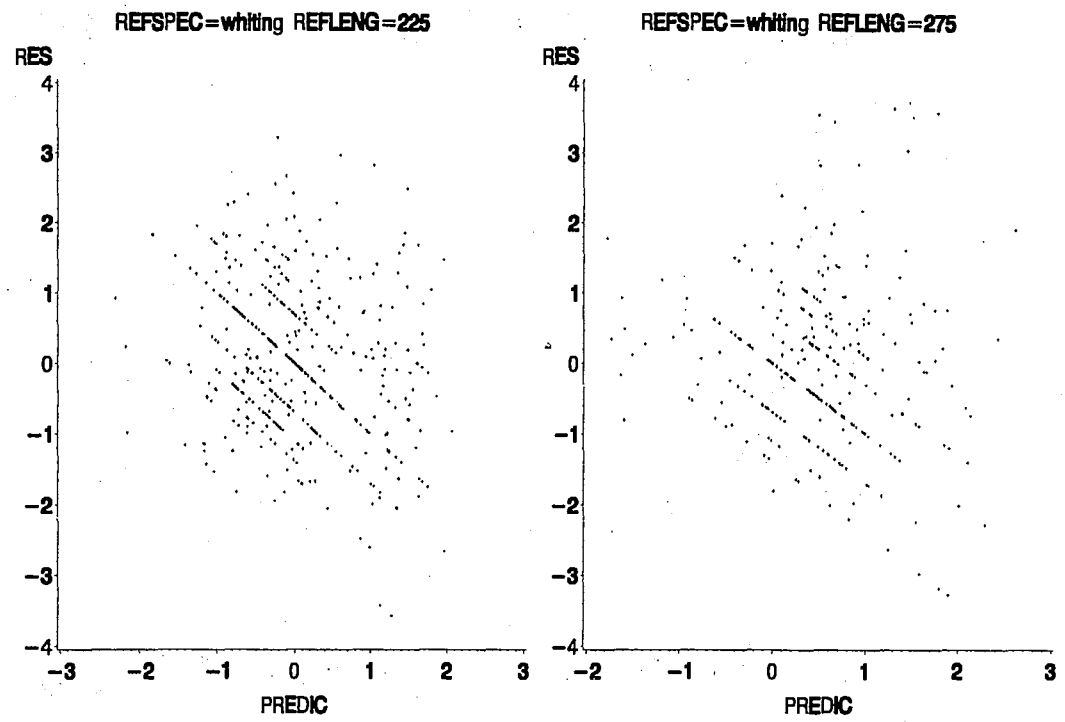


Fig. 6.3.1.2 continued. Residuals as a function of predicted value in the basic model for ratios.

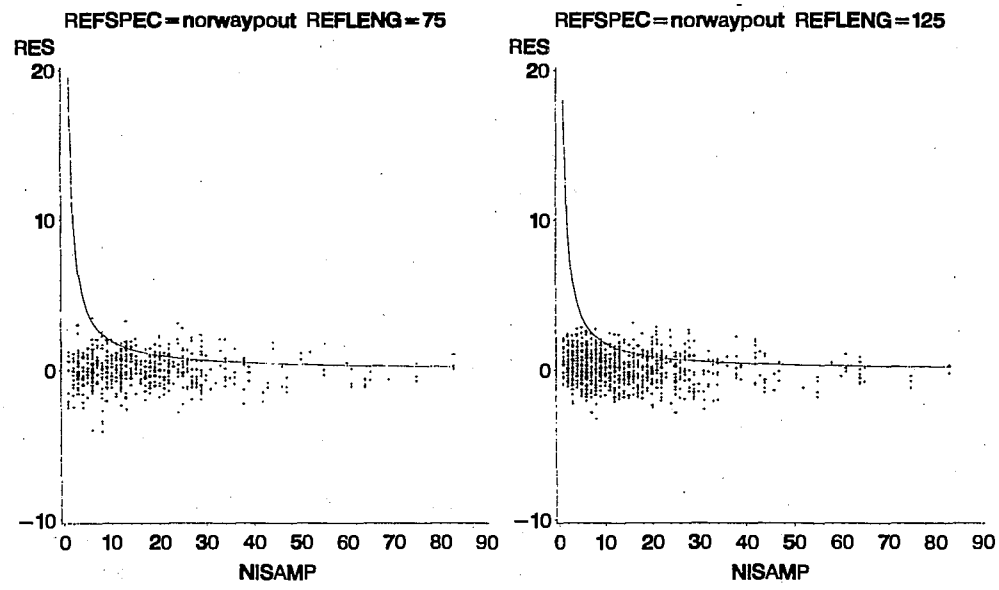


Fig. 6.3.1.3. Residuals as a function of number of stomachs in the sample in the basic model for ratios. Line: σ^2/(number of stomachs).

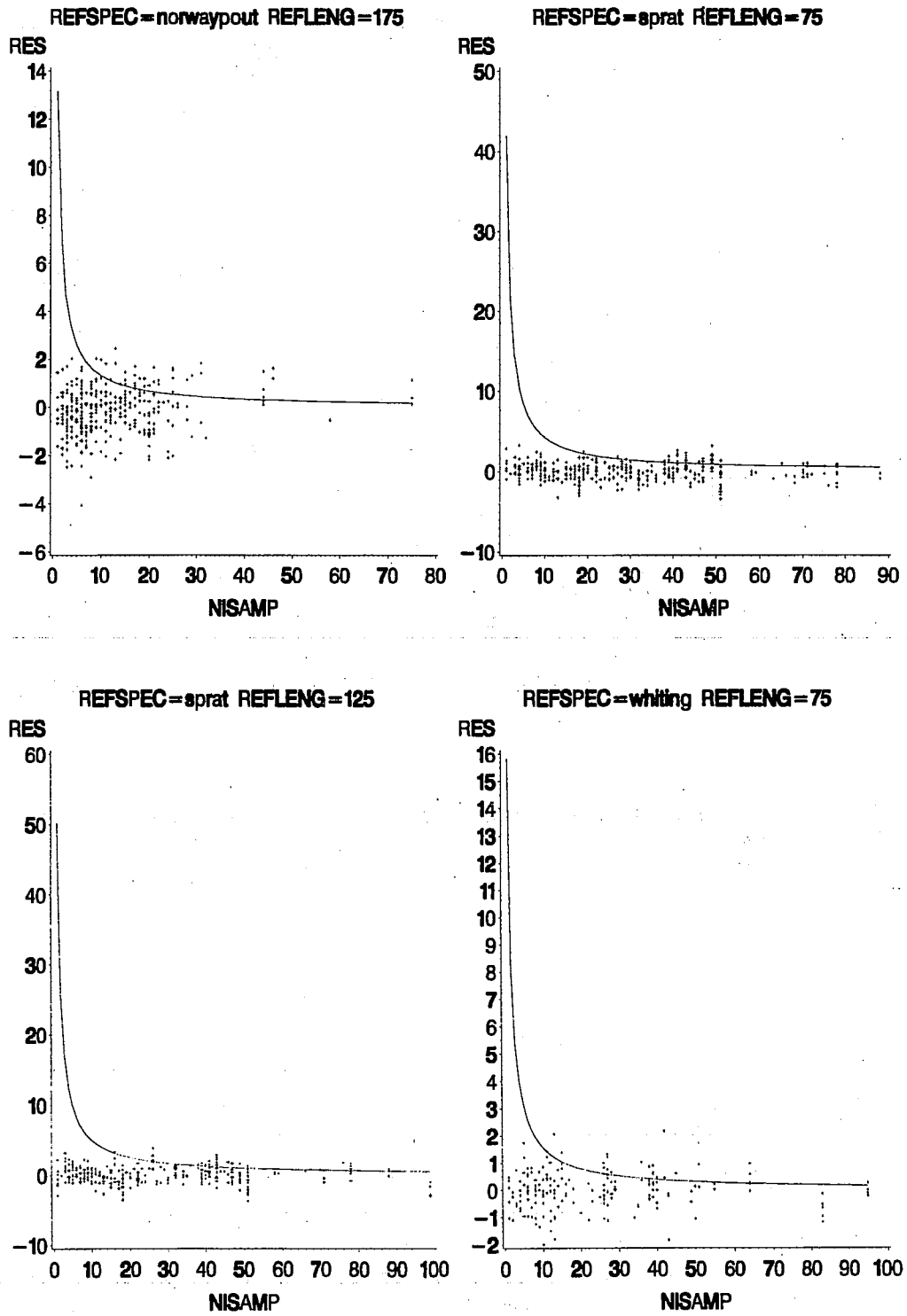


Fig. 6.3.1.3 continued. Residuals as a function of number of stomachs in the sample in the basic model for ratios. Line: σ^2/(number of stomachs).

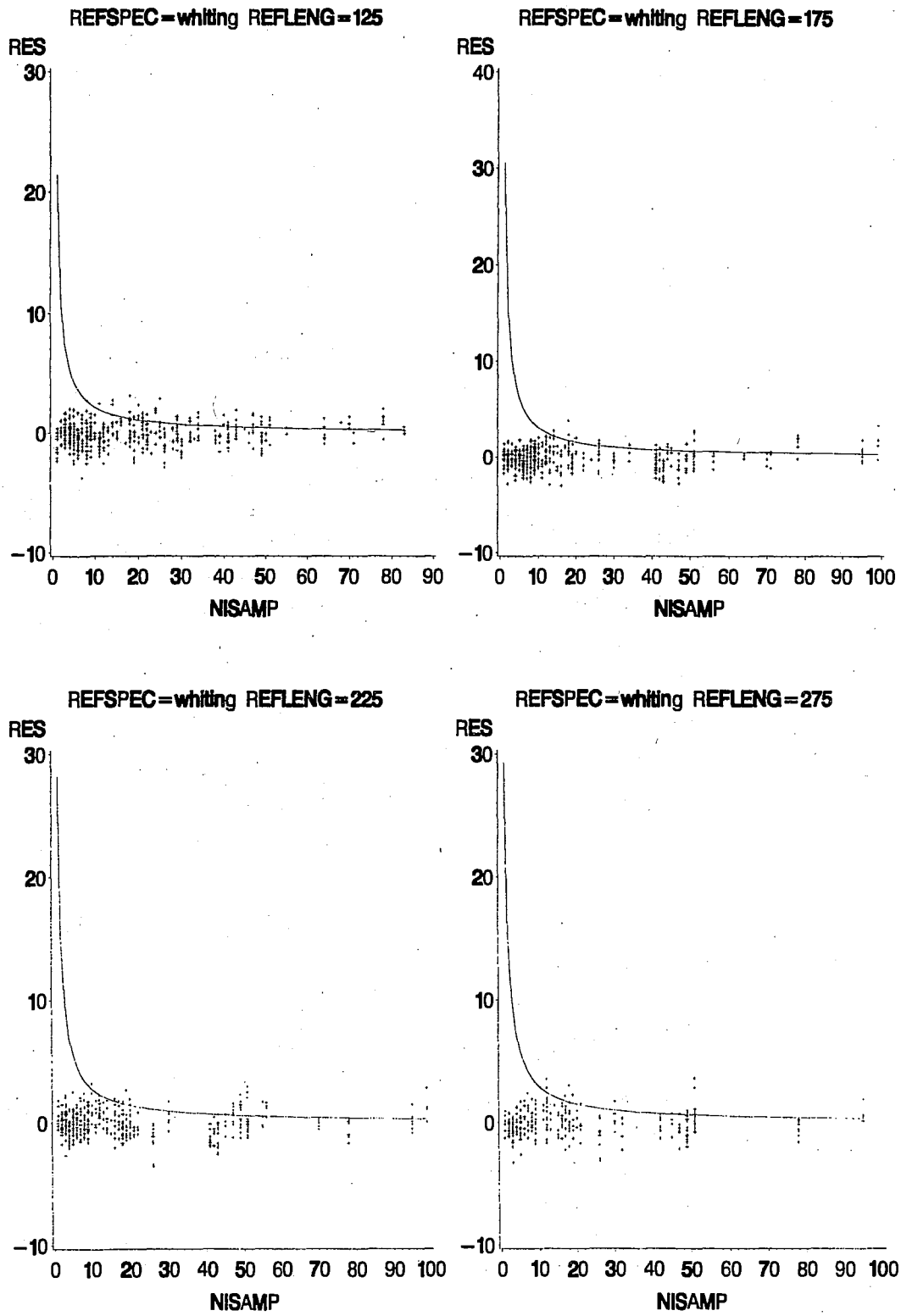


Fig. 6.3.1.3 continued. Residuals as a function of number of stomachs in the sample in the basic model for ratios. Line: σ^2/(number of stomachs).

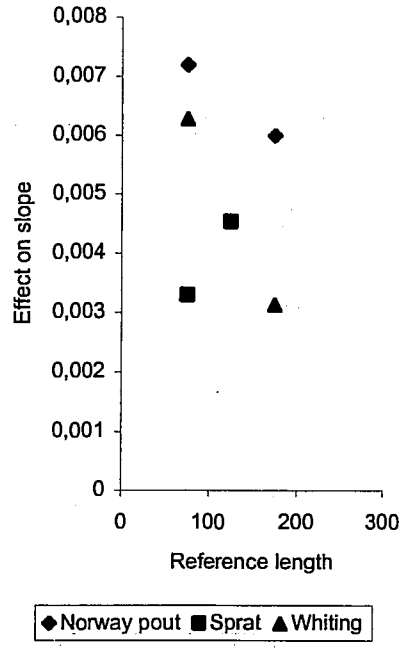


Fig. 6.3.2.1. The effect of number of stomachs on slope as a function of reference length. Resulting slope=slope+number of stomachs*effect.

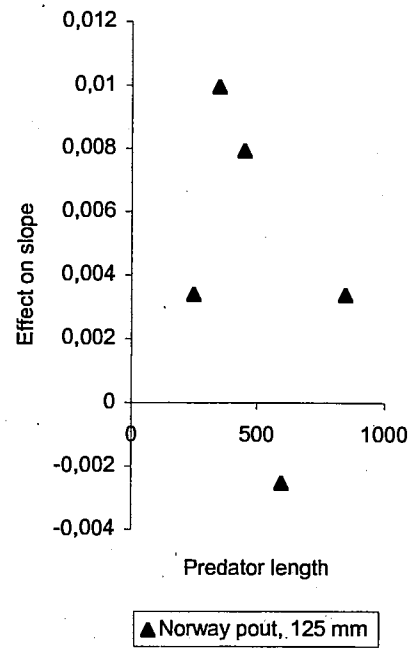


Fig. 6.3.2.2. The effect of number of stomachs on slope as a function of predator length. Resulting slope=slope+number of stomachs*effect.

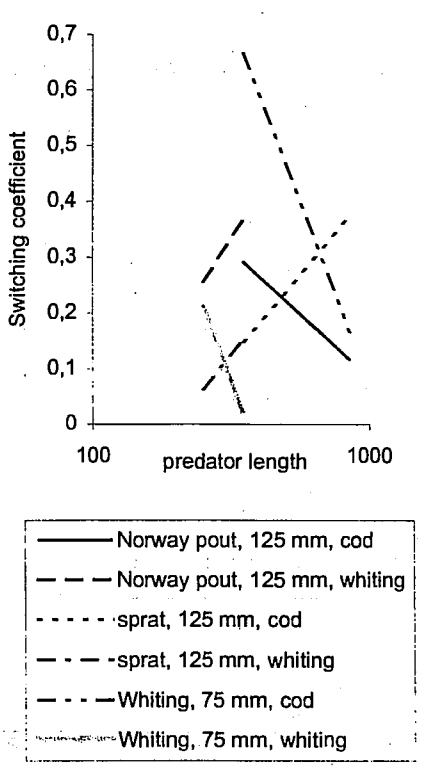


Fig. 6.3.5.1. Switching in the model describing dependence on length as polynomial. As a function of predator length for different references.

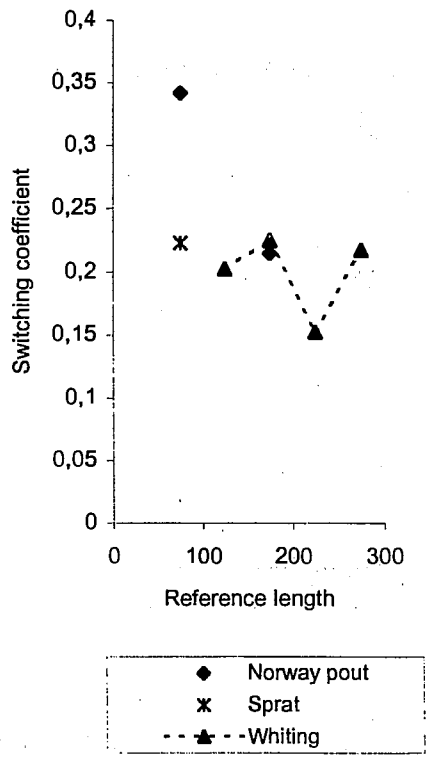


Fig. 6.3.5.2. Switching in the model describing dependence on length as polynomial. As a function of reference length.

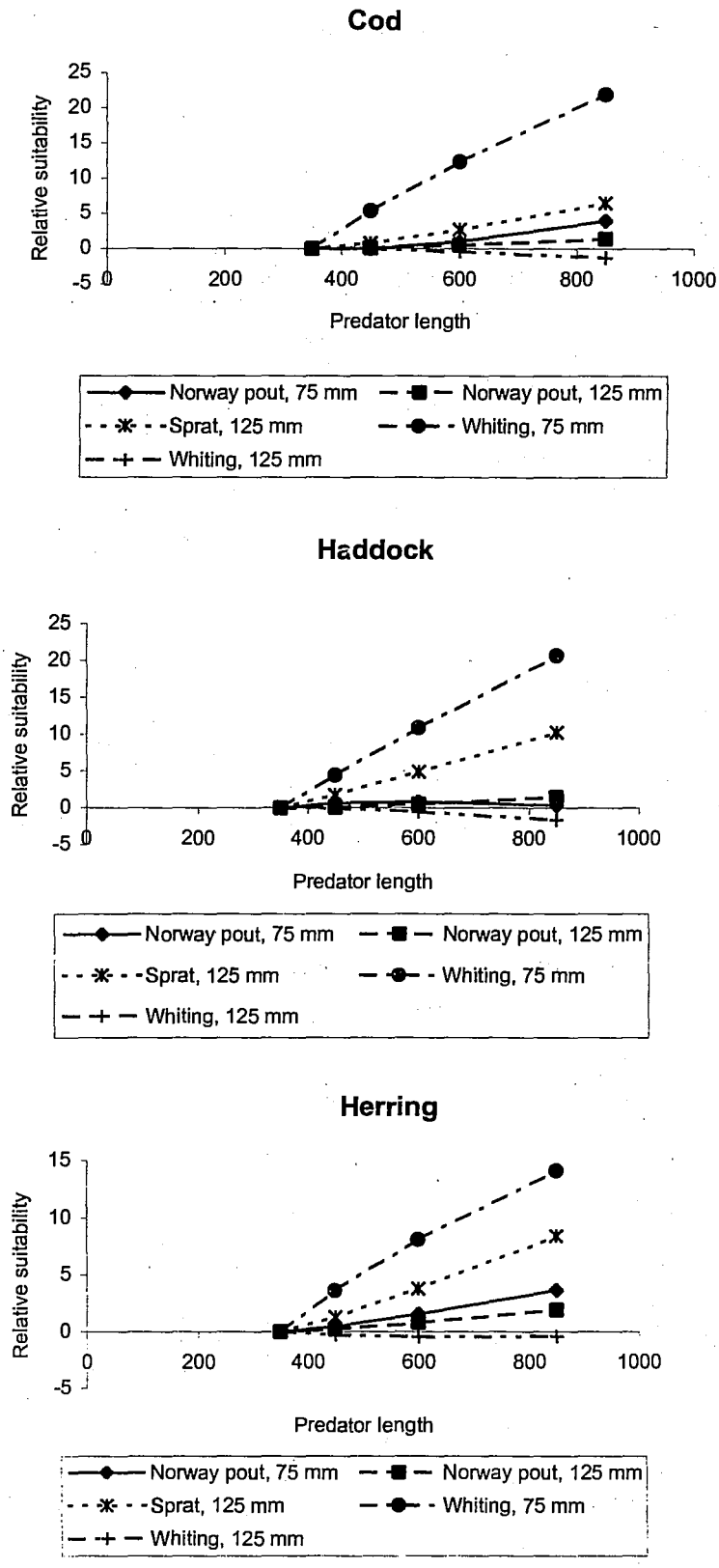


Fig. 6.3.5.3. Relative species suitabilities for different predator lengths.

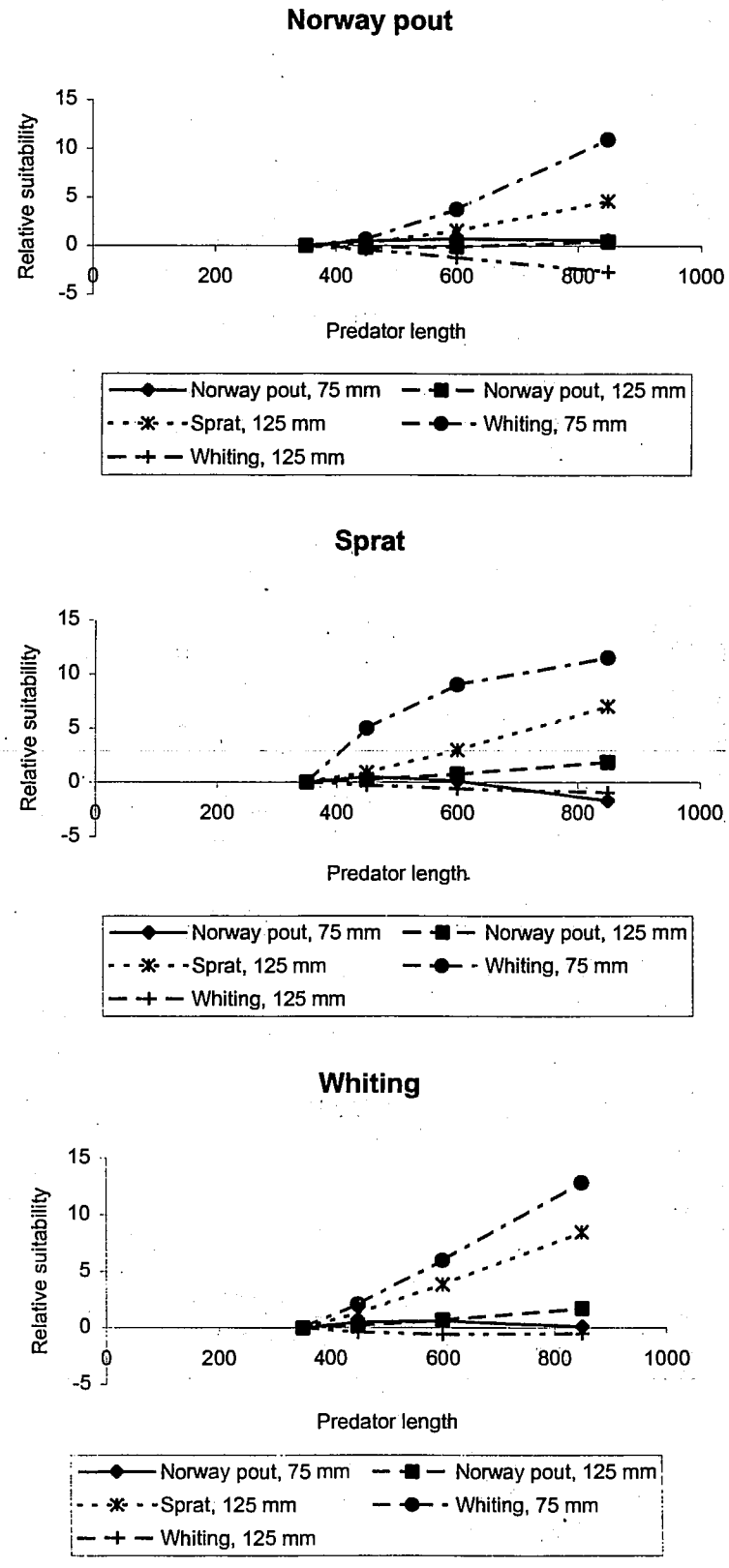
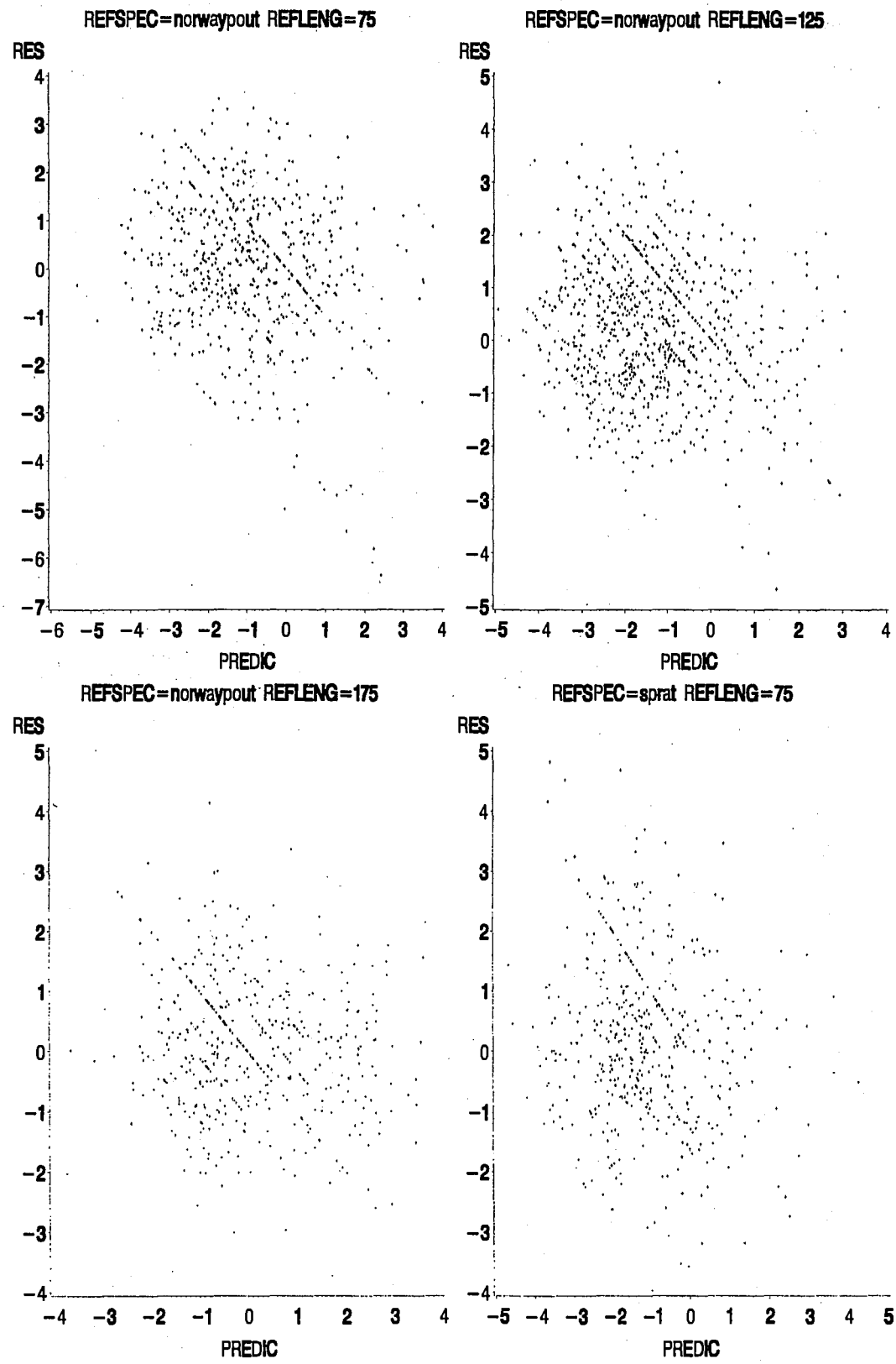


Fig. 6.3.5.3 continued. Relative species suitabilities for different predator lengths.



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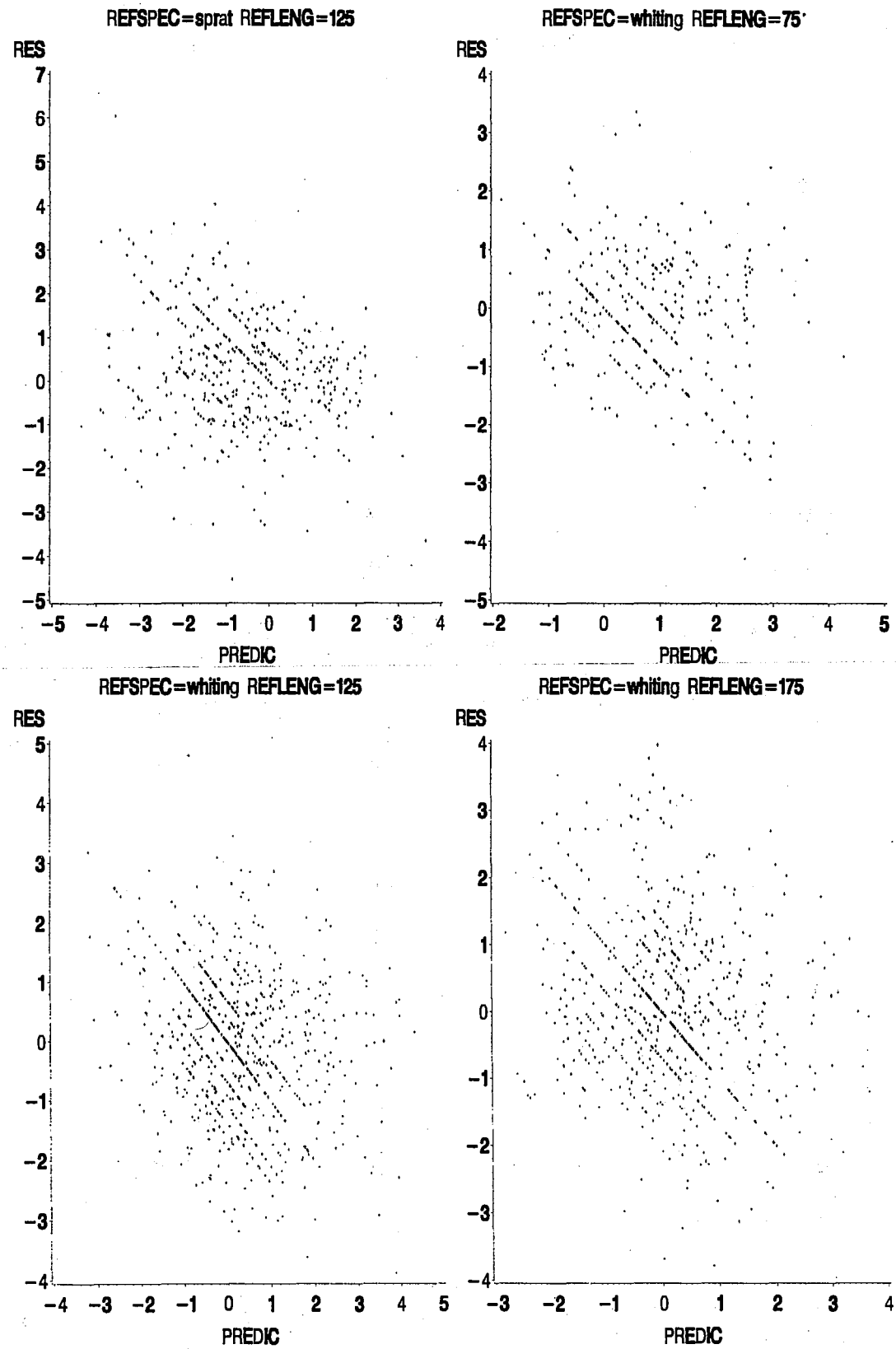

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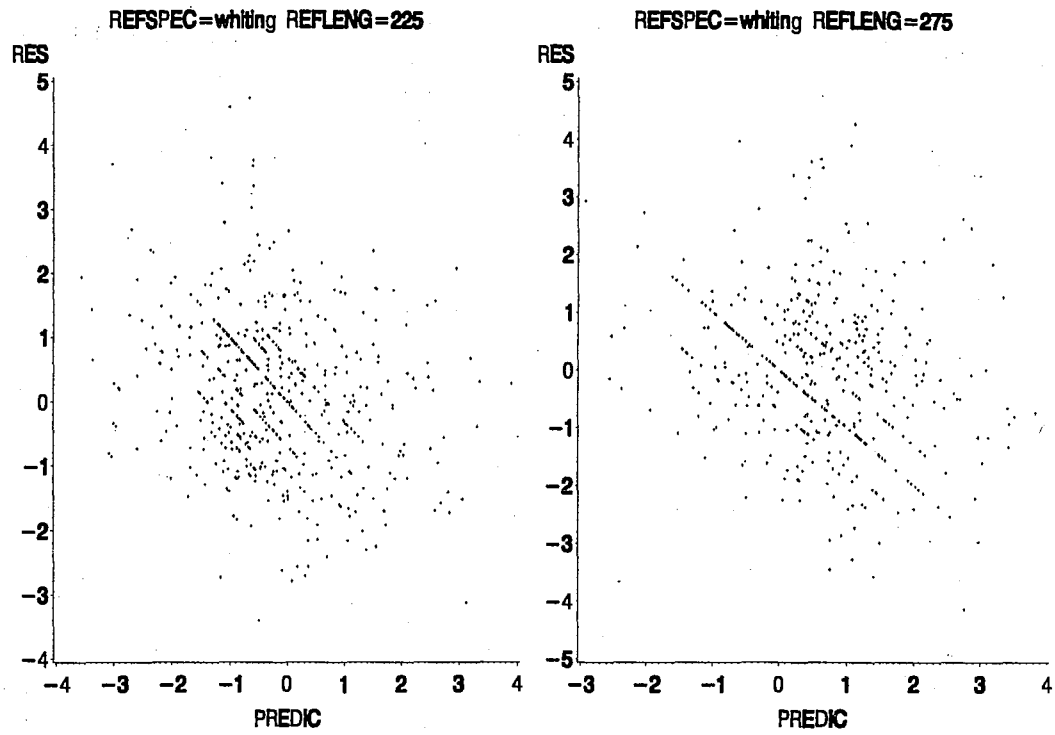

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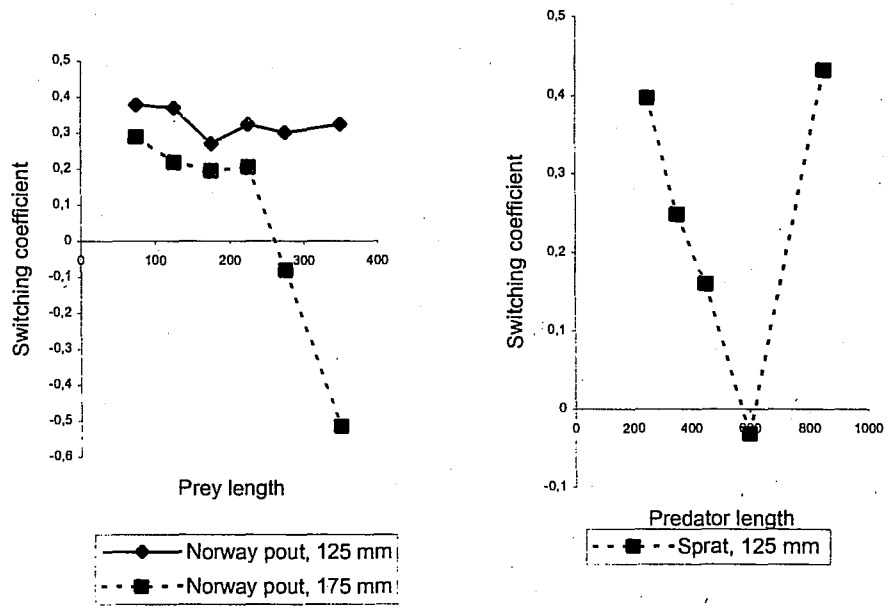

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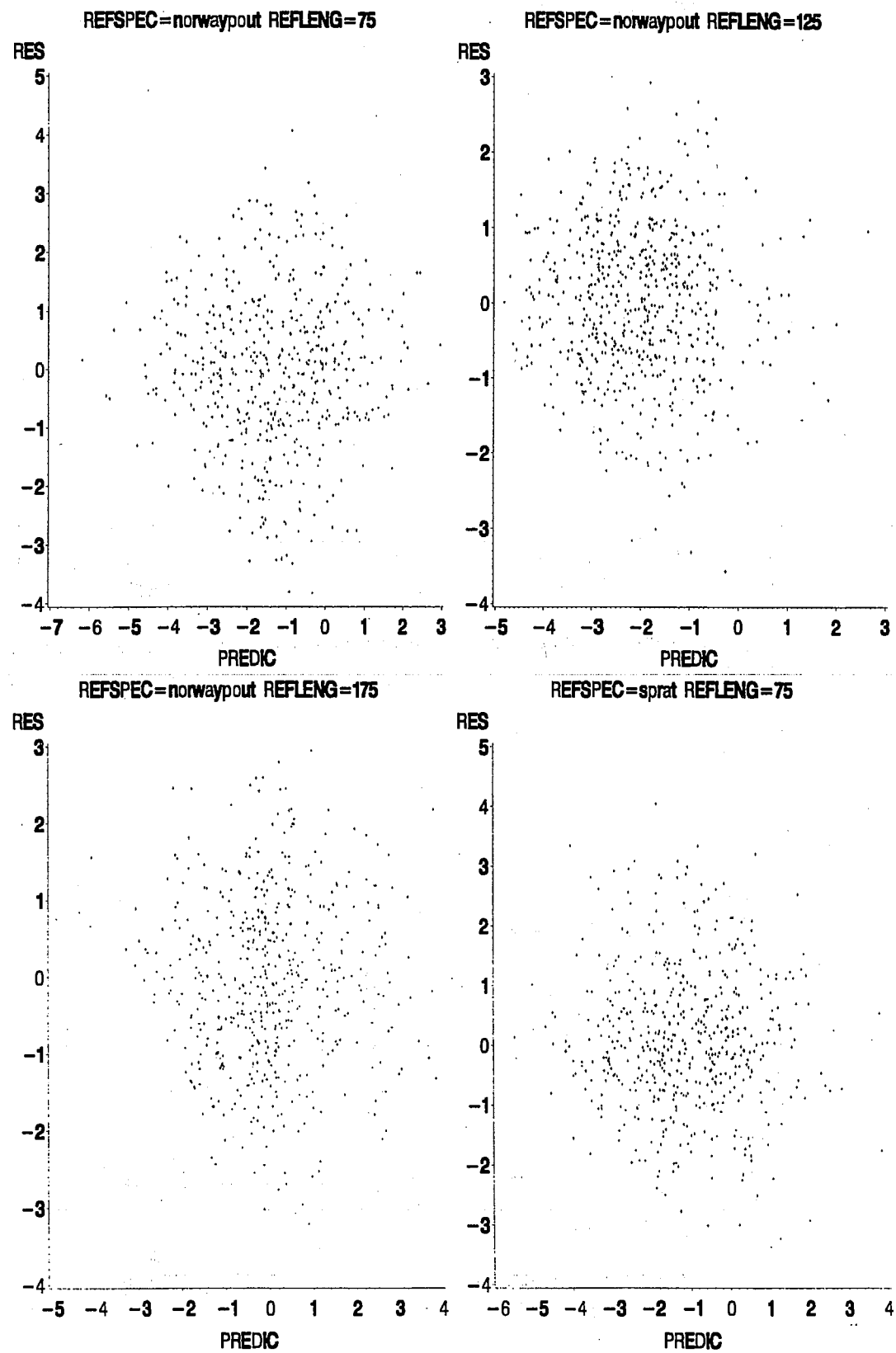


Fig. 6.3.6.3. Residuals from model of ratios build on North Sea scale as a function of predicted value.

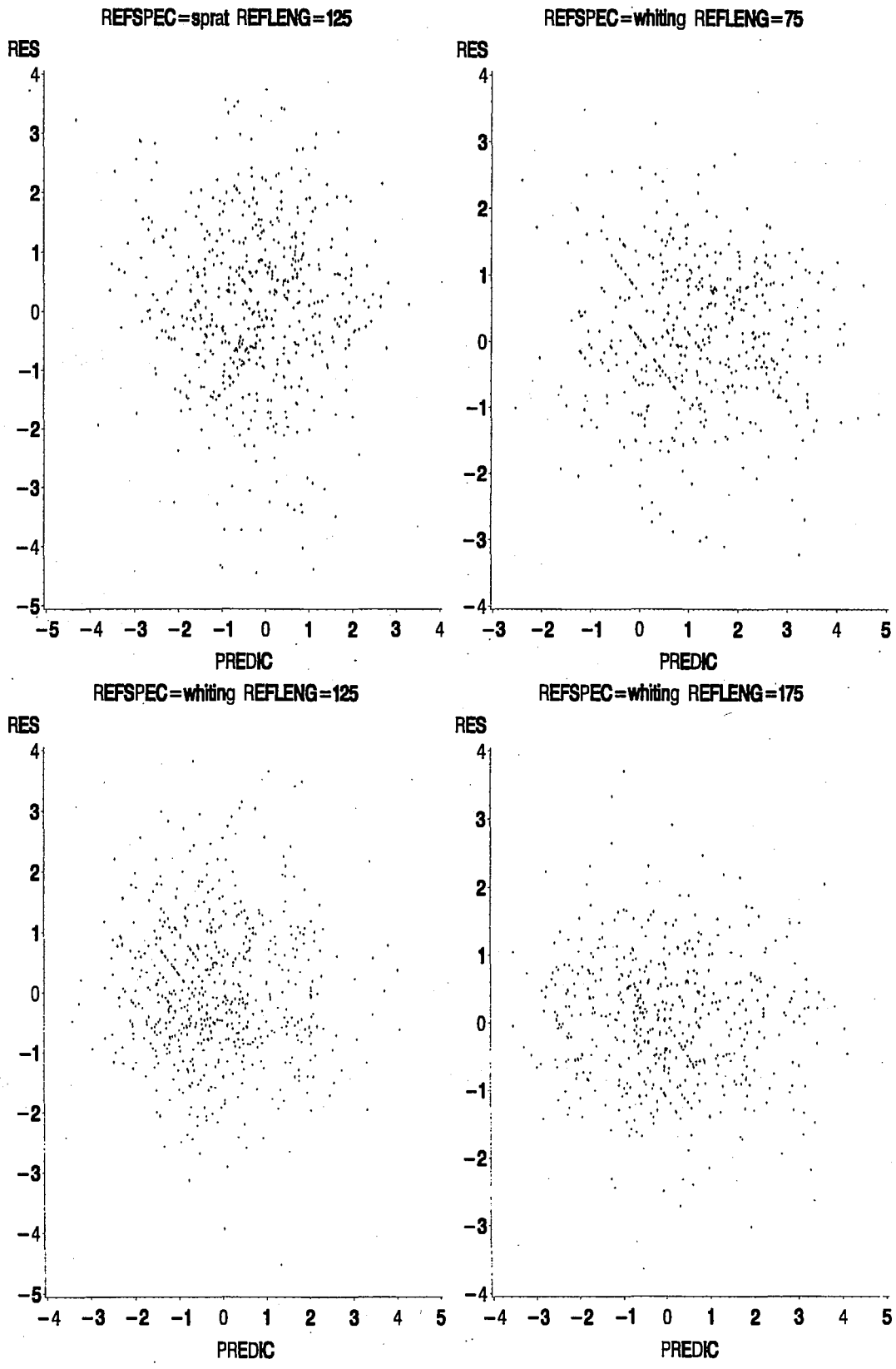


Fig. 6.3.6.3 continued. Residuals from model of ratios build on North Sea scale as a function of predicted value.

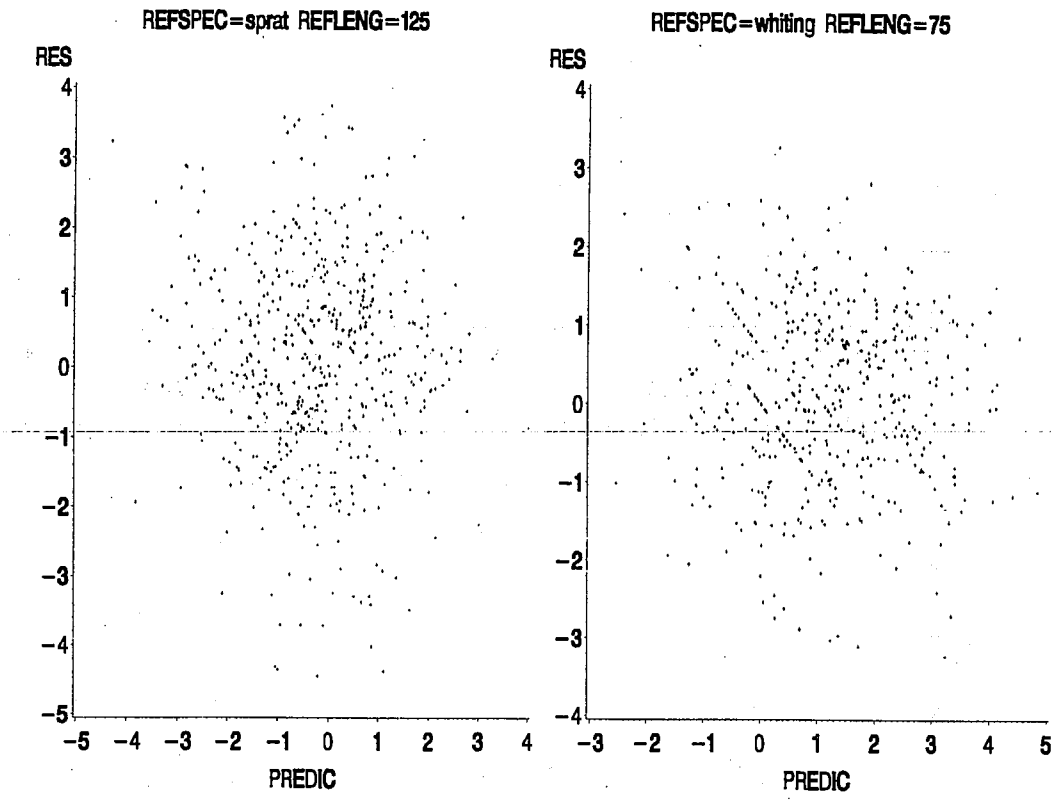


Fig. 6.3.6.3 continued. Residuals from model of ratios build on North Sea scale as a function of predicted value.

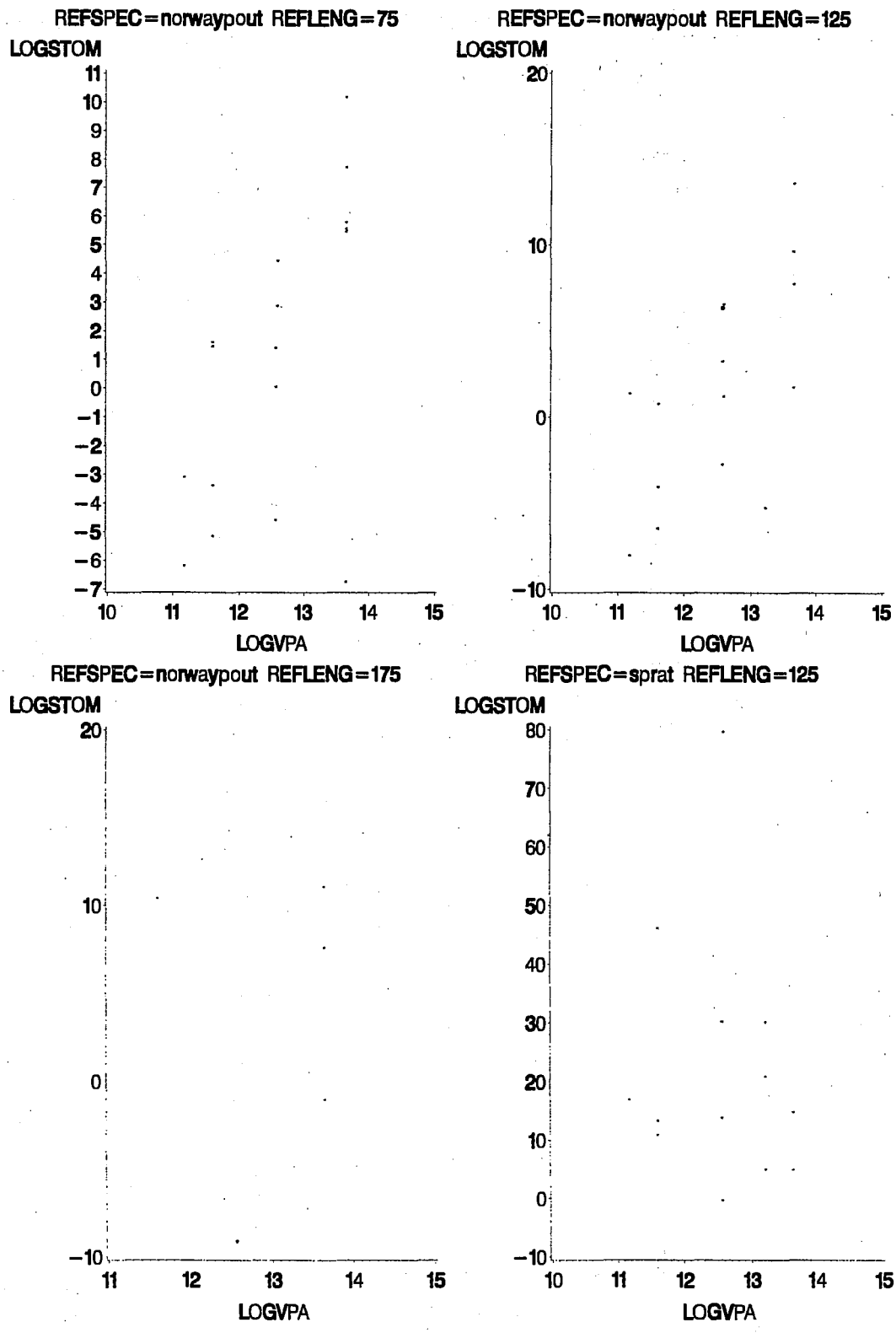


Fig. 6.3.7.1. Predicted average abundance of sandeel from the basic model as a function of VPA estimates. Each point represent a predator species and size-group.

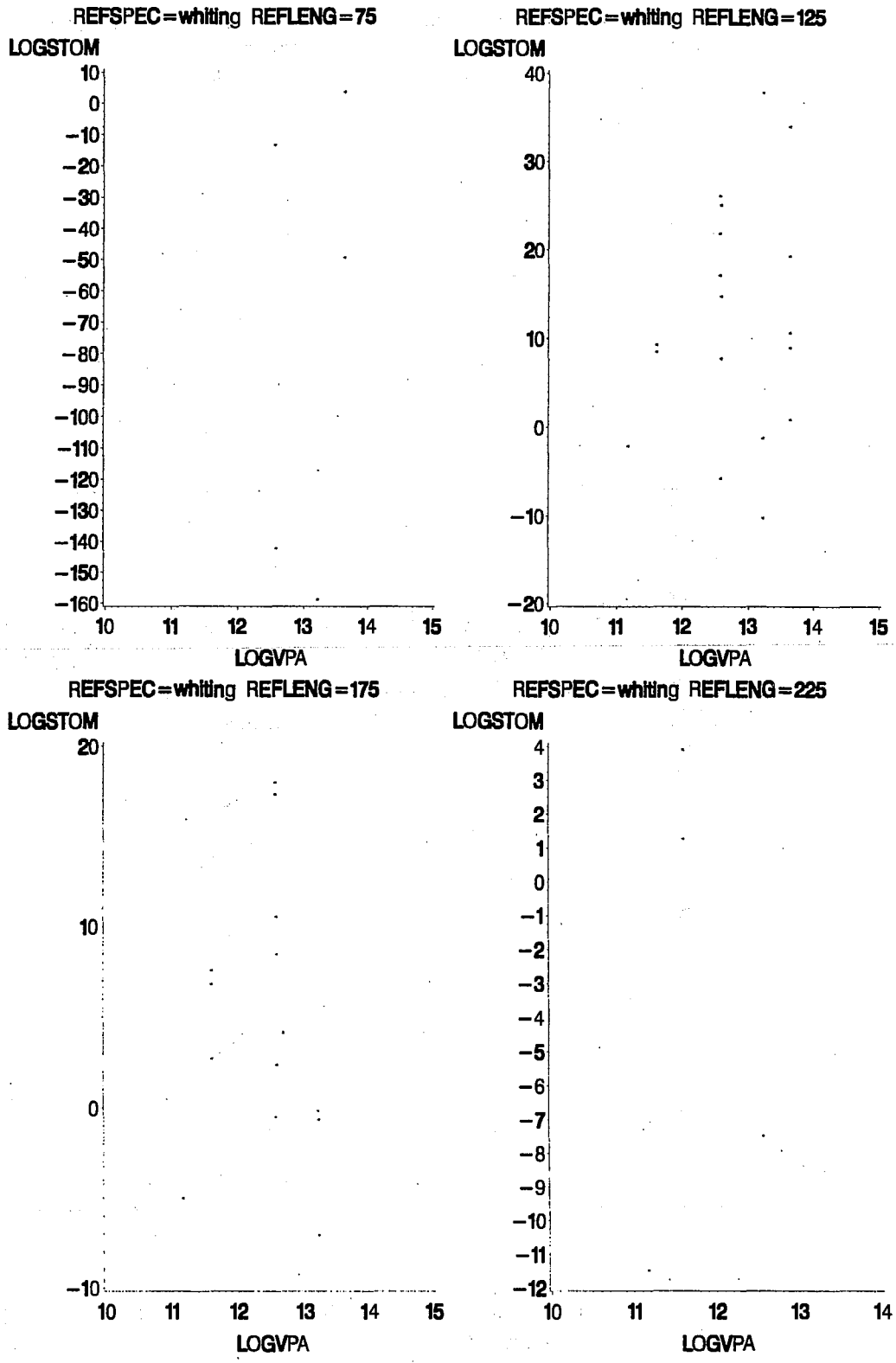


Fig. 6.3.7.1 continued. Predicted average abundance of sandeel from the basic model as a function of VPA estimates. Each point represent a predator species and size-group.

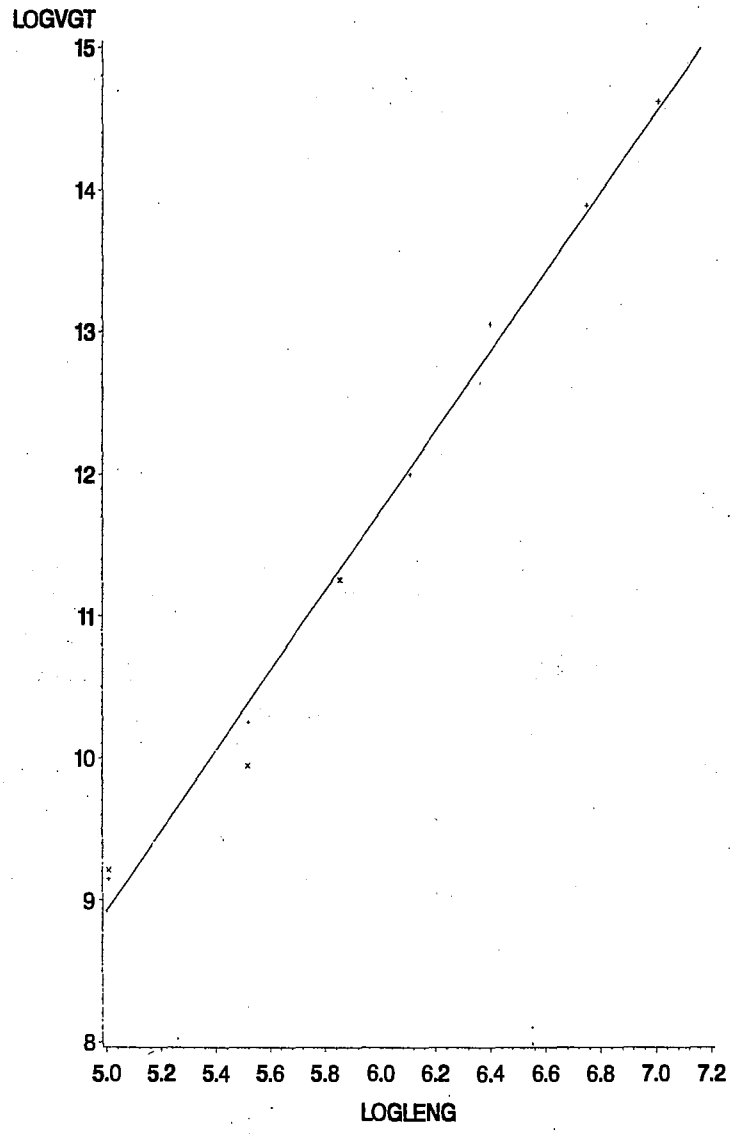


Fig. 6.4.1.1. ln(maximum weight of stomach content) as a function of ln(predator length). += Cod. x= Whiting. Line: predicted by model.

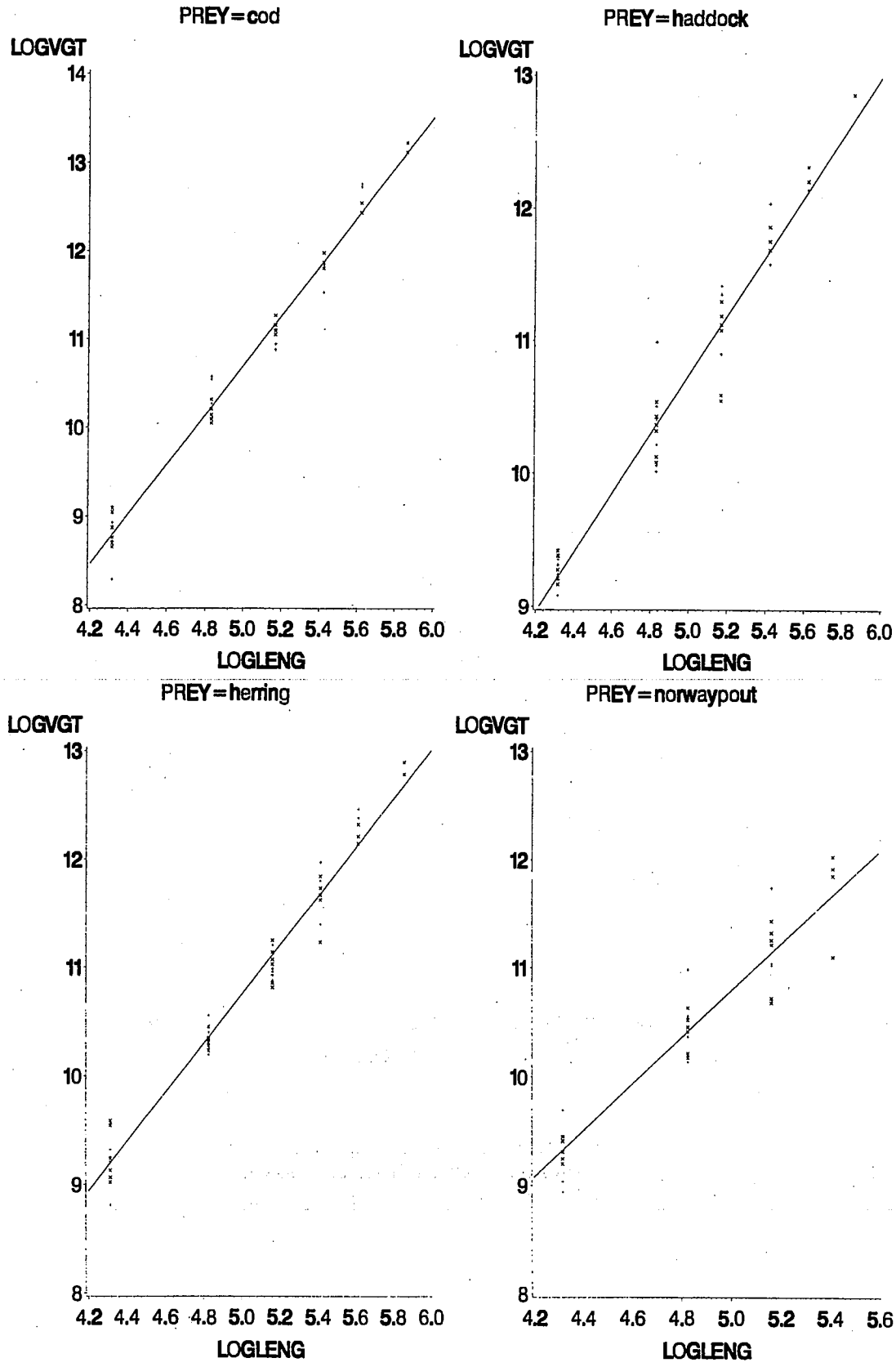


Fig. 6.4.2.1. ln(maximum weight of prey in the stomach) as a function of ln(prey length) for each prey species apart. Line: predicted by model.

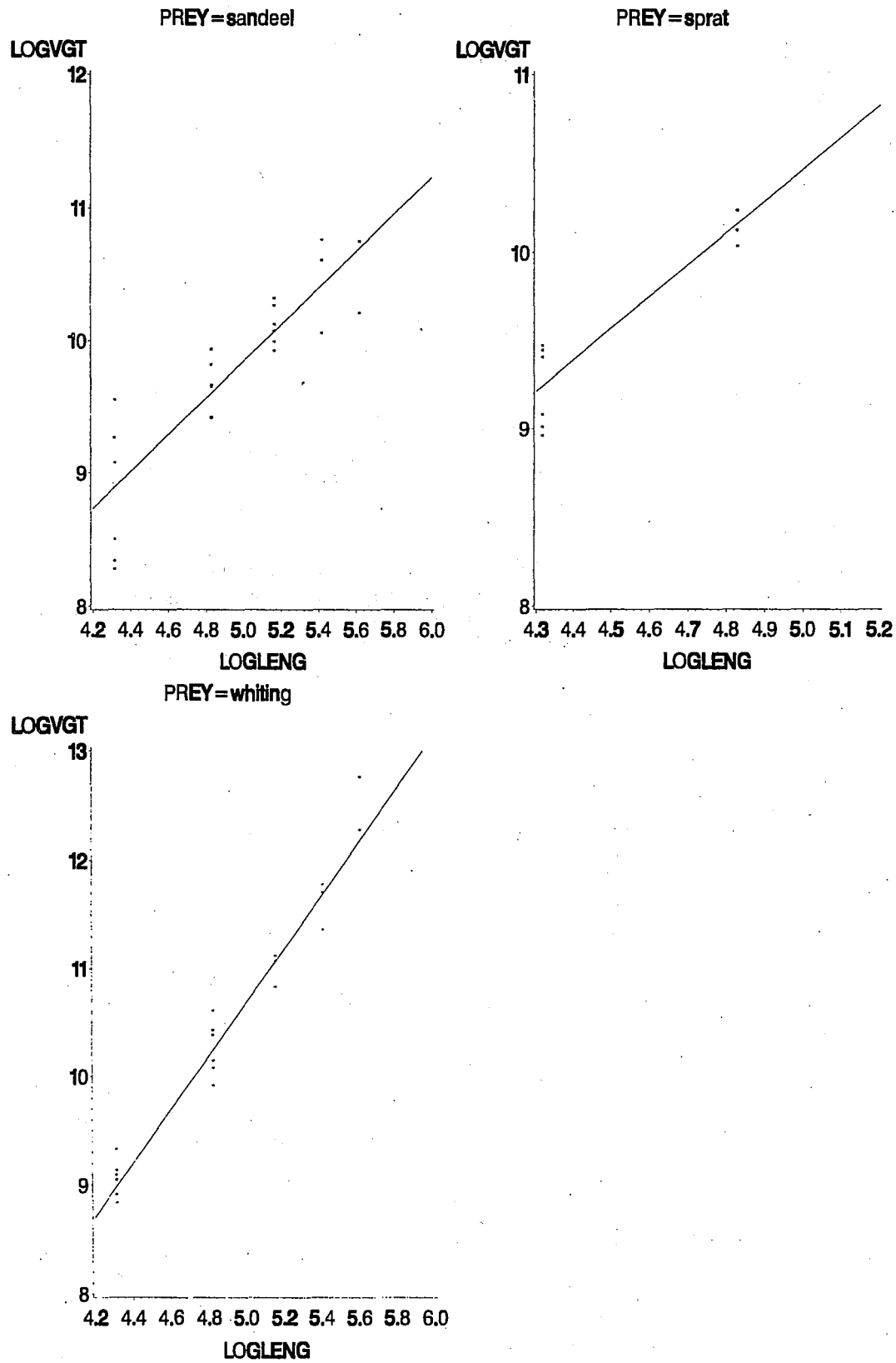


Fig. 6.4.2.1 continued. ln(maximum weight of prey in the stomach) as a function of ln(prey length) for each prey species apart. Line: predicted by model.

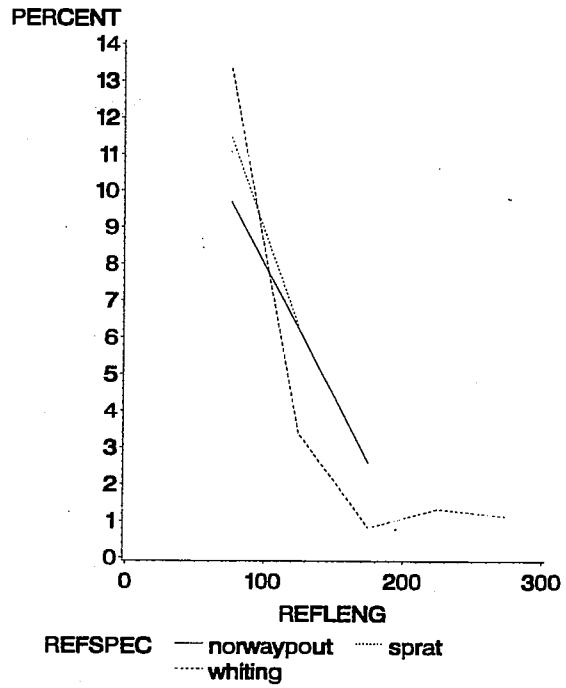


Fig. 6.4.2.2. Percentage of samples, where the average stomach can not contain another prey as calculated from the predicted weight at ingestion. All samples used in analyses for a reference included. Refspec= reference species. Refleng= reference length.

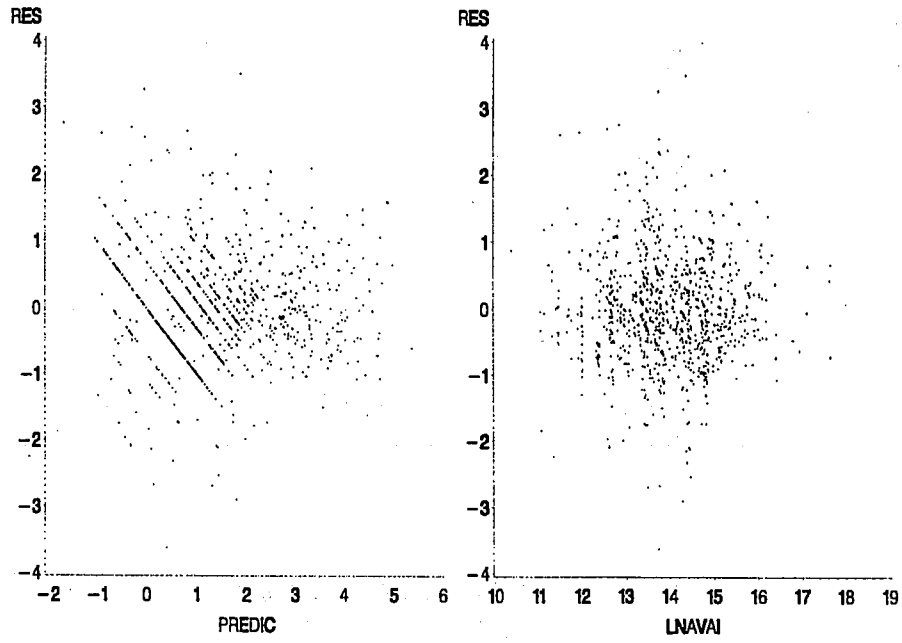
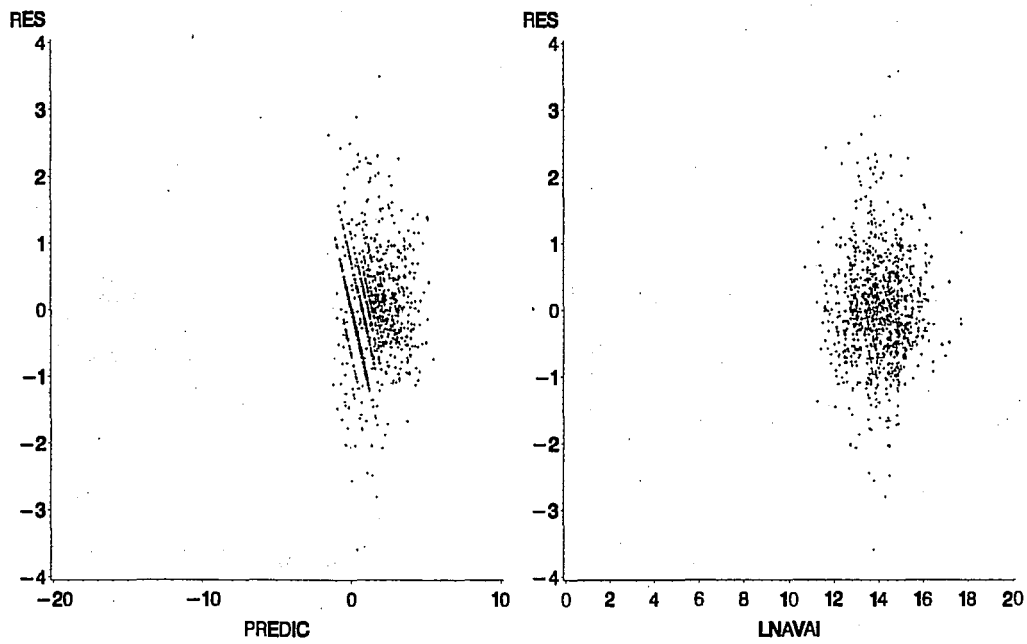


Fig. 6.4.3.1. Residuals from model of maximum ratio in the sample not taking the weight of the reference into account. Residuals as a function of predicted value (left) and ln(avai(w)) (right).



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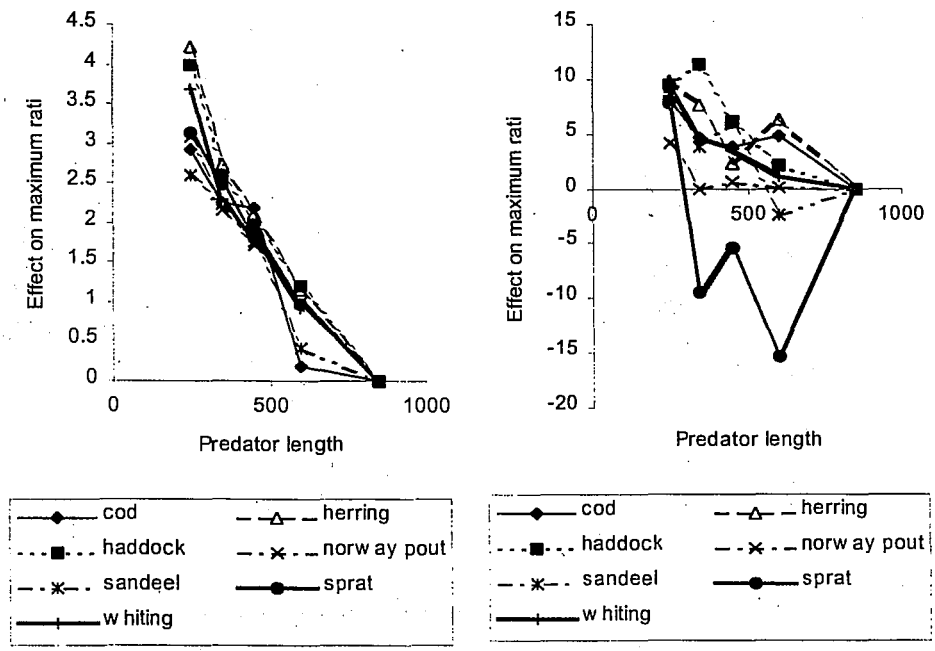

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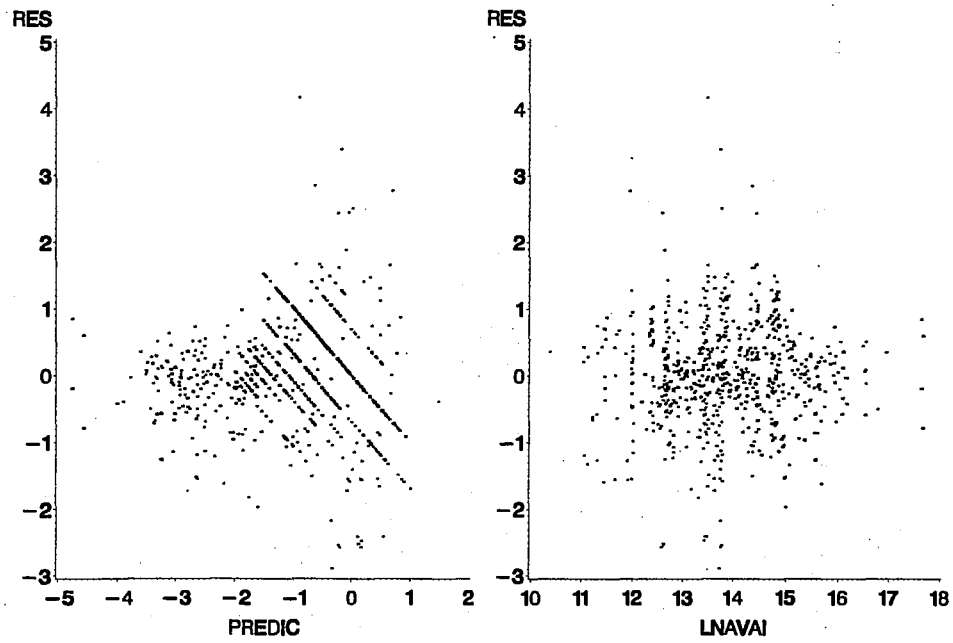

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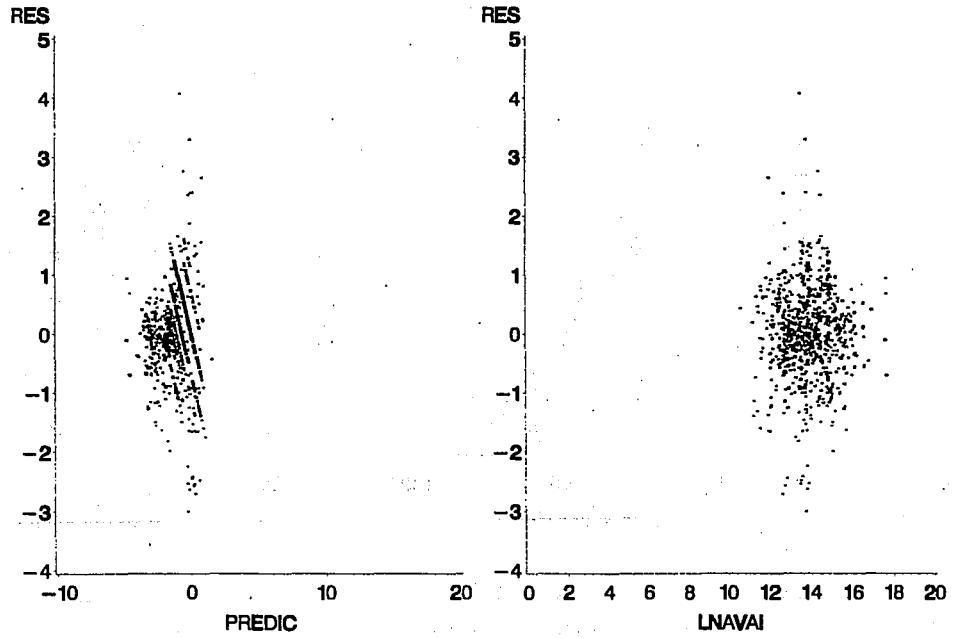

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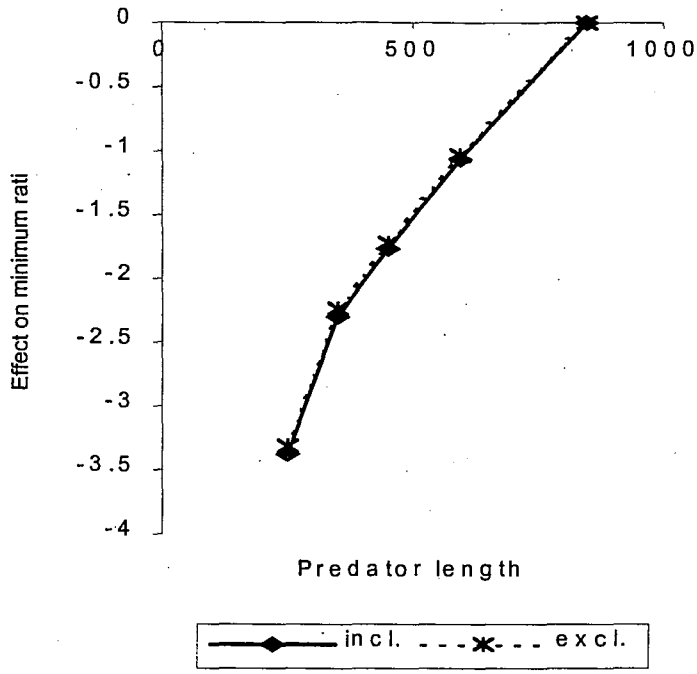

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