

ICES 1992

PAPER

C.M.1992/G:42
Demersal Fish Committee
ref. Pelagic Fish Committee



MSVPA and prey/predator Switching.

by

Jan Rene Larsen and Henrik Gislason

Danish Institute for Fisheries and Marine Research
Charlottenlund Castle, DK-2920 Charlottenlund, Denmark

Abstract

The effect of including prey/predator switching in the MSVPA for the North Sea is examined. Switching is modelled by making suitability a function of prey abundance. The results are evaluated by comparing observed and estimated stomach contents and by comparing estimates of year class strength with IYFS indices. Negative switching, where the suitability of a particular prey item declines as the abundance of the prey increases, results in a marginal reduction in the sums of squares of deviation between observed and estimated stomach contents. Regressions of suitability estimates versus prey biomass also point in the direction of negative switching. However, the result is not significant. The fit between MSVPA year class strengths and IYFS indices does not improve by introducing switching. It is concluded that additional stomach content data are needed to evaluate the significance of switching in the North Sea. Negative switching may be caused by changes in the relative spatial distribution of prey and predators as well as by changes in the behaviour of the predators. A spatially disaggregated MSVPA is needed to distinguish behavioral changes from changes in relative distribution.

1. Introduction.

The MSVPA described by Pope(1979), Helgason & Gislason(1979) and Sparre(1980) is a multispecies extension of the traditional VPA of Gulland(1965) in which predation of fish by fish is accounted for. In previous applications of the MSVPA food selection has been described by a model in which the suitability of a particular prey item to predation by a certain predator was assumed to be constant. This paper is an attempt to test a food selection model in which suitability is made a function of prey abundance, ie. where prey/predator "switching" is introduced.

Murdoch(1969) used the term "switching" to describe the situation where the ratio of the abundances of two prey species in the diet of a predator increases faster than proportionally with their ratio in the environment.

Let us consider a simple case where the predator faces two prey species at densities $N(1)$ and $N(2)$ and encounter and eat a certain number of individuals of each of these two species ($D(1)$ and $D(2)$). Usually the predator prefers one species over the other and this is reflected by a difference between the relative abundance of the two species in the environment and in the diet of the predator. This may be expressed as:

$$\frac{D(1)}{D(2)} = c \frac{N(1)}{N(2)}$$

(eq. 1)

where c is called preference. If c is larger than 1.0 prey 1 is preferred over prey 2. The preference c is a relative value, indicating the value that prey 1 has as a food item for the predator compared to prey 2.

If c is constant and does not depend on the abundance of either prey species no switching takes place. If c increases as $H(1)/H(2)$ increases switching is said to be "positive". In this situation the abundance of prey 1 in the diet increases faster than $H(1)/H(2)$. If c decreases as $H(1)/H(2)$ increases switching is said to be "negative". In order to investigate whether switching takes place, c is usually estimated at different values of $N(1)/N(2)$.

If positive or negative switching takes place it is necessary to modify eq. 1. As an example positive switching could be modelled by allowing c to increase proportionally to the ratio $N(1)/N(2)$ raised to some power b . If c' is a constant expressing the preference in the situation where the two prey items are equally abundant then :

$$\frac{D(1)}{D(2)} = c' \left(\frac{N(1)}{N(2)} \right)^{b+1}$$

(eq. 2)

2. Modelling switching in the MSVPA.

In the MSVPA the parameters of the food selection model are called suitabilities. However, suitabilities and preferences are closely related.

Suitability is defined by:

$$STOC_w(i) = \frac{SUIT(i)N(i)W(i)}{\sum_k SUIT(k)N(k)W(k)}$$

(eq. 3)

where $STOC_w(i)$ is the relative content of prey species i in the diet of the predator (weight basis), $SUIT(i)$ is the suitability of prey species i to the predator, $W(i)$ is the weight of prey species i at ingestion, and k is the total number of prey species. For notational convenience the indices for predator species, predator age and prey age has been omitted. Given data on food composition suitability is estimated within the MSVPA by inserting in:

$$SUIT(i) = \frac{\frac{STOC_w(i)}{N(i)W(i)}}{\sum_k \frac{STOC_w(k)}{N(k)W(k)}}$$

(eq. 4)

The number of prey individuals eaten may also be estimated:

$$D(i) = \frac{STOC_w(i)R_{pr}}{W(i)}$$

(eq. 5)

where R_{pr} is the ration of the predator.

Combining eq. 5 and eq. 3 allows the ratio of the number of individuals consumed to be expressed as:

$$\frac{D(1)}{D(2)} = \left(\frac{SUIT(1)}{SUIT(2)} \right) \left(\frac{N(1)}{N(2)} \right)$$

(eq. 6)

which compared to eq. 1 shows that c equals $SUIT(1)/SUIT(2)$.

Switching was introduced in the MSVPA by making suitability a function of prey abundance:

$$SUIT(i) = a(i) N(i)^b \quad (\text{eq. 7})$$

where a and b are constants. The *degree of switching*, b , can take negative or positive values for negative or positive switching. If b is 0, then $SUIT(i)$ is constant, indicating no switching. The expression for calculating the relative content of prey species i in the diet becomes:

$$STOC_w(i) = \frac{a(i)N(i)^{b+1}W(i)}{\sum_k a(k)N(k)^{b+1}W(k)} \quad (\text{eq. 8})$$

which in turn allows the computation of the constant a for known values of b :

$$a(i) = \frac{\frac{STOC_w(i)}{W(i)N(i)^{b+1}}}{\sum_k \frac{STOC_w(k)}{W(k)N(k)^{b+1}}} \quad (\text{eq. 9})$$

The number of prey individuals eaten may be computed from:

$$STOC_n(i) = \frac{a(i)N(i)^{b+1}}{\sum_k a(k)N(k)^{b+1}} \quad (\text{eq. 10})$$

For a system with 2 prey species the proportion, that species 1 constitutes of the diet (number basis) becomes:

$$\frac{D(1)}{D(1)+D(2)} = \frac{a(1)N(1)^{b+1}}{a(1)N(1)^{b+1}+a(2)N(2)^{b+1}} \quad (\text{eq. 11})$$

and the ratio of the number of individuals consumed becomes:

$$\frac{D(1)}{D(2)} = \frac{a(1)N(1)^{b+1}}{a(2)N(2)^{b+1}} = \frac{a(1)\left(\frac{N(1)}{N(2)}\right)^{b+1}}{a(2)}$$

(eq. 12)

which is similar to eq. 2.

Figure 1 shows how the food composition changes as a function of $N(1)$, $N(2)$ and b . In the case of no switching ($b=0.0$), the relationship between the proportion that species 1 constitutes of the diet and the relative abundance of species 1 is a downward concave curve. In the case of positive switching ($b>0.0$), the proportion of species 1 in the diet is lower than for $b=0.0$ when species 1 is rare compared to species 2; and higher when species 1 is more abundant than species 2. The situation is reversed for negative values of b . The situation where $b=-1.0$ is remarkable (and probably unrealistic), since in this case the food composition is independent of the relative abundance of the prey species.

3. Testing switching in the MSVPA.

The MSVPA was run with various values of b (the *degree of switching*) in order to evaluate whether switching improved the correspondence between the model output and independent data. In each run a single value of b was used for all predator and prey combinations.

Initially the intention was to test the model with values of b in the range from -1.0 to 1.0. However, due to problems with convergence, it was only possible to run the model with values of b between -0.6 and 0.4. The problems with the convergence are probably the same as identified by Hildén(1988) in a simplified MSVPA-like model in which a functional response of type III was introduced. Hildén's results show that in this case a range of cohort sizes and parameter values can produce, one, two or three solutions to the MSVPA-equations. Whether or not a unique solution exists depends on the values of b . Extreme values are most likely to result in non-unique solutions.

Three different measures were used to indicate the performance of the MSVPA at various degrees of switching: a) The correlation between stock estimates as given by the model and independent stock estimates b) The concordance between estimated and observed stomach contents and c) The consistency of the estimated suitabilities.

Except for the introduction of switching, the version of the MSVPA and the database were identical to the one used at the 1990 meeting of the Multispecies Assessment Working Group(Anon., 1991).

3.1 Correlation between MSVPA stock estimates and IYFS indices.

The MSVPA estimates of stock size were compared to independent stock estimates (IYFS-indices) as provided in Anon.(1989) for cod, haddock, and whiting, in Anon.(1990) for herring, and in Anon.(1991) for N. pout. Log-log regressions of MSVPA and IYFS estimates of year class strength were made in accordance with the model:

$$\ln(\text{MSVPA stock estimate}) = \alpha * \ln(\text{YFS-index}) + \beta$$

for various degrees of switching.

The results are shown in table 1.a and 1.b. Neither negative nor positive switching increase the correlation substantially. Moreover, the result show that curvilinearity (as measured by α) changes with the degree of switching, but that the magnitude of change differs from species to species, table 1.b.

3.2 Prediction of stomach contents.

Stomach content data for cod, whiting, and saithe are available from several years. It is therefore possible to estimate suitabilities on a subset of the data and use these suitabilities to predict the food composition. The predicted food compositions can then be compared to observations. However, additional feeding data are only available for some quarters and predators. Predictions of stomach content can therefore only be made for cod and whiting in the first and third quarter of 1981, 1985, 1986 and 1987 and for saithe in the third quarter of 1981, 1986 and 1987. For the remaining quarters and predators only one set of food composition data were available. As noted by Rice *et al.* (1991) the predicted stomach contents of cod, whiting and saithe are therefore not completely independent.

The deviation between predicted and observed stomach content was estimated at various values of b for all year and quarter combinations for which the predicted stomach content could be compared to observations. The frequency distributions of the deviations are shown in figure 2 for various degrees of switching. The deviations were then multiplied by the number of stomachs analyzed, squared, and summed.

Two different sums were calculated. One was the total squared deviation for each predator species:

$$SS(j) = \sum_y \sum_q \sum_d \sum_s \sum_a [N_{stom}(y,q,j,d) (STOC_o(y,q,j,d,s,a) - STOC_e(y,q,j,d,s,a))]^2$$

where $STOC_o(y,q,j,d,s,a)$ is the observed stomach contents (in kg) for predator species j , age d in year y , quarter q of prey species s , age a . $STOC_e(y,q,j,d,s,a)$ is the corresponding predicted (expected) value, and $N_{stom}(y,q,j,d)$ is the total number of stomachs sampled from predator species j , age d in year y , quarter q .

The other was the sum of squared deviation for each prey species:

$$SS(s) = \sum_y \sum_q \sum_j \sum_d \sum_a [N_{stom}(y,q,j,d) (STOC_o(y,q,j,d,s,a) - STOC_e(y,q,j,d,s,a))]^2$$

with symbols having similar meaning as in the previous formula.

In the output from the MSVPA, the contribution of a specific prey item to the stomach content of a specific predator, is given as a proportion of the weight of the total stomach content. By multiplying this proportion with the average weight of the stomach content, the total weight of the prey item in the stomach is obtained. If this number is divided by the weight of the individual prey at ingestion,

it is possible to estimate the number of prey individuals in the stomach. This means, that the SS 's could be based on prey weights as well as on prey numbers. During the test, however, it became obvious, that the use of the number of prey items was less desirable, since for some 0-groups division with the weight of one individual gave extremely high numbers which dominated the sums of squares. In order to give a more equal weight to all age groups the sum of squared deviations on a weight basis was used.

Figure 3 a) to c) shows values of $SS(j)$. For all three species the minimum in $SS(j)$ is found at negative values of b , ie. negative switching.

Figure 4 a) shows values of $SS(s)$. It is seen, that herring, N. pout, and sandeel contribute substantially to the sum of squares, in particular at positive values of b . In order to show the response of quantitatively less important prey species the $SS(s)$ for each species was normalised by dividing each value of $SS(s)$ with the sum of $SS(s)$, taken over all values of b , figure 4 b). For all prey species negative switching produces the lowest sums of squares.

3.3 Consistency of suitability estimates.

The suitabilities in the MSVPA are assumed to remain constant over time, and this is fundamental for the model (Rice *et al.*, 1991). If switching occurs, suitabilities should change as a function of prey abundance.

As mentioned in section 3.2, various subsets of stomach contents data exists. It is thus possible to compute independent estimates of suitabilities for cod and whiting in the first and third quarter of 1981, 1985, 1986 and 1987 and for saithe in the third quarter of 1981, 1986 and 1987. For the quarters and predators where no data were available, 1981 data were used.

The test was done with a *GLM* model in which the changes in $a(i)$ for a particular quarter-predator_species-predator_age-prey_species-prey_age combination were explained as resulting from a change in prey biomass. Thus a linear regression was made in which a unique intercept was estimated for each combination of quarter-predator_species-predator_age-prey_species-prey_age but with a common slope for each predator. If $a(i)$ is independent of prey biomass the slope is expected to be zero. In figure 5 the slope is plotted against b , the degree of switching. The standard deviation of the slope is also included. The slope is a decreasing function of b and becomes 0.0 for values of b in the range -0.35 to -0.05. However, the standard deviations show that for none of the degrees of switching tested here the slope was significantly different from 0.0.

4. Discussion.

The result show that switching does not improve the correlation between MSVPA estimates of year class strength and IYFS indices significantly. The comparisons of observed and estimated stomach contents indicate that positive switching is unlikely but that negative switching provided a marginal improvement to the fit to the observed food compositions. A b somewhere between 0 and -0.4 removes the correlation between suitability estimates and prey biomass. However, the latter result is not significant. For the time being the hypothesis of a constant suitability cannot be rejected. However, if switching does occur, negative switching is the most likely.

Suitability reflects both the relative spatial distribution of the predator and its potential prey and the probability that the predator will catch and eat the prey once it is encountered. If suitability is to

remain constant over time both of these components must remain constant.

Since the MSVPA considers the North Sea as one homogeneous area, changes in suitability may result from changes in abundance which affect the relative spatial distribution without an actual change in the size of the distribution area. Table 2.1.a shows a theoretical example of how changes in relative distribution could affect the suitabilities. Consider a situation with one predator and two prey species and divide the distribution area into two subareas, where prey *A* is found in only subarea 1, while the predator and its alternative prey, *B*, is found both in subarea 1 and 2. In situation I the biomass of prey *A* is 1.0 in subarea 1 and the biomass of prey *B* is 1.0 both in subarea 1 and 2. Let the predator be equally abundant in both of the two subareas, and let the suitability be 0.5 for both prey species. The relative food composition within each subarea might now be computed according to (eq. 3), which gives the values indicated in the table. The relative food composition for the whole area is computed as the average of the values for the two subareas since the predator is equally abundant in each of the two subareas. The overall suitabilities might now be computed according to (eq. 4), which gives the values 0.4 and 0.6 for prey *A* and *B*, respectively. In situation I the overall suitability of prey *A* has thus been estimated to 0.4, which is less than the within area suitability of 0.5. Not taking differences in spatial distribution into account may hence introduce a bias in the estimate of overall suitability. In situation II the biomass of prey species *A* in subarea 1 has doubled to 2.0. When the same computational procedure is applied, the result is an overall suitability of 0.33 for prey species *A*. Overall suitability is thus a declining function of prey biomass, i.e. the prey apparently becomes less attractive as its abundance increases.

In the North Sea, several species have changed their spatial distribution since the first set of stomach content data was sampled in 1981. Herring, which in 1981 was distributed mainly in the northern part of the North Sea became abundant throughout the area in 1985, 86, and 87. Sandeel also changed its distribution (Anon., 1990). In 1981 28% of the total North Sea biomass of sandeel was found in the northern area, while the corresponding percentages for 1985, 1986 and 1987 are 15, 20 and 35, respectively. It is probable, that similar changes have occurred for other species as well.

Changes in the probability of eating a prey once encountered may also take place. However, for fish the examples of density dependent changes in suitability are few (Murdoch and Bence, 1987) and positive switching would be the most likely result.

A third possibility for introducing changes in suitability over time results from the way in which suitability is estimated within the model. Since suitability is a non-linear function of food composition, the average suitability in a given year cannot be determined directly from the average stomach content of a given predator population, except if all the individuals share exactly the same array of suitabilities. Chesson(1984) showed, that a population may show switching, even though its individual members do not switch. If prey preferences are constant but differ between individuals, this is sufficient to cause switching at the population level. Differences in preferences between predator individuals may result in negative or positive switching, depending on the circumstances, but negative switching is the most likely result. Table 2.1.b shows an example of how within-predator differences affects the estimation of suitabilities at the population level. Two predator individuals (1 and 2) differ with respect to the suitability of two prey species *A* and *B*. When the abundance of prey species *A* increases, the fraction that the species constitutes of the food composition increases as well, but the overall result is a decrease in the suitability. From an overall point of view, negative switching has occurred without any change in the predators behaviour or in its spatial distribution relative to the prey.

At present the data do not allow switching to be rejected. It is therefore necessary to redo the analysis when the 1991 stomach content data become available. Given the preliminary results obtained here

the outcome could very well be that positive and zero switching has to be rejected. Since negative switching may result from year to year differences in the relative spatial overlap between the predator and the prey the development of an area based multispecies model should be encouraged. Without such a model it will be impossible to distinguish changes in suitability due to changes in behaviour from changes in suitability due to changes in spatial distribution.

References.

- Anon. 1989. Report of the Roundfish Working Group. ICES C.M. 1989/Assess:7. (mimeo.)
- Anon. 1990. Report of the Herring Assessment Working Group for the Area South of 62°N. ICES C.M. 1990/Assess:14. (mimeo.)
- Anon. 1991. Report of the Multispecies Assessment Working Group. ICES C.M. 1991/Assess:7. (mimeo.)
- Anon. 1991. Report of the Industrial Fisheries Working Group. ICES, Doc. C.M. 1991/Assess:14 (mimeo.)
- Chesson, P. L., 1984. Variable Predators and Switching Behaviour. *Theoretical Population Biology*, 26, 1-26.
- Gulland, J. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report. Coun. Meet. Int. Counc. Explor. Sea. 1965 (3):1-9. (mimeo.)
- Helgason, T. and Gislason, H. 1979. VPA-analysis with species interaction due to predation. ICES C.M. 1979/G:52 (mimeo.)
- Hildén, M., 1988. Significance of the functional response of predators to changes in prey abundance in multispecies virtual population analysis. *Can. J. Fish. Aquat. Sci.*, 45, 89-96.
- Murdoch, W. W., 1969. Predation and prey stability. *Ecological Monographs*, 39, 4, 335-354.
- Murdoch, W. W. & Bence, J. 1987. General predators and Unstable Prey Populations. In: W. Charles Kerfoot and Andrew Sih (eds.). *Predation. Direct and Indirect Impacts on Aquatic communities.* University Press of New England. p. 17-30.
- Pope, J. 1979: A modified cohort analysis in which constant natural mortality is replaced by estimates of predation levels. ICES C.M. 1979/H:16 (mimeo.)
- Rice, J. C., Daan, N., Pope, J. G., & Gislason, H., 1991. The stability of estimates of suitabilities in MSVPA over four years of data from predator stomachs. - *ICES mar. Sci. Symp.*, 193: 34-45.
- Sparre, P. 1980. A goal function of fisheries (legion analysis). ICES C.M. 1980/G:40. (mimeo.)

Table 1.a. R^2 resulting from fitting the model $\ln(MSVPA \text{ stock estimate}) = \alpha * \ln(IYFS\text{-index}) + \beta$ for the species indicated (age 1) at various degrees of switching.

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

Table 1.b. Estimates of α resulting from fitting the model $\ln(MSVPA \text{ stock estimate}) = \alpha * \ln(IYFS\text{-index}) + \beta$ for the species indicated (age 1) at various degrees of switching.

Predator species	Degree of switching (b)					
	-0.6	-0.4	-0.2	0.0	0.2	0.4
Cod	0.32	0.35	0.38	0.40	0.41	0.42
Whiting	0.40	0.45	0.49	0.53	0.56	0.58
Haddock	0.51	0.60	0.73	0.88	1.04	1.20
Herring	0.29	0.42	0.59	0.77	0.92	1.03
N. pout	0.25	0.29	0.33	0.39	0.45	0.51

Table 2.1.a. A theoretical example to show how overall suitability changes without a change in the behaviour of the predator. The spatial overlap of the predator and the prey changes from situation I to situation II as a result of an increase in the abundance of prey *A* in subarea 1. See text for further explanation.

Situation I

$SUIT(A) = SUIT(B) = 0.5$

Sub area	Biom(Prey A)	Biom(Prey B)	STOC(A)	STOC(B)	Ave. STOC(A)	Ave. STOC(B)	SUIT(A)	SUIT(B)
1	1	1	0.5	0.5	0.25	0.75	0.4	0.6
2	0	1	0.0	1.0				
Total	1	2						

Situation II

$SUIT(A) = SUIT(B) = 0.5$

Sub area	Biom(Prey A)	Biom(Prey B)	STOC(A)	STOC(B)	Ave. STOC(A)	Ave. STOC(B)	SUIT(A)	SUIT(B)
1	2	1	0.67	0.33	0.33	0.67	0.33	0.67
2	0	1	0.0	1.0				
Total	2	2						

Table 2.1.b. A theoretical example to show how overall suitability changes without a change in the behaviour of the predator. The two predator individuals has different suitabilities (SUIT_i) for the to prey species. The overall suitabilities are computed as an average of the two predator individuals. Since suitability is a non-linear function of food composition, the result of an increase in the abundance of prey A is a decrease in the population suitabilities for prey A (SUIT_p(A)). See text for further explanation.

Situation I

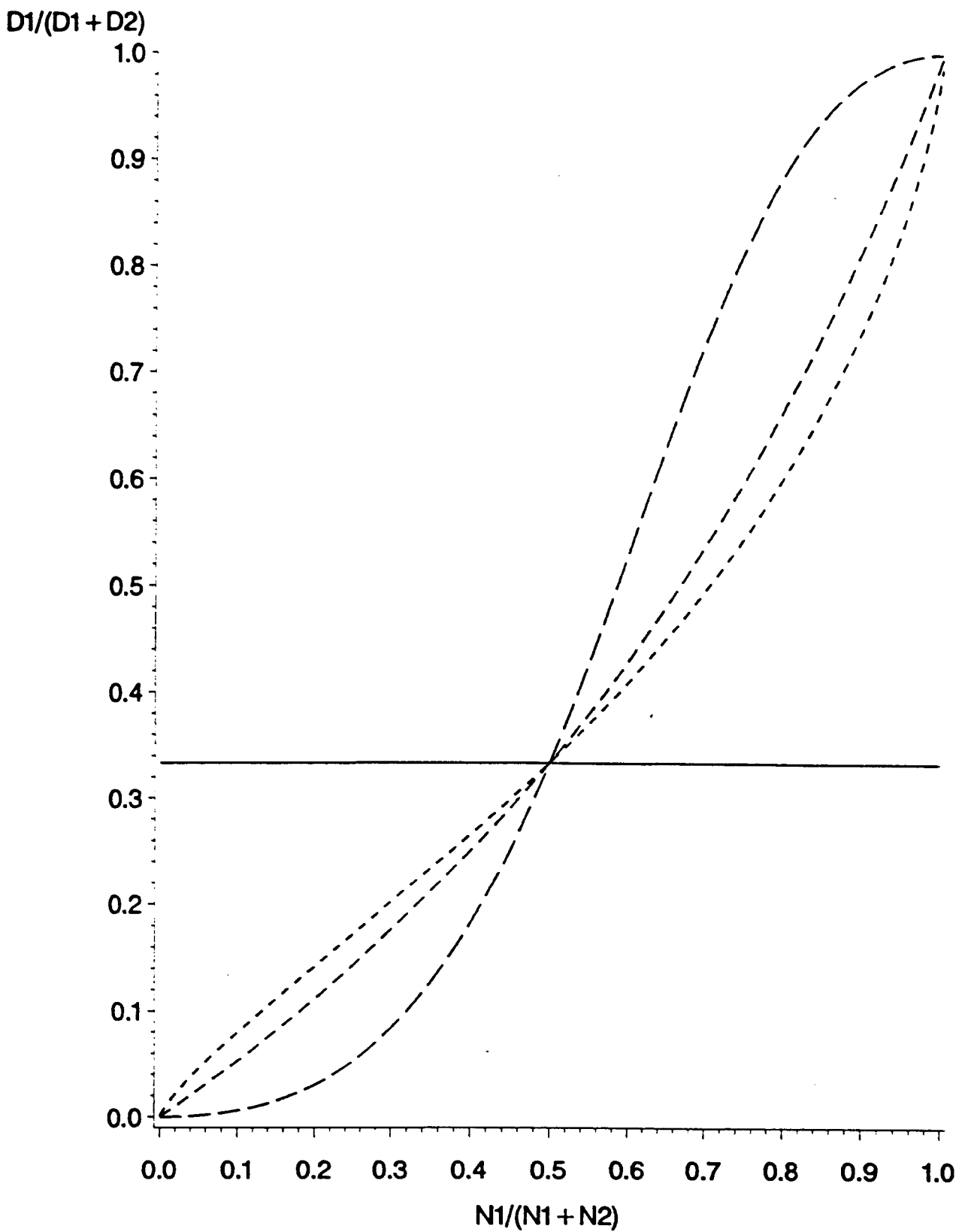
$\text{Biom}(\text{Prey } A) = \text{Biom}(\text{Prey } B) = 1$

Prodator	SUIT _i (A)	SUIT _i (B)	STOC(A)	STOC(B)	Ave. STOC(A)	Ave. STOC(B)	SUIT _p (A)	SUIT _p (B)
1	0.1	0.9	0.1	0.9	0.5	0.5	0.5	0.5
2	0.9	0.1	0.9	0.1				

Situation II

$\text{Biom}(\text{Prey } A) = 2, \text{Biom}(\text{Prey } B) = 1$

Prodator	SUIT _i (A)	SUIT _i (B)	STOC(A)	STOC(B)	Ave. STOC(A)	Ave. STOC(B)	SUIT _p (A)	SUIT _p (B)
1	0.1	0.9	0.182	0.818	0.565	0.435	0.393	0.607
2	0.9	0.1	0.947	0.053				



Deegree of switchina ——— -1.0 - - - - - -0.2 - - - 0.0 - · - · 1.0

Figure 1. Proportion of prey species 1 in the diet versus the proportion of prey species 1 in the environment estimated from $D1/(D1+D2) = (a(1)N(1)^{b+1}) / (a(1)N(1)^{b+1} + a(2)N(2)^{b+1})$ for different values of b (the *degree of switching*). Arbitrary values of $N(1)$, $N(2)$, $a(1)$ and $a(2)$.

SW=-0.6

SW=0

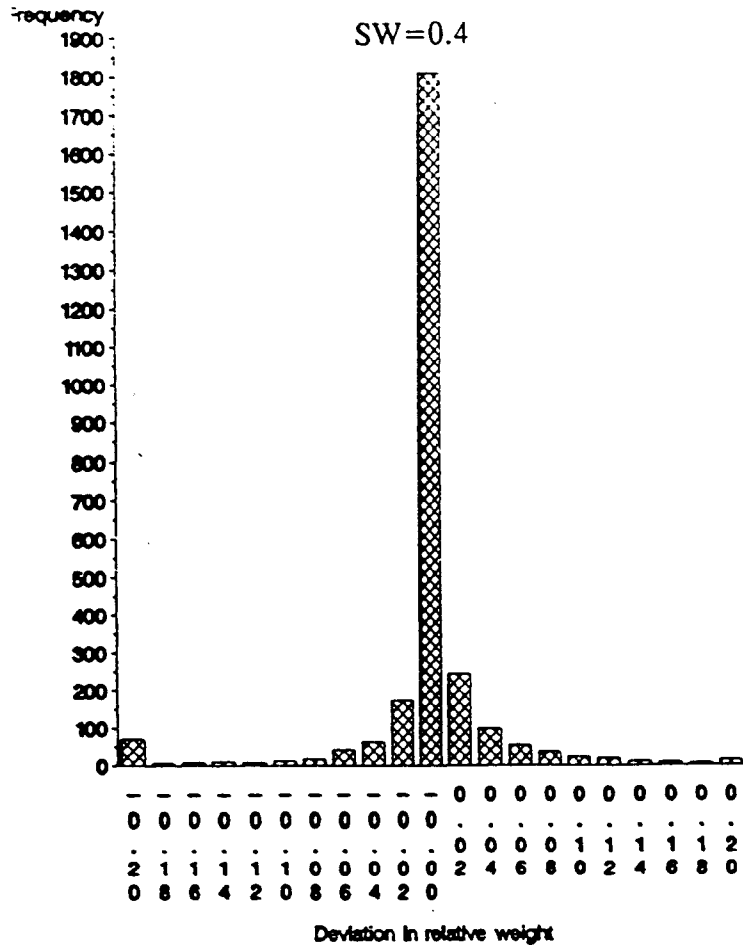
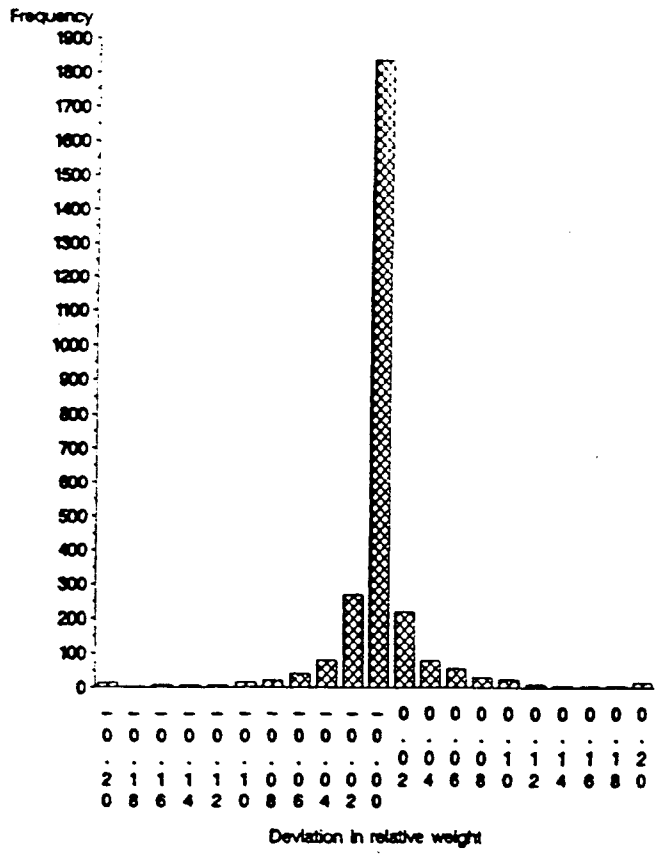
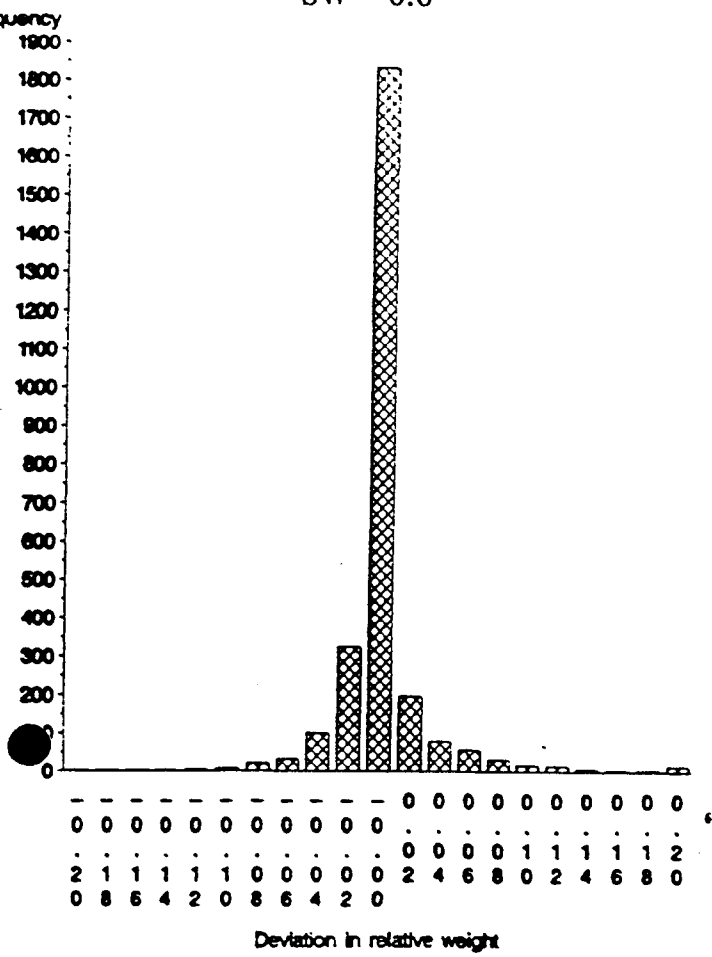
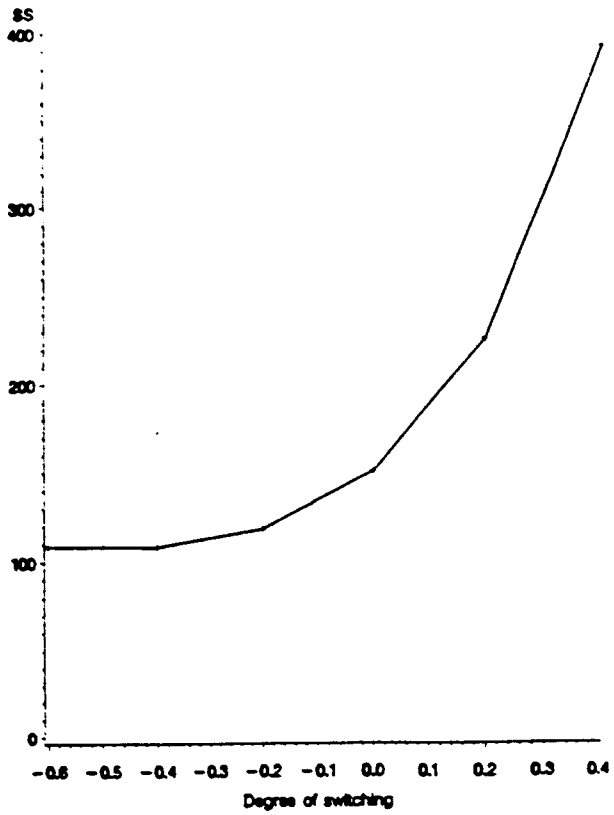
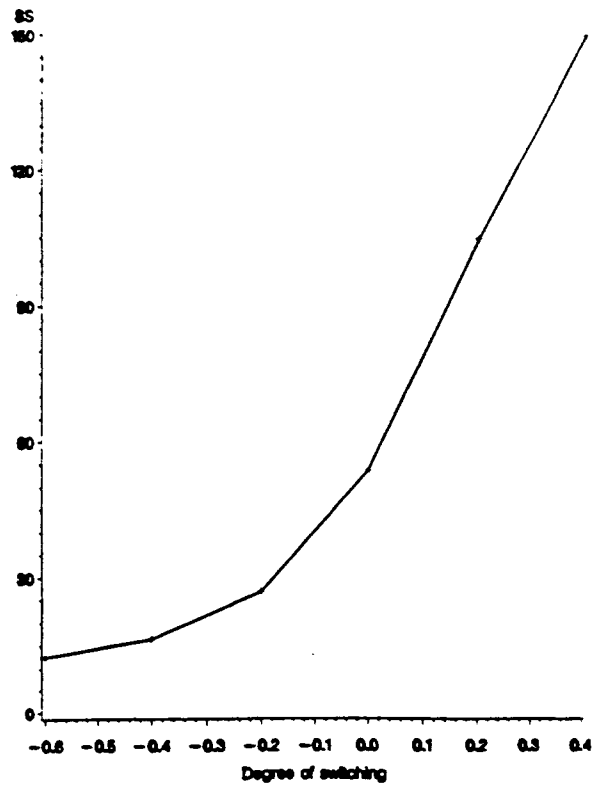


Figure 2. Distribution of differences between observed and estimated food composition at various degrees of switching.

3a: Cod



3b: Whiting



3c: Saithe

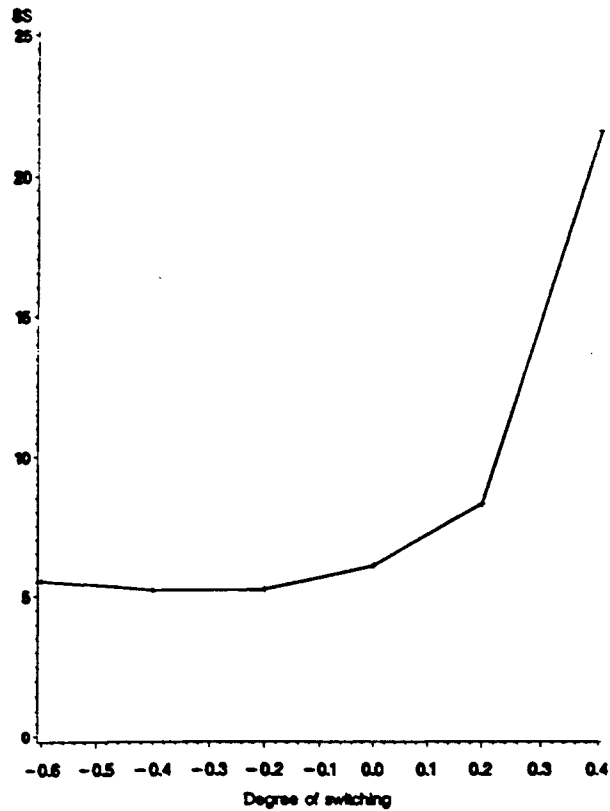


Figure 3a-c. Sum of squared deviations ($SS(j)$) between observed and estimated stomach contents for a) cod, b) whiting, and c) saithe at various values of b (the *degree of switching*). See text for further explanation.

Fig. 4a

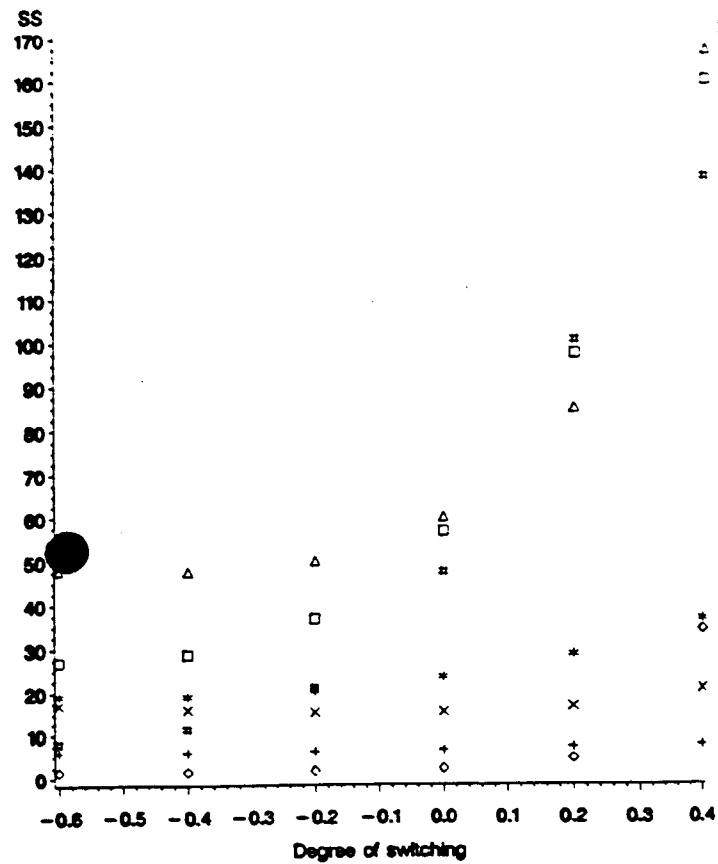
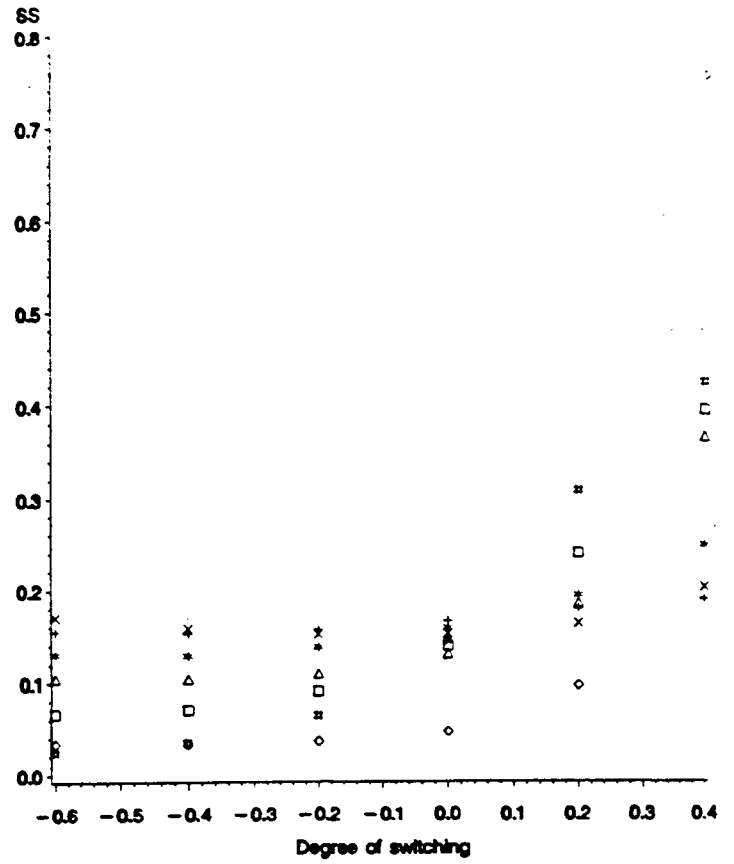


Fig. 4b



Prey species + + + Cod x x x Whiting - - - Haddock
 □ □ □ Herring ○ ○ ○ Sprat △ △ △ N. pout
 ■ ■ ■ Sandeel

Prey species + + + Cod x x x Whiting - - - Haddock
 □ □ □ Herring ○ ○ ○ Sprat △ △ △ N. pout
 ■ ■ ■ Sandeel

Figure 4a,b. Sum of squared deviations ($SS(s)$) between observed and estimated stomach contents for different prey species at various values of b (the *degree of switching*). The values in b) are normalised. See text for further explanation.

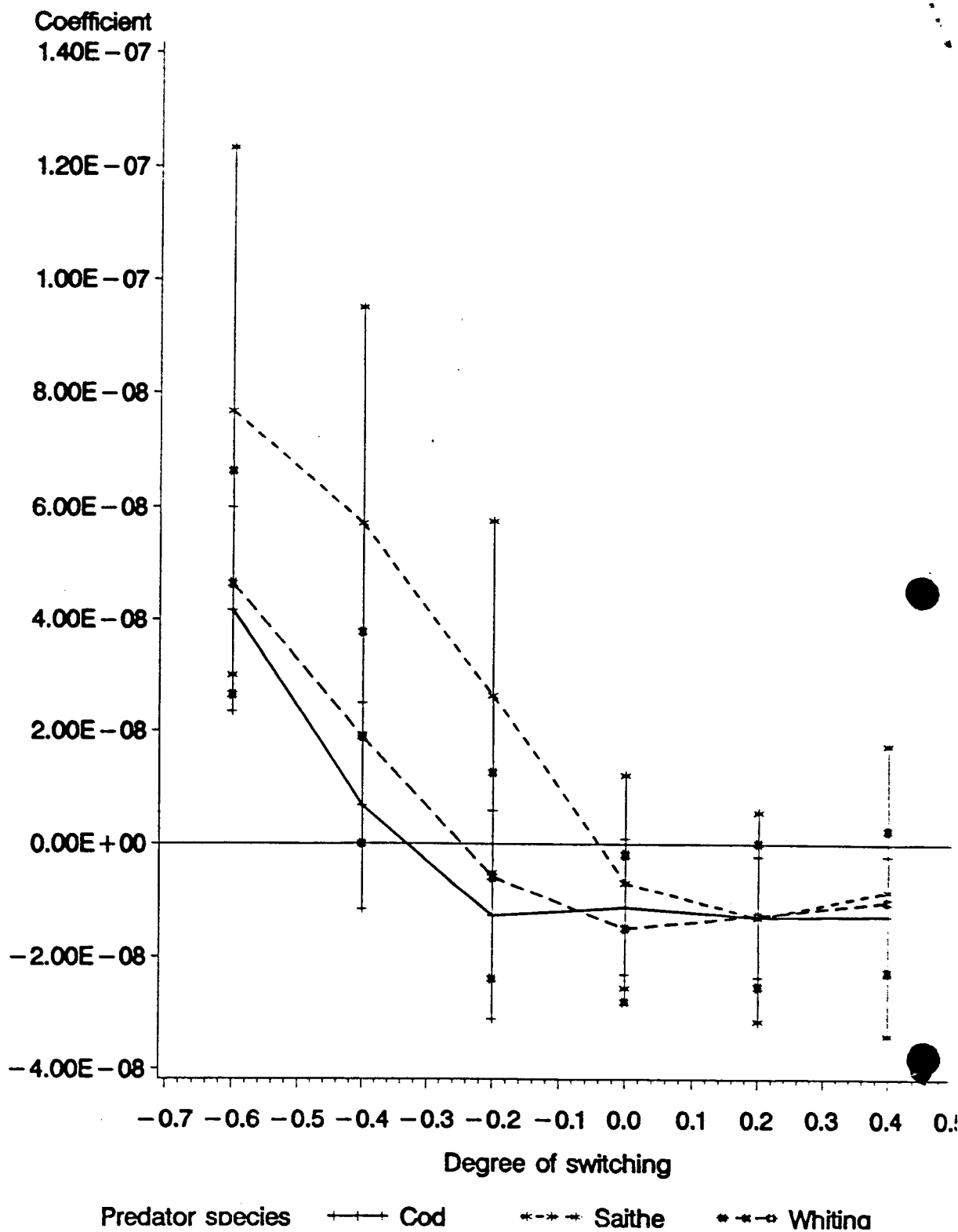


Figure 5. Slope of regression (\pm standard error) of $a(i)$ versus prey biomass plotted against the degree of switching for cod, whiting and saithe. See text for further explanation.