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Diet and prey selection of pikeperch (*Stizostedion lucioperca* (L.)) in Lake Vesijärvi analysed with a logit model

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Diet and prey selection of piscivorous pikeperch (*Stizostedion lucioperca* (L.)) was studied with a multicategory logit model. Statistically significant (log-likelihood statistics, $p < 0.05$) differences were found in the proportions of pikeperch feeding on different fish species at different seasons and at various weights. The differences among the two sampling years were found non-significant. The proportion of pikeperch feeding on perch (*Perca fluviatilis* L.) increased as the abundance of perch increased in the sampling area. It can be concluded that pikeperch are positively selective for perch. The logistic approach was found useful in order to analyse the feeding pattern of pikeperch.

1. Introduction

Predatory fish stock enhancement is widely used to manage fish communities. Reasons for this kind of stock enhancement include improvement of recreational fishing success, greater utilisation of forage fish production as well as food web management in water quality improvement by biomanipulation (Van Densen 1994). Pikeperch (*Stizostedion lucioperca* (L.)) has been managed and stocked in many eutrophic lakes in Europe in order to regulate forage fish stocks (Van Densen & Grimm 1988, Lammens *et al.* 1990, Brabrand & Faafeng 1993, Persson *et al.* 1993). It was first stocked in Lake Vesijärvi in southern Finland in 1984 in order to utilise the forage fish production and to increase the value of the fisheries. Later it was noted that predation of pikeperch could also help to balance the food web since the dense stocks of planktivorous and benthivorous fish were experimentally shown to be key factors to maintain the nutrient recirculation and thereby prevent the recovery of the lake (Horppila & Kairesalo 1990, 1992). When planning predatory fish stock management it is necessary to be able to estimate the predator–prey interaction and consider how the predatory pressure is distributed over different prey species. The present study was conducted in order to find suitable tools to estimate the factors that determine the feeding and prey selection (the influence of the prey species abundance on the pikeperch diet).

Models have been generated to predict the predation rates as a function of prey abundance based on the information of predator behaviour (Taylor 1984, Stephens & Krebs 1986, Walters 1986, Hart 1993). In this approach the feeding of a predator is divided into a sequence of successive events: searching and handling (pursuit, capture and manipulation) the prey between which a predator has to divide the total time available for feeding. With this information models like Holling's (1965) equations can be generated to describe the influence of increase in prey density on the fraction of the prey population eaten per predator per unit time i.e. functional response of predator on prey fish abundance. However, it remains questionable whether enough exact estimates for management purposes can be produced by linking together several assumptions of predator behaviour.

Another approach to analyse species interactions was taken in the present study. Logit model was applied to analyse the diet and prey abundance data of pikeperch. Logit model is a suitable method for analysing data represented in the form of proportions (Collett 1991). Usually the response in a logit model is binary, but the method can be generalised to the multicategory response case (e.g. Hosmer & Lemeshow 1989). Although the logistic approach is based on different origins than the one applying behavioural information the effect of preyfish abundance on predator feeding can also be modeled. The dependence of the foraging pattern on other categorical and continuous variables can be analysed. Additionally, with statistical tests the significance of these independent variables can be estimated.

2. Material and methods

The material of this study consisted of pikeperch stomach samples and samples of preyfish abundance taken from Lake Vesijärvi (southern Finland, 61°N, 25°30´E) in 1991 and 1992. The pikeperch were sampled by trawling and by gillnetting. Of the sampled pikeperch 416 specimens were from the pelagic trawl fishery in the Enonselkä basin of Lake Vesijärvi (Peltonen & Horppila 1992, Horppila & Peltonen 1994, Horppila *et al.* 1996). The trawls ranged from 8 to 12 meters in depth and had a cod end mesh size of 5 or 8 mm (bar). The trawl catches were also sampled in order to estimate the species composition of the trawling area by taking a sample of 2% or a minimum of 30 kg. In the year 1991, 83 catches were sampled and in 1992, 60 catches, respectively. The total catch was 268 tonnes in 1991 and 204 tonnes in 1992. The catch consisted mainly of roach (*Rutilus rutilus* (L.)), smelt (*Osmerus eperlanus* (L.)) and perch (*Perca fluviatilis* L.). Trawling was performed during the summer (June–August). In spring and autumn 255 pikeperch were collected with gillnetting. Hence, from the trawl catches and by gillnetting altogether 671 pikeperch ranging in weight from 41 to 3 330 g were collected during 1991–1992. The sampled pikeperch were frozen for later analysis. In the laboratory the pikeperch were weighed and the content of their stomach was analysed.

In order to analyse feeding of pikeperch on definite prey the pikeperch were classified according to the prey species they had eaten. The prey species categories were bleak *(Alburnus alburnus* (L.)), roach, smelt and perch. Another class consisted of the pikeperch that contained prey fish of several species. The pikeperch that did not contain any identifiable prey items or the ones that had regurgitated while they were trawled were not included. Neither were the five pikeperch included that contained other species than bleak, roach, smelt or perch.

The fractions of pikeperch feeding on different prey species were modeled using a logit model (Hosmer & Lemeshow 1989, Collett 1991). The response variable of the logit model had five possible categories (1 = several species, 2 = bleak, 3 = roach, 4 = perch and 5 = smelt). In the logit model the probability that a randomly chosen pikeperch falls into the diet category j is denoted by $\pi_j(x)$ where j = 1, 2, 3, 4 or 5. The fifth response variable class was used as the reference class and the logit model was thus:

$$\log\left(\frac{\pi_j(x)}{\pi_5(x)}\right) = \alpha_j + \beta_j x,$$

where $j = 1, \dots, 4$. The α_i are the intercept terms and vectors β_i contain the coefficients of the explaining factors. The vector $\boldsymbol{x}$ identifies the combination of values of the explaining factors. The model parameters were estimated using the programme Polychotomous Stepwise Logistic Regression (Moran *et al.* 1990) of the BMDP statistical software.

Two different logit models were fitted. The first one was fitted in order to analyse seasonal and pikeperch size dependent feeding patterns. Hence, the explaining factors were year (1991 or 1992), season of the year (May–June, July–August or September–October) and the weight of the pikeperch. The variable weight was transformed to logarithms (ln, natural logarithm) in order to eliminate the dominant effect of a few large specimens on the regression model.

The fit of a logit model containing the weight as explaining variable cannot be tested with the likelihood ratio test statistics (Collett 1991), and unfortunately, neither is the Hosmer-Lemeshow test (Hosmer & Lemeshow 1989) available in the polychotomous response variable situation. Hence, in order to study the fit of the first model described above, a modified model version with weight classified in three categories (< 500 g, 500–1 000 g, and > 1 000 g) was also fitted and the likelihood-ratio test statistics (deviance) was applied. Good fit is achieved if deviance is around its degrees of freedom (and thus, a large *p*-value is obtained). A good fit is, of course, conditional to the resolutive power provided by the sample size. With small samples substantial deviations may remain hidden while with large ones even negligible deviations indicate lack-of-fit.

The second model was fitted in order to estimate the effect of prey availability on the diet composition. The three most abundant diet categories (perch, smelt and roach) were included as response variable categories. Bleak was not included because only few pikeperch among the trawl samples contained bleak. The species composition of the daily trawl catches was assumed to indicate the prey fish availability. Prey fish abundance was only available from the trawl fishery in June–August and therefore independent variable season was not included, but year (1991 or 1992) and pikeperch weight (ln-transformed) were included. Hence, the biomass fractions of perch, smelt and roach in the catches were included as independent variables.

Difference of deviances was used to test the significance of the independent variables. Within a variable of a multicategory logit model there may be several parameter estimates, one for each response category. The significance of the parameters of the model was tested with Wald's test which is based on the confidence limits of the odds ratio (odds ratio = $e^{\text{parameter estimate}}$). The value one indicates the "no effect" situation. If odds ratio > 1 (< 1), the proportion of the corresponding response variable class increases (decreases) compared to the reference class (smelt) proportion. A parameter is different from zero ($p < 0.05$) if value 1 is not included in the 95% confidence limits of the odds ratio.

3. Results

The classified data included 249 pikeperch individuals. Most of the pikeperch did belong to the diet classes smelt and perch (Table 1). The analysis of the five-response category model (1st model) indicates that the independent variables season and weight (ln-transformed) were significant (difference of deviances, *p*-values 0.0036 and 0.0053, respectively) whereas the difference between years was non-significant ($p = 0.31$). Therefore, year as an independent variable was not included in the final model. The corresponding categorical weight model (three weight categories) where also season was included had a deviance 17.425 ($df = 16$) indicating a good fit. Although season as an independent variable was found significant, the individual coefficients for season are not very clear because, of the eight coefficients, only the coefficient of the response category bleak in September–October was found significant (Table 2). However, the overall fraction of pikeperch in the diet category bleak is relatively small and bleak is only little eaten except in the September–October season (Fig. 1).

Wald's test indicates that pikeperch weight is a significant ($p < 0.05$) factor when modeling feeding on roach, perch and several species, but not in the response category bleak (Table 2). The proportions of the diet categories perch, roach and several species increase as the pikeperch grow larger but the proportions of diet category smelt decreases concomitantly (Fig. 1).

Year effect was not significant (likelihood-ratio-test, $p = 0.33$) also in the three-response category model (2nd model) which included the prey-fish abundance (proportion of each species in a trawl catch), neither were the proportions of smelt

Table 1. The numbers of pikeperch in each prey species category in 1991 and 1992. The pikeperch size classes are < 500 g, 500–1 000 g and > 1 000 g.

Year	Species category	May–June			July–August			September–October		
		< 500	500–1 000	>1 000	< 500	500–1 000	>1 000	< 500	500–1 000	>1 000
1991	Several	6	0	1	1	2	1	1	1	0
1991	Bleak	0	0	0	0	0	0	2	7	0
1991	Roach	0	1	1	1	1	0	0	5	0
1991	Perch	0	0	1	16	17	1	2	7	5
1991	Smelt	14	0	1	30	4	0	2	6	1
1992	Several	2	3	0	2	1	1	0	2	4
1992	Bleak	0	1	0	2	1	0	0	1	1
1992	Roach	1	3	0	0	0	0	0	0	2
1992	Perch	6	13	1	8	5	0	2	4	7
1992	Smelt	2	4	3	7	3	0	5	6	7

and roach in the trawl catches significant factors (p-values 0.84 and 0.74, respectively). After omitting these factors the model included the proportion of perch (p = 0.0193) and ln-weight of pikeperch (p = 0.0102) as independent variables (Table 3). As in the five-category model, it can be seen that the small pikeperch mainly feed on smelt while the large ones feed on perch and roach (Fig. 2). The proportion of pikeperch feeding on perch increases and the proportion feeding on roach decreases sharply as the proportion of perch in the trawl catches increases. The respective decrease in the proportion of smelt as a function of perch abundance in the catches is not as sharp though

Table 2. The parameter estimates of the logit model (1st model). The symbols for the parameters refer to the presentation of the model. The prey category smelt is used as the reference. The parameter estimates are given with respective standard errors, odds ratios and confidence limits**.** A coefficient is different from zero when the value 1 is not included in the confidence limits. Significant parameters are in boldface. The effect of the variable season is parametrised using the May–June season as the reference. Thus, the coefficient $\beta_{i(\mathrm{SEASON2})}$ is the difference in logits between July–August and May–June, whereas $\beta_{i(\mathrm{SEASON3})}$ is the difference between September–October and May–June. $\beta_{i(\mathrm{WEIGHT})}$ is the coefficient of the ln-transformed predator weight (in grams).

Outcome	Parameter	Estimate	*S.E.*	Odds ratio	95% *c.l.* of odds ratio	
					Lower	Upper
Several	α_1	– 5.036	1.93	–	–	–
	$\beta_{1(\mathrm{SEASON2})}$	– 0.7773	0.539	0.46	0.16	1.3
	$\beta_{1(\mathrm{SEASON3})}$	– 0.9064	0.562	0.40	0.13	1.2
	$\beta_{1(\mathrm{WEIGHT})}$	**0.7100**	0.303	2.0	1.1	3.7
Bleak	α_2	– 3.637	2.27	–	–	–
	$\beta_{2(\mathrm{SEASON2})}$	0.5150	1.19	1.7	0.16	17
	$\beta_{2(\mathrm{SEASON3})}$	**2.202**	1.10	9.0	1.1	78
	$\beta_{2(\mathrm{WEIGHT})}$	0.07796	0.343	1.1	0.55	2.1
Roach	α_3	– 6.552	2.70	–	–	–
	$\beta_{3(\mathrm{SEASON2})}$	– 1.422	0.873	0.24	0.043	1.3
	$\beta_{3(\mathrm{SEASON3})}$	– 0.3987	0.656	0.67	0.19	2.4
	$b_{3(\mathrm{WEIGHT})}$	**0.8388**	0.418	2.3	1.0	5.3
Perch	α_4	– 3.722	1.22	–	–	–
	$\beta_{4(\mathrm{SEASON2})}$	0.3905	0.38	1.5	0.70	3.1
	$\beta_{4(\mathrm{SEASON3})}$	– 0.1983	0.422	0.82	0.36	1.9
	$\beta_{4(\mathrm{WEIGHT})}$	**0.5907**	0.194	1.8	1.2	2.6

Table 3. The parameter estimates of the logit model (2nd model) with respective standard errors, odds ratios and confidence limits. The symbols for the parameters refer to the presentation of the logit model. The prey category smelt is used as the reference. $\beta_{i(\mathrm{WEIGHT})}$ is the coefficient of the ln-transformed predator weight (in grams) and $\beta_{i(\mathrm{PERCH})}$ is the coefficient of the proportion of perch of the total trawl catch. A coefficient is different from zero when the value 1 is not included in the confidence limits. Significant parameters are in boldface.

Outcome	Parameter	Estimate	*S.E.*	Odds ratio	95% *c.l.* of odds ratio	
					Lower	Upper
Roach	α_1	– 7.091	4.27			
	$\beta_{1(\mathrm{WEIGHT})}$	0.9825	0.627	2.7	0.78	9.2
	$\beta_{1(\mathrm{PERCH})}$	– 9.632	8.18	0.000066	0.67×10^{-11}	0.64×10^{3}
Perch	α_2	– 4.311	1.58			
	$\beta_{2(\mathrm{WEIGHT})}$	**0.6466**	0.243	1.9	1.2	3.1
	$\beta_{2(\mathrm{PERCH})}$	**4.187**	2.03	66	1.2	3600

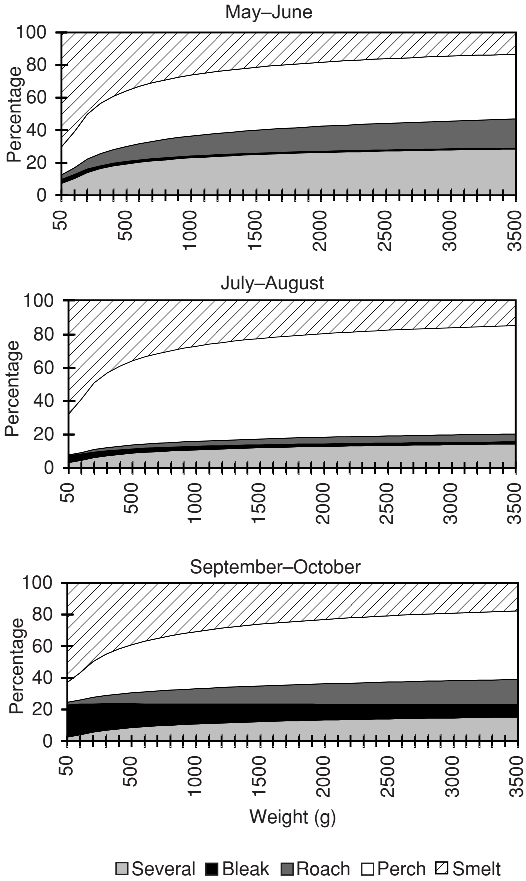

Fig. 1. Estimates of the proportion (based on logit model) of pikeperch in different prey categories during the three seasons as a function of pikeperch size.

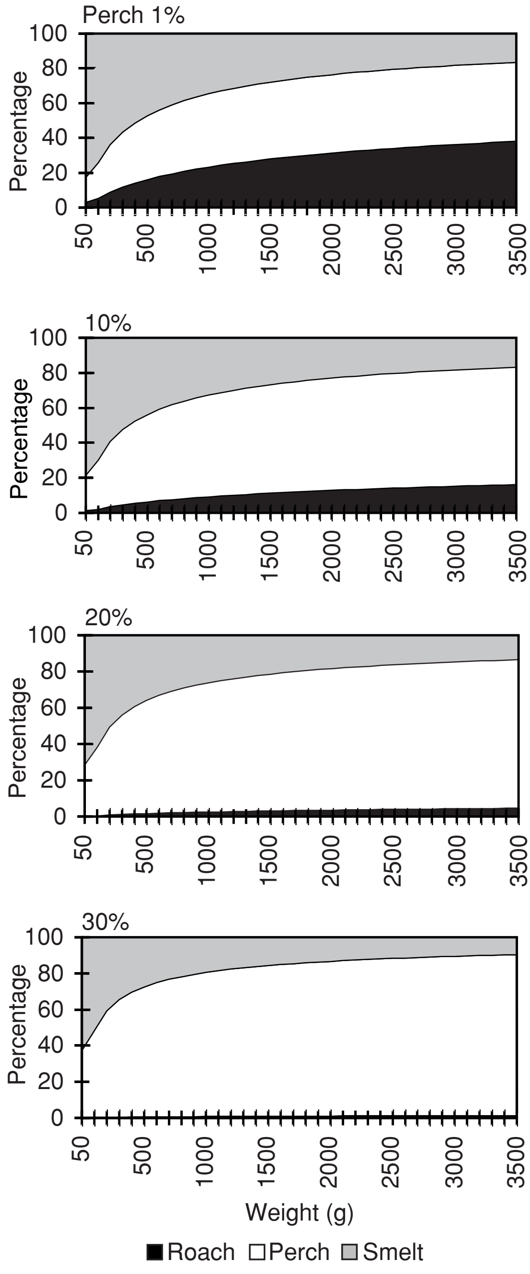

Fig. 2. Estimates of the proportion (based on logit model) of pikeperch feeding on smelt, roach and perch as a function of predator size and the percentage of perch in the trawl catches.

clear anyway. The confidence limits of odds ratios in diet category roach indicate that the parameter estimates are non-significant (Wald's test, $p > 0.05$, Table 3). On the other hand, the parameter estimates are significant in diet category perch.

4. Discussion

The results indicate that the multicategory logit model is a suitable tool to analyse feeding of predatory fish. With the statistical analysis underlying feeding patterns were found from the data sets of pikeperch diet and prey abundance. The application of the analysis is appropriate if the predator feeds on relatively few prey items and generally takes items of only one category at a time. The analysis can be used to find the factors that have the largest effect on the feeding of a predator and those that are redundant. Thereby the studies of trophic interactions can be further developed and sampling schemes can be enhanced.

The logit model can be applied to analyse the influence of abundance of different prey species on the diet of a predator. The logistic approach also accommodates the gradual shift of the predator from one prey species to another as the abundance of a prey changes. It is more realistic to assume this kind of shift than to assume that a predator abruptly changes its feeding as the density of a prey population changes. This is because there is always some variance included in prey selection i.e. a predator catches not only the most profitable but also energetically some less profitable items (Townsend & Winfield 1985, Stephens & Krebs 1986).

Application of stomach contents data in order to estimate prey selection has been criticized because it is difficult to take representative samples of the forage fish abundance and stomach contents of the predator. In the present study the trawl selectivity may induce underestimates of the abundance of especially young-of-the-year smelt. The trawl selectivity of roach or perch in not as large a problem because they are larger than smelt and their pelagic populations are relatively homogenous in size structure.

In foraging studies it also remains questionable whether the predator has been feeding in the same location where the sample of prey abundance is taken. Although perch would not occur in trawl catches, the model predicts some feeding on perch. Therefore, the estimates given by the logistic model in which perch abundance is included are only local, i.e. extrapolation beyond the observed perch percentages (1–58% of the daily trawl catches) may not be appropriate. The wide confidence limits of the coefficients in this model where preyfish abundance was included (the second model) may at least partly be explained by the small number of specimens in diet category roach ($n = 7$) compared with the numbers falling in diet categories perch ($n = 66$) and smelt ($n = 58$).

Another reason that has the potential to bias the results of a feeding study is that a predator may feed while in trawl during the fishing. It is obvious that in this study the pikeperch were not substantially feeding while in the trawl because the abundance of roach or smelt in the trawl catches did not show in the feeding of pikeperch like the abundance of perch.

In the five-category logit model the diet category several species also contains some specimens that had eaten perch, roach, smelt and bleak. Therefore, it slightly underestimates the fractions of pikeperch feeding on these species. If a larger data set had been available it would have been possible to further analyse the structure of the fifth response category.

The influence of the pikeperch weight on diet can be largely explained by the morphology of pikeperch and the available prey. Especially, the small pikeperch may not be able to eat the large individuals of deep-bodied prey species such as roach and perch but they can forage on the more elongated species as smelt and bleak. Because, normally there are only few large pikeperch in a population, the deep-bodied prey fish may avoid predation by growing to large sizes i.e. escape to a size refuge (Van Densen & Grimm 1988, Hambright *et al.* 1991, Van Densen 1994). Although roach dominates the fish assemblage in the pelagic zone, the small roach that would be suitable food for pikeperch are hardly at all found in the pelagic area (Peltonen & Horppila 1992, Horppila & Peltonen 1994, Malinen & Peltonen 1996) and practically all the roach in the pelagic areas are > 10 cm in total length. In several lakes the large roach (> 100–150 mm) have been unaffected by the predation of pikeperch while the smaller ones have been clearly reduced and restricted to the littoral habitats (Lammens *et al.*, 1990, Brabrand & Faafeng, 1993, Persson *et al.* 1993). In Lake Vesijärvi the predation of pikeperch on roach may not be sufficient to regulate the roach population. However, pikeperch may have induced behavioural changes in roach so that the young age groups are more delimited to the shallow areas. Pikeperch may thereby limit the feeding rates of roach in the pelagic areas and thereby influence on the food-web dynamics.

The perch in the pelagic zone are generally 70–120 mm in length. Hence, they may be more suitable prey items than roach. The results suggest that pikeperch are positively selective for perch because the fraction of pikeperch feeding on perch increases as the abundance of perch increases. Because of this kind of response pikeperch may have a balancing effect on the perch stock. However, a balancing effect may only exist if the functional response curve is sigmoid (Holling 1965, Taylor 1984) resembling a curve produced by a logit model. Even then a predator may have a balancing effect only near the equilibrium density, but as the prey populations are dense any change in the predatory behaviour cannot be effective (Taylor 1984). The predation of pikeperch has been observed to exhaust a perch stock (Lammens *et al.* 1990), but on the other hand it has been observed to shift the dominance from roach to the dominance of perch (Brabrand & Faafeng 1993).

There are only few smelt larger than 120 mm in the research area which makes smelt an ideal prey for especially the small pikeperch. Smelt may coexist with pikeperch in spite of heavy predation because it compensates for the predation by maturing at a young age (Lammens *et al.* 1992). In Lake Vesijärvi smelt has a very high production-biomass ratio (Horppila *et al.* 1996) and this acts as a stabilising factor preventing the collapse of the smelt stock.

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