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Analysis of otter (*Lutra lutra*) spraints: Part 1: Comparison of methods to estimate prey proportions; Part 2: Estimation of the size of prey fish

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(With 1 figure in the text)

Contents

Part 1: Comparison of methods to estimate prey proportions

The accuracy of five different methods used in spraint analysis for estimating prey proportions is tested through a feeding experiment with three otters in captivity. Estimated prey proportions are compared to the actual diet of the otters. The results of analysing 362 spraints and the time budget indicated a score-bulk estimate to be the most appropriate method of estimating prey proportions in otter diet. However, all five methods showed rather high similarities to the actual diet and it is concluded that dietary studies using different methods can be compared in broad outlines. The relations between the methods are confirmed in the analysis of 978 spraints, collected in the field.

Introduction

Numbers of the European otter (*Lutra lutra* L.) have declined throughout Europe over the past

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three decades. Many studies of the dietary habits of otters have been made in the last 25 years with a view to increasing the general knowledge of otter ecology (review in Jenkins, Walker & McCowan, 1979; Mason & MacDonald, 1986; Adrián & Delibes, 1987; Callejo, 1988; Taylor *et al.*, 1988; Kyne, Smal & Fairley, 1989; Kemenes & Nechay, 1990; Beja, 1991; Libois & Rosoux, 1991; Hansen & Jacobsen, In prep.).

Dietary studies of otters have been made by direct observation (Kruuk, Conroy & Moorhouse, 1987) and by stomach content analysis (Fairley, 1972; Erlinge & Jensen, 1981; Skarén, 1992; Jacobsen & Hansen, In prep.), but most have been based on spraint (faeces) analysis where there is a large renewable source of material. In spraint analysis, it is not only important to determine what kinds of prey are represented, but also the proportion of each prey category.

Several methods exist for estimating the proportions of each prey category in spraints. The relative frequency of occurrence method (Erlinge, 1967) is the most commonly used; this method has previously been tested (Erlinge, 1968) and showed reasonable agreement between food given to otters and spraint analysis. Greater accuracy in the estimation of proportions of prey can be obtained through other more quantitative methods (Jenkins *et al.*, 1979; Wise, Linn & Kennedy, 1981), but these are more time consuming.

This study aimed to compare the most commonly used methods in estimating proportions of prey, and to find whether any of the methods give a better estimate of the actual diet than any other. The aim was fulfilled through a feeding experiment with otters under semi-natural conditions. Further, the methods of estimating proportions of prey were applied to field-collected spraints in order to determine whether the experiences from the feeding test can be transferred to natural conditions.

Materials and methods

The feeding experiment was done at Otter-Zentrum, Hankensbüttel, Germany, where the individual otters were held in separate enclosures under semi-natural conditions. Each enclosure (*c.* 250 m^2) contained natural vegetation and a pond (*c.* 50 m^2) with aquatic plants and overgrown banks. The otters had some fixed sprainting sites where most spraints were deposited.

The experiment included 3 adult otters, 2 females (A, B) and a male (C), and lasted 6 days. The enclosures were cleaned of old spraints prior to feeding. To avoid the use of food markers, the otters were fed chicken for 2 days prior to and for 3 days after the experiment. Normal rations were 1000 g of food per day, but in order to ensure that all test material was eaten, the animals were offered only 700–900 g once a day.

The test feed consisted mostly of fish, because this is the predominant prey item of otters in northern Europe (review in Mason & MacDonald, 1986; Hansen & Jacobsen, In prep.; Jacobsen & Hansen, In prep.). A few frogs (*Rana temporaria*) were also included because they are frequently taken by otters (Jenkins & Harper, 1980; Fairley, 1984; Adrian & Delibes, 1987; Weber, 1990; Hansen & Jacobsen, In prep.; Jacobsen & Hansen, In prep.). The 3 otters were given different diets corresponding to the prey compositions in different freshwater habitats in Denmark. These were a mixed diet (otter A), a diet consisting predominantly of cyprinids (Cyprinidae) (otter B), or trout (*Salmo trutta*) (otter C) (Table I). Each species of fish was represented by different sizes, corresponding to the size range of fish found in Danish streams. The lengths and weights of all prey items were measured before being given to the otters. Table I shows both the number of specimens and the biomass of each prey category; cyprinids and trout accounted for a high proportion of the total diet, sticklebacks and frogs only made up very small proportions. A total of 13·257 kg of fish ($n = 234$) was used in the experiment.

The otters occasionally left some of their food on the ground; this was removed and excluded from the calculations. All spraints were collected once a day during and for 2 days after the experiment.

TABLE I

The diet for each otter A, B, and C individually and the pooled diet for all three otters (total). The figures in the first column relate to biomass, the second, number of specimen. The fish include: cyprinids[1], roach, bream; percids[2], perch, ruffe, pike-perch; trout, eel, and stickleback. The frogs are the common frog

	Otter A:		Otter B:		Otter C:		Total (A, B, C)	
Diet	grams	no.	grams	no.	grams	no.	grams	no.
Cyprinids[1]	1770	37	3509	36	186	4	5465	77
Percids[2]	583	34	208	16	106	3	897	53
Trout	1273	12	0	0	3459	25	4732	37
Eel	775	19	745	14	541	7	2061	40
Stickleback	23	11	6	3	30	12	59	26
Frog	32	4	0	0	11	1	43	5

A total of 362 spraints with 678 occurrences of prey were analysed.

It can be a problem in spraint analysis to separate spraints from each other, when they are placed in a pile. There are also general differences in spraint size; some spraints appear only as small droppings, whereas other spraints are much larger deposits from bowel evacuations (Watson, 1978; Veen, 1986).

In this experiment, the spraints from the three otters differed in number and size (dry weight)—female otter A—114 spraints, 0·46 g mean dw; female otter B—112 spraints, 0·70 g mean dw, and the male otter C-131 spraints, 0·39 g mean dw. This difference occurred because males use spraints for marking to a higher degree and therefore deposit more spraints of a smaller size than females (Green, Green & Jefferies, 1984; Hillegaart, Östman & Sandegren, 1985).

Identification and estimation of proportions of food items

Otter spraints contain undigested prey remains. Fish can be identified using vertebrae, otoliths, jawbones, pharyngeal bones, operculae, and scales, and frogs are easily identified by their characteristic bones. A reference collection (including photos (Hansen & Jacobsen, 1992)) was made of all hard parts of the fish species in question to supplement the literature (Maitland, 1972; Webb, 1976; Härkönen, 1986) on identification.

Identification of cyprinids and percids (Percidae) to species level can only be made if otoliths, pharyngeal bones or operculae were present. Because this was only possible for a limited number of spraints, it was necessary to pool all roach (*Rutilus rutilus*) and bream (*Abramis brama*) as cyprinids, and all perch (*Perca fluviatilis*), ruffe (*Gymnocephalus cernuus*) and pike-perch (*Lucioperca lucioperca*) as percids in order to allow a comparison to the actual diet. Because the remaining families were represented by only one species, there were no problems in identifying to species level.

Spraints were allowed to stand in a detergent solution for 7 days, were washed out through a 1 mm sieve, and the remains analysed in a petri dish with water. After analysis, the spraints were dried (60 °C, 48 h) and weighed.

The 5 methods tested in this experiment differ according to time budget and the degree of detail in the assessment of each prey category in the single spraint. All methods were applied to the total amount of spraints.

Method Ia—frequency of occurrence

The prey categories were noted for each spraint. The number of occurrences of a prey category was expressed as a proportion (%) of the total number of occurrences of all prey categories in a sample, the sum of the frequencies being 100 (Erlinge, 1967). This is the simplest and quickest way of analysing spraints.

Method Ib—frequency of occurrence × dry weight (DW)

As above, but all values were multiplied by the dry weight of the spraint and then expressed as percentage of the total number of occurrences of all items in a sample, the sum of the frequencies being 100. This is a way of overcoming the problems of differences in spraint size (dry weight), but has not been used in otter studies to our knowledge.

Method II—score-bulk estimate

The proportion of each prey category was estimated visually. Each prey category represented was given a score from 1–10, so that the total score for one spraint is 10. The scores for each prey category were then multiplied by the dry weight of the spraint and the resulting figures were summed for each prey category and expressed as a percentage (Wise *et al.*, 1981).

Method III—range-bulk estimate

The contribution of each prey category to the total bulk in a spraint was estimated visually into 1 of 4 equal ranges (0–25%, 26–50%, 51–75%, and 76–100%) (Jenkins *et al.*, 1979). These ranges were used by Jenkins *et al.* (1979) to illustrate graphically not only the frequency of each prey category, but also the abundance of the prey category in the spraint. Because ranges could not directly be compared to the other methods, which all were expressed as exact figures, the mean values of the ranges were used to calculate a comparable result. The total value of a spraint would therefore not necessarily give 100%. The mean range values were multiplied by the dry weight, summed for each prey category and expressed as a percentage.

Method IV—area counting

The spraint was spread out in a petri dish marked into 24 equal areas and the number of areas in which a certain prey category was present was counted. The values for each prey category in all spraints were summed and expressed as a percentage. This is the most time-consuming of all the methods, since it takes time to search for every prey category in all areas. This method is an attempt to quantify the proportion of prey categories in a spraint in an objective way, but has not been applied to otter spraint analysis to our knowledge.

In addition to the methods of estimating prey proportions tested in this study, a few other methods have been used in otter spraint analysis, attempting to calculate different correction factors to convert volume or weight of the hard parts in the spraints to actual biomass of prey (van der Zee, 1981; Bekker & Nolet, 1990; Libois & Rosoux, 1991). Besides being very laborious, conversion factors are considered problematic (Kyne *et al.*, 1989; Reynolds & Aebischer, 1991) and were not tested in our study.

The biomass of each prey category offered to the otters was used to calculate the relative proportions of the prey categories in the diet. The results of the spraint analysis were tested against these relative proportions and this was done for the results of the 3 otters pooled (total), as well as separately (Table II).

Statistics

The Kendall Rank-Order Correlation Coefficient, τ, (Huhta, 1979; Siegel & Castellan, 1988) was calculated to test the efficiency of the 5 different spraint analysis methods. The τ-value was tested to show if there was a significant correlation between the sets of data ($P < 0{\cdot}05$ or $P < 0{\cdot}01$). This was done for sets of data from the otters both individually and pooled.

TABLE II

*The relative proportions (biomass) of prey categories in the actual diets and estimated prey proportions, by use of five different methods. (For further details see methods section). The results are shown for the otters A, B, and C separately and pooled (total). [1]Roach and bream; [2]perch, ruffe, and pikeperch. *) Kendalls τ showed significant correlation ($P < 0.05$) between the spraint analysis and the actual diet. **) Kendalls τ showed significant correlation ($P < 0.01$)*

	The actual diet offered to the otters (%)	Method Ia, frequency of occurrence (%)	Method Ib, frequency of occurrence (× DW) (%)	Method II, bulk-score estimate (%)	Method III, rank-bulk estimate (%)	Method IV, square-counting (%)
Otter A:		*)	**)	**)	**)	
Cyprinids[1]	39·7	31·7	30·7	42·0	39·3	29·2
Percids[2]	13·1	19·3	17·3	12·6	13·5	15·9
Trout	28·6	24·8	26·4	21·3	22·1	41·3
Eel	17·4	18·7	19·7	20·4	20·2	11·0
Stickleback	0·5	3·3	2·9	1·6	2·4	1·6
Frog	0·7	2·1	3·1	2·0	2·5	1·0
Otter B:		**)	**)	**)	**)	*)
Cyprinids[1]	78·5	46·7	45·1	69·8	64·1	64·5
Percids[2]	4·7	23·8	21·0	13·0	15·2	21·0
Trout	0	1·7	1·7	0·5	0·8	0·8
Eel	16·7	25·0	28·9	16·0	18·3	12·6
Stickleback	0·1	2·9	3·4	0·8	1·6	1·0
Otter C:		*)	*)	*)	*)	
Cyprinid[1]	4·3	13·2	15·5	10·0	10·8	10·4
Percids[2]	2·5	1·6	0·3	0·1	0·1	0·3
Trout	79·8	61·6	53·3	64·3	61·3	71·5
Eel	12·5	18·4	26·6	22·3	24·6	13·8
Stickleback	0·7	3·7	2·8	1·7	1·7	2·0
Frog	0·3	1·6	1·4	1·7	1·6	2·0
Total:		**)	**)	**)	**)	**)
Cyprinids	41·2	31·76	33·4	44·9	38·4	40·9
Percids	6·8	16·26	15·3	9·3	9·4	16·1
Trout	35·7	26·64	21·9	24·5	29·3	26·3
Eel	15·6	20·70	24·7	19·0	21·1	13·9
Stickleback	0·5	3·28	3·1	1·3	1·8	1·8
Frog	0·3	1·32	1·5	1·1	0·9	1·0

Renkonens Index of Similarity (Krebs, 1989) was used to illustrate the degree of similarity between relative frequencies of prey categories in the food offered to the otters and the frequencies of prey categories in the corresponding spraint analysis. The index is calculated as:

$$P = \sum \text{minimum}\,(p_{1i}, p_{2i})$$

where P = percentage similarity between sample 1 and 2
p_{1i} = percentage of species i in community sample 1
p_{2i} = percentage of species i in community sample 2

The Index describes the amount of overlap between relative proportions of diet; total overlap will give an index of 100%. This index was also used to illustrate the similarity between the different methods both for the experimental data and field data.

TABLE III

Renkonens Index of Similarity between food offered to the otters (in total) and the results from the methods used in the spraint analysis. (For further details see methods section)

	Method Ia, frequency of occurrence	Method Ib, frequency of occurrence (× DW)	Method II, bulk-score estimate	Method III, range-score estimate	Method IV, area-counting
Index of Similarity	81·5%	78·4%	88·8%	90·8%	88·6%

Results

The spraint analysis results obtained by the five methods of estimating proportions of prey are shown in Table II; the results are presented for each otter separately and for the three otters pooled.

When the results of the individual otters were tested against their actual diet, all methods showed a significant correlation with the actual diet composition ($P < 0{\cdot}05$), except method IV which was rejected for otters A and C. When data from the three otters were pooled and tested against the pooled diet, all methods correlated significantly ($P < 0{\cdot}01$).

The deviations between methods and actual diets for the individual otters illustrate the same pattern of over- and under-estimations as the pooled results, with a few exceptions. The following comments on Table II will therefore be based on the pooled results. The cyprinids showed a very low value when methods Ia and Ib were used, whereas the other methods showed a higher similarity with the proportion of cyprinids in the actual diet. All methods over-estimated the proportion of percids in the diet and this over-estimation was particularly pronounced with methods Ia, Ib, and IV. Eel (*Anguilla anguilla*) was also over-estimated by most methods, but to a lesser extent than percids. The proportion of trout was clearly under-estimated for all methods. Stickleback (*Gasterosteus aculeatus*) and frog were over-estimated by all methods, these deviations being most pronounced with methods Ia and Ib.

The Indices of Similarity between the actual diet (all otters in total) and the results of each method are given in Table III. The table shows that method Ia and Ib had the lowest degree of similarity to the actual diet. The other methods all showed a similarity to the actual diet of about 90%. Method III showed the highest value.

The degree of similarity in the results obtained from the different methods is shown in Table IV. These similarities do not reflect the usefulness of the methods, but illustrate how much the methods resemble each other. For example, two methods that make the same overestimation for a prey category will show a high degree of similarity.

TABLE IV

Renkonens Index of Similarity between the five methods tested in the feeding experiment. All calculations are based on the results for all three otters pooled. (For further details see methods section)

			Method Ib	Method Ia 94·1%
		Method II	83·0%	86·9%
	Method III	93·3%	88·5%	91·2%
Method IV	89·7%	90·7%	87·2%	90·8%

TABLE V

Renkonens Index of Similarity between the five methods used on material from Danish freshwater localities. (For further details see ***Methods*** *section)*

			Method Ib	Method Ia 87·4%
		Method II	85·6%	77·1%
	Method III	95·8%	88·3%	80·0%
Method IV	80·0%	79·4%	89·0%	90·5%

The indices in Table IV illustrate that all methods had a high degree of similarity to each other, in particular method Ia and Ib, but also methods II and III showed a high degree of similarity. The lowest similarity was between method Ib and method II.

The five methods used in the present experiment were also applied to a larger material representing a wider variety of prey categories, collected at Danish freshwater localities (number of spraints, 978; number of occurrences, 1696).

The different methods were compared to each other with the Renkonens Index of Similarity. This was done to determine whether the methods illustrated the same relations as seen in the feeding experiment (Table IV).

The similarity indices between the five methods (Table V) indicated that methods II and III resembled each other most. The lowest agreement was seen between method Ia and method II. In general, these field results confirmed the relations between the methods in the feeding experiment.

Discussion

When an experiment like this is performed in relatively open areas with natural vegetation and water conditions it will not be possible to find all spraints. During the spraint analysis it became obvious that not all bones from the fish fed to the otters appeared in the spraints. Vertebrae were missing from all categories of prey and from all sizes of prey, indicating that some spraints had not been found. The ground was thoroughly searched every day; remains of spraints left on the ground could not have been sufficient to account for all the missing spraint material. Part of the explanation is probably that the otters defecated in the water: this has been observed for otters in nature (Jenkins & Burrows, 1980) and Kruuk & Conroy (1987) stated that many otters defecate most often in the water. Both for otters in nature and in captivity, defecating in water is especially the case when a female otter is rearing cubs (Östman, Hillegaart & Sandegren, 1985), but it has also been observed with single adult otters in captivity (Östman *et al.*, 1985; Christensen, 1989).

Because it is impossible to collect all spraints from an otter in the field (Jenkins & Burrows, 1980; Kruuk & Conroy, 1987), this feeding experiment was subject to the same restrictions as spraints analysis in the field. Nevertheless, we believe that the proportion of spraints available for the analysis was representative of all spraints.

Missing vertebrae from larger prey fish could also be due to the otter showing caching behaviour (Harper & Jenkins, 1982) or dropping part of a prey fish in the water while playing. This is further discussed in Part 2.

Comparison of the five methods to estimate prey proportions

The methods tested in the present study represent different ways of assessing the relative proportions of each prey category.

The frequency of occurrence method (Ia) is the most commonly used. In method Ib, this method is combined with the dry weight, trying to take into account differences in spraint size. The dry weight is also a multiplier in methods II and III, but not in method IV, because this method already takes into account the different sizes of the spraints because large spraints show remains from the prey category in more areas than smaller spraints.

The differences between the methods and what is presumed to be the actual diet, reflect both dissimilarities between the methods and more general discrepancies associated with the individual prey categories. The overall pattern is the same for each otter as a separate sample and for the total result, and therefore only the pooled results of all three otters are discussed below.

General deviations for all methods, but to a different extent, are due to a variation in the amount of recognizable hard material between prey categories. This variation is due in part to some species having outstanding features, but also to small prey having a higher bone to flesh ratio than large prey. Over-estimation of frog and stickleback is due to small size and characteristic bones; percids are over-estimated owing to many characteristic scales; and eel is over-estimated owing to the relatively large number of vertebrae compared to other fish species. The under-estimation of trout is due to the relatively few characteristic remains in the spraints. Trout scales are small and some were probably lost in sieving and many of the trout used in the feeding experiment were large and had consequently low bone to flesh ratios.

The problem of minor prey categories (frequently appearing in the spraints but in small amounts) being over-estimated, and major prey categories (frequently appearing in the spraint in large amounts) being under-estimated is a well-known disadvantage (Erlinge, 1967) of method Ia. This was confirmed by our study so that a lower similarity to the actual diet for both methods Ia and Ib compared to methods II, III, and IV was seen. This was well illustrated for the cyprinids, which were a major prey category in this study.

Finally, an under-estimation of one prey category may induce an over-estimation of the other prey categories in the diet, when relative proportions of prey are compared.

To sum up, the accuracy of the estimation of the prey proportions can be improved if a little more time is spent on spraint analysis. Methods II, III, and IV show high similarities to the actual diet, all of them being improvements compared to methods Ia and Ib. The fact that method IV was not correlated significantly with the actual diet for two of the otters, taking into account the time budget of the method, leads to the conclusion that method IV may be inappropriate in analysis of otter spraints. However, method IV shows a high similarity to the pooled results, so that any improvement giving a reduction in analysis time would increase its utility. Methods II and III closely resemble each other. Neither is more time-consuming than the other, but because method II is a little more detailed and the calculations can be made directly, we prefer this method for future studies.

Other observations from the feeding test

The feeding of insects in otter spraints has been discussed in several studies and most small insects are often considered to be indirect prey items (Hamilton, 1961; Foster & Turner, 1991). In our study, 10 spraints consisted entirely of the hard exoskeleton of big 3–4 cm dragonfly nymphs

(*Odonata*) numbering up to 12–14 in a single spraint. Because no fish remains were present together with insects in the spraints, and because the otter was seen to dive to the bottom of the pond catching something, insects may have been consumed deliberately. These observations may confirm that otters are able to forage on large aquatic insects.

In the analysis of spraints from the feeding test, some vertebrae from smelt (*Osmerus eperlanus*) were found. Because smelt was not offered to the otters, they may have come from the stomach of another fish. This proves that some of the prey items found in otter spraints are not eaten by otters, but are consumed indirectly. This can contribute to the over-estimation of small prey items in spraint analysis, because some small fish, for instance stickleback, may have been eaten by a larger fish which was consumed by the otter.

Part 2: Estimation of the size of prey fish

A method used in otter spraint analysis to estimate the length frequency distributions of prey fish by measuring fish vertebrae (Wise, 1980) is tested through a feeding experiment (see Part 1). The otters were fed a known diet of fish of various lengths. The length distributions of the fish in the diet were compared to the results of a subsequent analysis of 362 spraints. The length frequency distributions found by the spraint analysis were similar to the length frequency distribution in the diet for cyprinids and percids but not always for trout or eel and generally for large specimens of fish. With these reservations, it is concluded that this method can be applied to otter spraint analysis.

Introduction

Northern Europe otters (*Lutra lutra* L.) eat mainly fish (Mason & MacDonald, 1986; Kyne *et al.*, 1989; Hansen & Jacobsen, In prep.; Jacobsen & Hansen, In prep.). The fish composition in the diet is often estimated through spraint analysis, but a detailed dietary study of the otter also requires information on prey fish size.

Wise (1980) developed a method to estimate prey size, and concluded through a laboratory test with mink (*Mustela vison*) that the basic premise behind the method was correct. This laboratory test was made with three species of fish in a limited size range, but the regression formulas of Wise (1980) have been used for more species and larger sizes of fish in several studies of otters in the field (Jenkins *et al.*, 1979; Jenkins & Harper, 1980; Wise, Linn & Kennedy, 1981; Murphy & Fairley, 1985; Adrián & Delibes, 1987; Kyne *et al.*, 1989; Kemenes & Nechay, 1990).

This study aimed to test this size estimation method with a greater variety of species and sizes of prey. The aim is fulfilled through a feeding experiment with otters under semi-natural conditions.

Materials and methods

The feeding experiment was carried out with 3 otters in captivity for 6 days as described in Part 1.

Measurement of fish vertebrae present in spraints allows an estimation of prey size due to the correlations between vertebrae length and fish body length. Regression relationships were calculated (Wise, 1980) for roach, perch, trout, pike, and eel. Wise (1980) calculated correlation factors for both abdominal and caudal vertebrae, respectively, but also the mean correlation factor for all vertebrae was found. In our study, the length frequency distribution of prey fish was estimated by use of the mean correlation factors calculated by Wise (1980). All body lengths of fish refer to fork length.

The cyprinids used in the test were mainly roach but some bream were also included. No correlation factor was available for bream from the literature and in our reference collection the number of bream was too small to calculate a separate correlation factor. However, since we found that the reference bream matched the correlation for roach, both cyprinids were treated as roach. Similarly, the only correlation factor available for the percids was for perch. We found that our reference ruffe and pike-perch matched the correlation for perch.

In each spraint, the vertebrae from each prey category were measured with a digital slide calliper (±0·01 mm). For each prey category, the vertebrae were divided into vertebrae length intervals equivalent to 3 cm intervals of fish length (6 cm intervals for eel).

We estimated the length frequency distribution of prey fish by use of the actual number of vertebrae. In each spraint, all vertebrae were counted, whereafter the vertebrae, according to their length, were recorded in the different fish length intervals.

Sometimes one spraint included vertebrae from the same fish category, but belonging to more than one length interval. This could reflect that the otter had actually eaten 2 or more different sizes of the same fish species, but it could also reflect the variation in vertebrae size in one fish. This variation therefore involves the risk of placing the prey fish in the wrong length interval. However, this risk applies to all spraints and the problem was therefore believed to be neutralized, since the same method was used for the whole material.

To justify this method, 2 alternative methods of estimating the length frequency distribution of prey fish were tried. First, Wise (1980) calculated minimum and maximum lines in the regression relationships to account for the variation in vertebrae length in one fish. Taking these minimum and maximum values of each length interval into account, we tried in each spraint to assess whether all vertebrae from the same prey category in a spraint could have belonged to the same fish. If this were the case, all vertebrae were recorded in the length interval concerned. Thereafter, the number of vertebrae for each length interval for each prey category was summed for all spraints and the length frequency distribution was expressed as a percentage.

Instead of using the actual number of vertebrae, the occurrence of each length interval present in a spraint was noted. Therefore, secondly, in order to give a more quantitative result, the dry weight of the spraint concerned was multiplied by the occurrences in the spraint. Thereafter, the occurrences were summed for all spraints for all length intervals for each prey category and the length frequency distribution expressed as a percentage.

All 3 methods of calculation were compared to the length frequency distribution of the actual diet, but neither of the 2 alternative methods gave a more accurate result. We therefore decided to use the first method described, where the actual number of vertebrae was counted, because this was considered to be an objective way to determine the length frequency distribution.

The length frequency distributions of fish offered to the otters were calculated based on the number of individuals in each length interval. Because the number of vertebrae in one individual of the same species is almost constant, the length frequency distributions in the actual diet and in the spraints can be compared directly.

The Kendall Rank-Order Correlation Coefficient, τ, (Huhta, 1979; Siegel & Castellan, 1988) was calculated to test the length estimation method (Wise, 1980). The τ-value was tested to find if there was a significant ($P < 0{\cdot}05$ or $P < 0{\cdot}01$) correlation between the sets of data.

Results

The length frequency distribution estimated from the spraint analysis is compared to that of the fish in the feed. These comparisons are shown for each fish category in Fig. 1.

The cyprinids are shown in Fig. 1a. There was a significant correlation ($P < 0{\cdot}05$) between the length frequency distribution estimated from the spraint analysis and that of the actual diet but minor deviations are seen. For instance, the spraint analysis overestimates the length of the smallest cyprinids, underestimates the length of the larger cyprinids, and the largest cyprinids do not seem to turn up in the spraints at all.

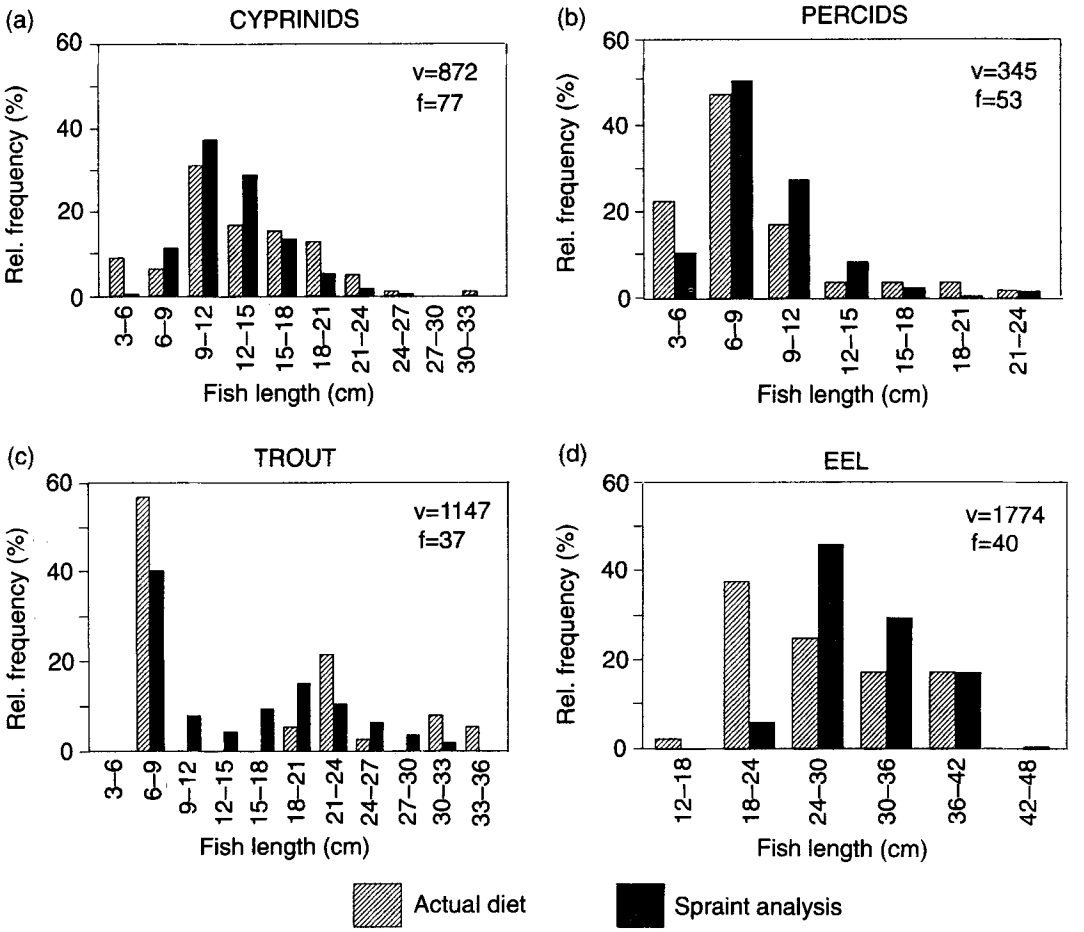

FIG. 1. (a–d) Comparison of the length frequency distributions of fish in the spraints and in the actual diet. v = number of vertebrae and f = number of fish, on which the distributions are based.

The estimated length distribution of percids (Fig. 1b) was significantly correlated ($P < 0{\cdot}01$) with the actual length distribution. The spraint analysis tends to over-estimate the length of the smallest and medium-sized percids and to under-estimate the length of the largest percids.

There is no significant correlation between the two distributions of length of trout (Fig. 1c). The figure illustrates that the length of the smallest trout was over-estimated and the length of large fish (> 30 cm) was clearly under-estimated. Further, the length distribution in the spraints places some fish in the length intervals between 9–18 cm, although no fish of these lengths were fed to the otters.

The length distributions for eel (Fig. 1d) were not significantly correlated. The length of small eels (< 24 cm) was clearly over-estimated, inducing an over-estimation of eels in the 24–30 cm and 30–36 cm intervals. The proportion of eels larger than 36 cm seems to match the actual diet very well.

Discussion

The results of this feeding test showed that the degree of applicability of the method varied between the fish species in question. We found it reasonable to use the method with cyprinids and percids, but some reservations should be taken with smaller eels and especially trout.

The deviations between the length frequency distributions estimated from the spraints and in the actual diet can be explained by different causes. For example, uncertainties of the length intervals can appear when using the mean correlation factors (Wise, 1980) for all vertebrae instead of using the correlation factors for anterior and caudal vertebrae, respectively, which were also estimated by Wise (1980).

The deviation for small eel is obviously due to the great variation in vertebrae length along the column of an eel, and it seems that using the mean correlation for all vertebrae is not very suitable for eel. Larger intervals for eel could reduce the problem, as recommended by Murphy & Fairley (1985).

In the case of percids and cyprinids, deviations could arise, because the regression relationships for roach and perch were also used for related species. However, this simplification does not seem to influence the results, since cyprinid and percid match the actual length distribution very well.

The general uncertainties of the correlation factors are believed to account for the deviations in the length distributions for trout. The correlation factors are best for small fish; the largest specimens are therefore less accurately classified in the correct length interval. However, missing vertebrae from large trout in the spraints is a specific problem which cannot only be explained by the poor correlation factor for large fish.

This specific loss of vertebrae from large fish it also seen for cyprinids and it is possibly due to the fact that otters can eat the flesh and leave the vertebral column intact (Chanin, 1985). By contrast, in the case of eel, otters have to eat the whole eel in order to obtain flesh at all (Jenkins *et al.*, 1979). This is illustrated in the accuracy of the length estimation of larger eels. It appears therefore that the otters in some way have avoided consumption of the vertebrae from the largest fish. However, no remains of large fish were found on the ground in the enclosures, so that the otters must have dealt with the remains in another way.

Captive otters sometimes show caching behaviour (Harper & Jenkins, 1982), hiding some of the prey in holes in the banks of a pond, which has also been observed in Otter-Zentrum (Barbara Heins, pers. comm.). In addition, otters have been observed playing with the prey in the water (Weir & Banister, 1973; pers. obs.), and it is therefore a possibility that some of the fish remains were dropped into the pond and were never consumed by the otters.

During the spraint analysis it became obvious that remains generally were missing from all sizes and species of fish. It seemed, therefore, that not all spraints had been found, even though the ground was properly searched every day. The otters might have been defecating in the water, which is further discussed in Part 1. This problem could also account for some of the uncertainties in the test, since the estimation of length of prey fish in otter spraints goes into further details compared to estimating prey proportions in otter diet.

To sum up, this experiment suggests that the method of estimating prey size (Wise, 1980) is usable under natural conditions, even though only some of the spraints are available. The regression relationships are accurate for cyprinids and percids, but less accurate for trout and eel or generally for large fish.

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