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Stomach contents analysis—a review of methods and their application

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Methods for analysing fish stomach contents are listed and critically assessed with a view to their suitability for determining dietary importance—this term is defined. Difficulties in the application of these methods are discussed and, where appropriate, alternative approaches proposed. Modifications which have practical value are also considered. The necessity of linking measurements of dietary importance to stomach capacity is emphasized and the effects of differential digestion upon interpretation of stomach contents outlined. The best measure of dietary importance is proposed as one where both the amount and bulk of a food category are recorded.

I. INTRODUCTION

Study of the diet based upon analysis of stomach contents is now standard practice in fish ecology but surprisingly little literature exists upon the range of methods which may be employed. Review papers by Hynes (1950), Pillay (1952) and Langler (1956), all consider the methods in use at those times. However, since then more refined techniques of dietary analysis have come into operation. Windell (1968) and Windell & Bowen (1978) review this subject, and whilst the latter is more up-to-date, the coverage of both papers lacks critical discussion of the techniques outlined.

An attempt is made here to describe the methods of analysis in use at present and to examine each, illustrating its advantages and disadvantages. Before undertaking this review, however, it is pertinent to categorize studies employing stomach contents analysis, thereby allowing a fuller understanding of their aims and the type of data required.

II. TYPES OF STUDY

Two main categories of study exist. Firstly, those which examine the diet of a fish population with a view to assessing the species' nutritional standing in the context of the fish community. Such a study may consider seasonal variation in the diet and/or dietary comparison either between different sub-groups of the same species, e.g. year classes or different species living in the same or comparable habitats. In both instances the aim may be to discern whether there is competition for food. This category also includes studies which monitor the feeding intensity of a fish population throughout the day to discern the diel rhythm or feeding periodicity (e.g. Staples, 1975).

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The second category is concerned with studies which attempt to estimate the total amount of food consumed by a fish population (e.g. Allen, 1951). This may involve calculation of daily ration or energy budget, based upon field (Staples, 1975), or laboratory determinations (Gerking, 1972; Morgan, 1974; Elliott, 1976), or both (Cameron *et al.*, 1973; Swenson & Smith, 1973). Such studies are largely beyond the scope of this review and the reader is referred to Beamish *et al.* (1975), Elliott & Persson (1978) and Windell (1978) for up-to-date discussions of the various approaches employed.

OCCURRENCE METHODS

Possibly the simplest way of recording data gleaned from stomach contents is to record the number of stomachs containing one or more individuals of each food category. This number may then be expressed as a percentage of all stomachs (Frost, 1946, 1954; Hunt & Carbine, 1951) or all those containing food (Dineen, 1951; Dunn, 1954; Kennedy & Fitzmaurice, 1972).

The advantages of the frequency of occurrence method are that, provided food items are readily identifiable, it is quick and requires the minimum of apparatus. However, it gives little indication of the relative amount or bulk of each food category present in the stomach. Despite this, the method provides a somewhat crude qualitative picture of the food spectrum (e.g. Crisp, 1963; Fagade & Olaniyan, 1972).

Johnson (1977) has used this method as an indicator of interspecific competition by assuming that where the occurrence of a food item exceeded 25% in two or more predators competition was likely. The method has also been utilized to illustrate seasonal changes in diet composition (e.g. Frost, 1977).

A modification, devised by Frost & Went (1940), is the dominance method. Here the proportion of stomachs where a particular food category is 'dominant by bulk' is determined and expressed as a percentage of the total stomachs or filled stomachs examined. This method also fails to indicate the actual amount or bulk of each food category. There is the additional problem of which criteria to employ in assessing dominance.

Number (Blake, 1977) volume (Etnier, 1971; McCaskill *et al.*, 1972) and weight (Newsome & Gee, 1978) have all been used. Since different investigators have used various criteria of dominance, comparability between studies is limited. Additionally, if bulk is measured directly, no benefit is derived from employing the dominance method and more information would result from consideration of actual bulk measurements and the same argument applies where number is the dominance criterion.

NUMERICAL METHODS

The number of individuals in each food category is recorded for all stomachs and the total is expressed as a proportion, usually a percentage, of the total individuals in all food categories (e.g. Crisp *et al.*, 1978; Ikusemiju & Olaniyan, 1977). The mean number of individuals per stomach in each food category may be calculated (Bulkley *et al.*, 1976; Neill, 1938; Smyly, 1952; Straskraba *et al.*, 1966).

The numerical method is relatively fast and simple to operate providing identification of prey items is feasible. In some situations it may be the most appropriate method, for example, where prey items of different species are in the same size range, e.g. in piscivorous fishes (Beyerle & Williams, 1968) or planktonivorous fishes (Guma'a, 1978). The tedium of this method in the latter situation may be overcome by sub-sampling (Engel, 1976; Starostka & Applegate, 1970). Micro-organisms are usually suspended in a known volume from which the sub-sample is taken. The number of organisms may be determined using a Sedgwick-Rafter counting cell (Brazo *et al.*, 1978; Levesque & Reed, 1972; McComish, 1966). Priegel (1970) devised his own counting cell for this purpose. Ball (1961) suggested that numerical methods give a better indication of the amount of effort exerted in selecting and capturing different organisms.

Other factors prevent the use of this method in isolation as an index of ' dietary importance '. Firstly, as has been generally recognized in the literature (Crisp *et al.*, 1978; Hynes, 1950; Mann, 1973; Mann & Orr, 1969), numerical estimates overemphasize the importance of small prey items taken in large numbers. Crisp *et al.* (op. cit.) omitted micro-crustacea from their numerical analysis for this reason, but small organisms may be very important since they are digested more rapidly than large ones (Sikora *et al.*, 1972).

Secondly, for many stomachs it is difficult to estimate numbers in each category because of mastication of the food, especially in cyprinids, before it reaches the stomach, and/or the effects of the digestive process. In this situation, percentage occurrence may provide as reliable an indication of diet (Crisp *et al.*, 1978; Stickney, 1976), alternatively percentage volume composition may be used (Bonneau *et al.*, 1972).

Thirdly, fish size is not taken into account. Lastly, this method is not suitable for dealing with food items such as macroalgae and detritus which do not occur in discrete units (Arawomo, 1976).

VOLUMETRIC METHODS

Volumetric analysis falls into two categories: direct and indirect estimation. In the former, the displacement of each food item or group of items sorted from the stomach contents, is measured, usually in some type of graduated measuring device (e.g. Wolfert & Miller, 1978), this displacement volume being equal to that of the food item(s). Alternatively the ' settled ' volume of the stomach contents may be measured by allowing them to settle in a graduated measuring vessel (Jude, 1971).

Where direct estimation is impractical, e.g. where small items are prevalent in the stomach, indirect volumetric analysis may be employed. This can be done by comparing food items with blocks of known volume (Larimore, 1957). Calculation of the mean dimensions of prey species, based on measurement of a number of individuals, allows determination of mean volume. The formula employed depends upon which three-dimensional shape the organism most closely resembles (McComish, 1966; Starostka & Applegate, 1970).

The total volume of a food category taken by the fish population is usually given as a percentage of the total volume of all stomach contents (e.g. Hunt & Jones, 1972; Ikusemiju & Olaniyan, 1977; Pedley & Jones, 1978). Some authors have opted to use only stomachs of a particular fullness in volumetric determinations (e.g. Le Drew & Green, 1975; Sauvonsaari, 1971). Mean stomach volumes have been used to indicate seasonal changes in feeding activity (Voigtlander & Wissing, 1974).

A major problem with direct estimates of volume based on displacement is that the water trapped within the item may cause large errors in the estimate. Excess water can be removed by blotting items on filter paper before volume determinations are attempted, but, especially in the case of small items, this water is often difficult to extract.

Methods for measuring small stomach volumes have been described by Chubb (1961), Graham & Jones (1962) and Hellawell & Abel (1971). In each case the stomach contents are squashed on a plate to a uniform depth and the area of the squash is measured. This area may be enlarged using a micro-projector (Hellawell & Abel, 1971). The sources of error in this method have been discussed by Hellawell & Abel (op. cit.); overall these appear to come to about 3·5%. Where stomach contents are readily separable, food category volumes can be estimated using the same technique but this becomes difficult in cyprinid fishes where food is macerated and categories are largely inseparable. Hellawell & Abel (op. cit.) have used a modified points technique in this instance (see later). Centrifugation has been employed to separate contents into distinguishable layers, thereby allowing estimation of percentage volume composition (Bonneau *et al.*, 1972).

When stomach contents are of a nature which prevents volumetric estimation by direct means, e.g. well digested matter or particulate matter such as detritus or sewage, the method of McComish (1966) and Klarberg & Benson (1975) may be adopted. Here total volume of stomach contents and volume of each of the separable components is estimated. The difference between the former and the sum of the latter values gives an estimate of the volume of the remaining stomach contents.

The combination of direct determination of the total volume of stomach contents and estimation of the contribution of food categories has widely employed (e.g. Desselle *et al.*, 1978). Volumetric techniques probably give the most representative measure of bulk and may be applied to all food items.

GRAVIMETRIC METHODS

In gravimetric analysis of stomach contents, the weight of food may be determined ' wet ' or ' dry '. Glenn & Ward (1968) found that wet weight correlated highly significantly with dry weight for five different prey species.

In dietary studies where large amounts of material are collected, wet weight is probably the more convenient measure; dry weight estimation is more time-consuming and is usually employed where accurate determinations of calorific intake are required (e.g. Li & Brocksen, 1977). Berg (1979), however, states that dry weight gives a lower error margin in bulk determination of the food of planktonivorous fishes.

Dry weight is obtained by evaporating water until constant weight is achieved. The temperatures at which this has been carried out include 60° C (Efford & Tsumura, 1973; Jones, 1973; Man & Hodgkiss, 1977), 65° C (Allen, 1951; Cameron *et al.*, 1973; Elliott, 1967), 80° C (Pemberton, 1976), 85° C (Craig, 1978), 100°C (Sikora *et al.*, 1972), 105° C (Moore & Moore, 1975*a*, *b*) and 150° C (Glenn & Ward, 1968). Higher temperatures (> 80° C) may result in the loss of volatile lipids (Windell & Bowen, 1978), and are more time-consuming. Freeze drying of food items in a lyophilizer also gives an accurate measure of dry weight (Adams, 1976; Elliott, 1967).

When wet weight determinations are made, surface water is most often removed from prey items, by blotting them on tissue paper (Parker, 1963); however the variation in the amount of moisture removed has been identified as a major source of error in weight measurements (Parker, op. cit.). Other methods which have been employed in removal of water are drip drying (Sugden, 1967), pre-drying on a warming plate (Bellinger & Avault, 1971), and centrifugation (Howmiller, 1972; Peck, 1974). These methods, especially the first two, tend to be time-consuming where there are large samples involved; Herke (1973) has proposed a scaled-up version of centrifugation employing a household washing machine for spin drying.

The total weight of a food category can be expressed as a percentage of the overall weight of stomach contents, where weight is either 'wet' (Gibbons & Gee, 1972) or 'dry' (Jones, 1973; Pemberton, 1976). Alternatively food category weight may be expressed 'wet' as a proportion of body wet weight (Fagade & Olaniyan, 1972; Thorpe, 1977) or body dry weight (Adams, 1976); Foltz & Norden (1977) and Gibson & Ezzi (1978) expressed food category dry weight as a proportion of body dry weight. Values, incorporating body weight are probably more useful since they are a measure of food intake relative to fish size (see later). In the case of fish where the amount of stomach contents is too small to be weighed practically an overall picture of dietary composition can be obtained from the pooled weight of each food category.

Mean weight of stomach contents has been employed (Straskraba *et al.*, 1966). Smyly (1952) working on perch fry, with only a small amount of stomach contents, calculated mean weight of contents collectively i.e. as:

$$\frac{\text{Total stomach contents weight}}{\text{Total fish weight}} \times 100.$$

Sikora *et al.* (1972) determined mean dry weight for prey species and expressed this as 'biomass units'. Variation in the mean total weight of stomach contents relative to fish size is frequently used in determining the diel rhythm of feeding behaviour (e.g. de Silva, 1973; Gordon, 1977*a*, *b*; Keast, 1970; Staples, 1975). Changes in mean weight of stomach contents through the year indicate differences in feeding intensity (Man & Hodgkiss, 1977).

Gravimetric measurement of stomach contents is usually considered to overemphasize the contribution of single heavy items to the diet (George & Hadley, 1979; Hellawell & Abel, 1971). This may be true in studies of 'food importance', but in 'energetic' studies the contribution of dietary items should be measured as calorific value. In this instance weight to energy regressions can be employed. Gravimetric methods give a reasonable estimate of bulk and, in the case of larger prey items, are relatively easy to apply; they have the advantage of being applicable to almost all prey items though they are perhaps less so than volumetric techniques.

Where material is preserved in formalin, an overall increase in weight occurs (Parker, 1963), therefore errors could result if weight of preserved stomach contents is compared to that of 'fresh' contents or is expressed relative to 'fresh' body weight; although the latter is permissible if the procedure is consistent throughout the study.

SUBJECTIVE METHODS

The tedium involved in processing large amounts of material using numerical, volumetric or gravimetric methods has led to the development of techniques of subjective estimation of the contribution of a food category to the diet. The percentage contribution by volume of each food category to the total contents may be estimated by eye (Pillay, 1952). The points system, first employed by Swynnerton & Worthington (1940) and fully discussed by Hynes (1950) is a similar approach; here each food category is awarded points proportional to its estimated contribution to stomach volume.

Frost (1943) modified the technique to take into account differences in stomach fullness. An estimate of stomach fullness, (ranging from empty to full), was made and the points total for the stomach altered proportionally. Rice (1962), Dipper *et al.* (1977) and Kislalioglu & Gibson (1977) have all included an increased points total for distended stomachs. Ball (1961) proposed a set of criteria for visually assessing fullness which has been modified by Haram & Jones (1971).

Where the fish possesses no well-defined stomach the fullness of the whole gut can be assessed. Robotham (1977) divided the gut into ten equal regions and expressed the number of full sections as a 'mark out of ten'. Whether or not stomach fullness is assessed, the points allocated to a food category are summed and expressed as a percentage of the total points awarded. Rice (1962) used mean points total to compare feeding intensity of populations from different areas and at different seasons. The allocation of points proportional to volume has been criticized because of its subjectivity (Hynes, 1950; Windell & Bowen, 1978) but while consideration of direct volumetric data would yield a less subjective and doubtless more accurate estimate, the points system has the advantage of being simple and rapid to apply.

In attempts to minimize subjectivity and standardize points allocation a number of verifying procedures have been adopted: the accuracy of fullness estimates can be ascertained by comparing the wet weight of contents for stomachs in each fullness state. Kislalioglu & Gibson (1977), employing such a method, found that the points system generally overestimated bulk, but Schmidt-Nielsen (1939) expressed weight of contents as a proportion of fish weight, and in so doing found no overlap between the figures for different fullness states. Similarly, Craig (1978) plotted dry weight of contents against fish wet weight for each fullness category and obtained highly significant regression coefficients.

To standardize points allocation, Broadway & Moyle (1978) took undigested representatives from each size class of a common prey species and embedded them in plastic for use as a reference collection. The smallest size class was designated one point and the points for larger individuals increased according to volume. Elston & Bachen (1976) designated the average smallest prey item as one point. Weight has also been used in this way, Smyly (1952) designated the mean dry weight of the lightest food category as one point and allotted points in proportion to this. Subjectivity may also be reduced by placing food items on a calibrated dish (Keast, 1965), or a graduated slide (Gibson & Ezzi, 1978) and using the area covered as an aid to determining volume.

III. DISCUSSION

A number of authors (Hynes, 1950; Mann & Orr, 1969) have stated when discussing methods of stomach analysis that important items in the diet will be obvious irrespective of the method of stomach analysis employed. This statement hinges on the definition of 'important items in the diet' (see later): each method will show items important in the diet according to the attribute it was designed to measure. However, where small samples are taken and the variation in food categories is large, different methods may produce quite different results, (see e.g. Radforth, 1940).

The term 'importance in the diet' is often employed in the literature but has been ill-defined. Dragovitch (1970) used the criteria of frequency of occurrence in stomachs, stomach volume, and number of individuals in assessment of dietary importance. Tyler (1972), on the other hand, considered the important items as 'major food-energy sources' and his criteria for defining these were based on prey items exceeding specific levels of occurrence, weight relative to fish weight and percentage wet weight.

The 'importance' of a food category is here taken to mean the amount (number) and bulk (volume or weight) in the diet. This definition is intended to apply to studies attempting to describe or compare diets; nutritional importance in 'energetics' terms may be otherwise defined. By considering both bulk and amount in association a more accurate picture of dietary importance will be gained. These criteria of importance appear to be broadly in agreement with Berg (1979).

It seems realistic to base assessment of dietary importance upon these unrelated methods, and Windell (1971) has stated that indices combining values from different sources are more representative. Such a measure is the 'index of relative importance' (IRI) (Pinkas *et al.*, 1971; Prince, 1975) which incorporates percentage by number (N), volume (V) and frequency of occurrence (F) in the formula:

$$\mathrm{IRI} = (\%N + \%V) \times \%F.$$

George & Hadley (1979) employed the 'relative importance index' (RI) which is based on the 'absolute importance index' (AI) as follows:

$$\mathrm{AI} = \%\ \text{frequency occurrence} + \%\ \text{total numbers} + \%\ \text{total weight},$$

$$\mathrm{RI} = 100\ \mathrm{AI} / \sum_{1}^{n} \mathrm{AI}$$

where n is the number of different food types.

It seems somewhat unlikely that either of these methods is a more accurate index of dietary importance since they confound two sources of error and variation. A single value of dietary importance is useful when comparing the diets of different fish species using non-parametric ranking tests, however since such compound indices of dietary importance are not widely used, comparisons between studies are limited.

The difficulties associated with using numerical counts in dietary assessment are relatively few and largely centre on the situation where food is digested so making counts difficult. This may be overcome by making a subjective estimate of number (Pillay, 1952) or by counting only particular body parts resistant to digestion (Blake, 1977), which could, however, lead to an overestimate (see later). To avoid this frequency of occurrence can be used instead of numerical estimates (Stickney, 1976).

Numerical counts are not suitable in every situation, for example where plants are among the principal food components (Klarberg & Benson, 1975). Where fish are concentrating upon a few food categories, frequency of occurrence may be equally valid (Frost, 1977).

Neither volume nor wet weight are totally valid indicators of nutritional bulk, since both include in the measurement non-digestible material such as exoskeleton, shell etc. In an attempt to overcome this, some authors have determined the weight of molluscs less shells (Moore & Moore, 1974; Keast, 1978) and trichopterans less cases (Keast, op. cit.).

One variable which exerts a considerable influence on the bulk of food present in a stomach is the rate of digestion. A number of factors have been found which affect this: long periods of food deprivation (Elliott, 1972; Griffiths, 1976; Windell, 1966); the hard parts possessed by the food item (Hess & Rainwater, 1939); the fat content of the prey (Elliott, 1972; Hess & Rainwater, 1939; Kitchell & Windell, 1968; Pandian, 1967; Reimers, 1957; Windell, 1966); and lastly, water temperature (Baldwin, 1957; Markus, 1932; Reimers, 1957; Sokolov & Chvoliova, 1936).

Differential digestion has been found to cause errors in the determination of dietary importance. For example, Gannon (1976) showed that *Daphnia,* as a consequence of their digestibility, are under-represented in stomachs of the Alewife, *Alosa pseudoharengus* (Wilson). This had a considerable effect on the calculation of electivity indices (Ivlev, 1961). Similar observations have been made for other zooplankters (Berg, 1979; Doud, 1974).

Errors in bulk measurement resulting from differential digestion may be minimized in two ways. Firstly, by computation of mean wet weight (Mathur, 1973), mean dry weight (Efford & Tsumura, 1973; Elliott, 1967), or mean volume (Eder & Carlson, 1977; Hellawell, 1972; Hunt & Jones, 1972) for each prey category, based on undigested specimens. An estimate of weight/volume is then calculated from the number of individuals and the mean bulk. The errors may be considerable, due to deviation in the size of food eaten from that employed in calculation of the mean. Horton (1961), in an attempt to avoid this, determined mean dry weight for five size classes of prey items.

An alternative approach is calculation of regressions for each prey category of weight on length, or some other parameter, e.g. appendage length. Measurement of length of items from stomachs is often difficult and Berg (1979) outlines more sophisticated methods which may be employed in this context. Other examples from the literature of the use of regressions in calculation of prey bulk are: use of opercular bones to estimate prey length (Newsome, 1977), and use of gizzard weight to determine total length and weight of prey (Minckley & Paulson, 1976).

Neither of the above methods helps to compensate for food items which are rapidly digested, for example, oligochaetes (Kennedy, 1969). Calculation of mean length and volume for intact individuals and estimation of number and hence volume has been employed in this situation (Klarberg & Benson, 1975).

Since both methods depend ultimately upon counts of organisms present in the stomach, where parts of a food organism are resistant to digestion and are counted as whole animals (Klarberg & Benson, 1975; Loftus & Leon, 1977; Minckley *et al.*, 1970), the importance of some food categories may be overemphasized. Kionka & Windell (1972) found that large chitinous pieces from *Asellus* exoskeletons were retained in the stomach after associated organic matter had been evacuated. Similarly, Miller (1974) showed that chironomids and simuliids remain recognizable in the stomach, by virtue of their chitinous head capsules, after other contents are indistinguishable.

If dietary importance is a consequence of both number and bulk it seems inadvisable to base both measurements ultimately upon the same feature, i.e. number, thus introducing a double over-emphasis. The error introduced into estimates of dietary importance by differential digestion may be minimized by sampling fish during, or immediately after their period of peak feeding; this can be determined by frequent regular sampling over a 24 h period. Differences in the state of digestion of prey have been used as an indicator of peak feeding (Eggers, 1977; Outram & Haegele, 1972; Sekavec, 1974; Swenson & Smith, 1973), and some authors have devised arbitrary scales of digestion (Darnell & Meierotto, 1962; Magnuson, 1969; Mathur & Robbins, 1971). Usually the proportion of undigested food is used as an indicator of maximum feeding activity (Mathur & Robbins, op. cit.).

The relative rate of degradation of food organisms in digestion has been studied experimentally by Le Brasseur & Stephens (1965) using swine pepsin. Another approach adopted is force feeding fish and examining stomach contents at frequent intervals (Lewis *et al.*, 1974).

The implications of differential digestion rates of prey species on the use of weight as an indicator of dietary importance have been discussed by Berg (1979). Swedberg & Walburg (1970) found weight easier to determine, and derived a volume estimate by utilizing a weight : volume ratio of 1 : 1.

Food category volume is often estimated as a percentage of the total contents volume: this may be done subjectively, or the total volume may be measured directly or indirectly. Both procedures give an indication of the bulk of a food category relative to the others in the stomach. However, the food category volume described in this way provides only a limited amount of information on dietary importance, since the bulk relative to stomach capacity is not known. The same argument applies to gravimetric analysis. In order to determine the relative importance of a category by bulk, the estimate must be related to stomach capacity or fish size.

A number of methods have been employed to measure stomach capacity. Magnuson (1969) fed starved fish items of known volume until satiated. By plotting total food volume of stomachs examined against body length and fitting a regression line to the edge of the points cluster, Hellawell (1971; 1972) determined the relationship between body length and stomach capacity. Using this, he converted the contents volume of all fish to the equivalent for a specific fish size.

A similar relationship was constructed by Kimball & Helm (1971), but stomach capacity was experimentally determined for different fish lengths, by measuring the amount of water that could be injected into an empty stomach prior to bursting. A linear relationship between stomach capacity, measured in the same way, and body wet weight has also been found (Flowerdew & Grove, 1979; Jobling *et al.*, 1977).

Using any of these methods food category volume may be expressed as a percentage of stomach capacity. A mean percentage can be calculated for the sample or the total percentage for the category expressed as a proportion of the total for all categories. Volume is the only measurement of bulk which can be employed in this way, unless fish weight is incorporated into the measurement, when either weight or volume may be used.

In this case, bulk is expressed as a proportion of fish body weight (Andrievskaya, 1957; Spanovskaya & Gryorash, 1977; Thorpe, 1974); the total bulk, expressed in this way, of each category is then calculated as a percentage of the total bulk of all stomach contents. This method of expressing bulk in units of body weight has been employed by some authors (Keast & Welsh, 1968; Smyly, 1957) to give a measure of stomach fullness which can be compared for fish of different sizes. Such an ' index of filling ' can then be used to demonstrate changes in stomach fullness with time which may reflect changes in feeding activity (Tugarina & Yel'tsova, 1975). A subjective ' index of fullness ' was used by Tippetts & Moyle (1978); total points awarded to a stomach was expressed in units of fish length.

It is difficult to relate food category bulk to fish size where volume and weight are difficult to determine. In such situations a subjective estimate of actual volume must be made. This can be done by determining total contents volume directly, estimating the contribution of a food category as a proportion of this and multiplying to obtain an estimate of volume (Spiers, 1974). Alternatively, the actual volume may be estimated and the subjectivity reduced by comparison with samples of known value.

Estimates of stomach fullness based upon the points method have been used to illustrate seasonal changes in feeding activity (Ball, 1961; Dipper *et al.*, 1977; Sinha & Jones, 1967). In most cases, mean number of points per stomach was used as a fullness index for the sample. However, the usefulness of fullness estimates in determination of dietary importance appears to be a source of confusion in the literature.

Since, in most instances, stomach fullness estimates are largely subjective, this prohibits useful comparisons between studies. Furthermore, it appears that an estimate of stomach fullness based upon measurements of gut dimensions is not reliable (Berg, 1979).

Using points assessment, when fullness is determined, food category volumes are expressed as a proportion of this i.e. points are awarded relative to stomach fullness. When the stomach is full, the relative points are equivalent to a proportion of stomach capacity, and, in other instances, for example a half-full stomach, food category points volume is also relative to this, i.e. to the stomach capacity. The method of points assessment combined with stomach fullness fails to take account of differences in stomach capacity. In two fish the actual food category volume, which may be 50% of the stomach contents in both cases, is less in the fish with the smaller stomach capacity even although the food category forms the same proportion of the contents in both cases; the points should be allotted in proportion to the actual volume. This may be overcome by the method of Cadwallader (1975) where different points totals are allotted to the same fullness category in fish of different sizes.

In one approach to examining competition between populations, the amount or bulk of a food category in the diet is related to a corresponding estimate of the potential food of that type in the environment; the ' availability ' (Allen, 1940). Most methods could be employed to estimate this although weight (Elliott, 1967) and number (Allen, 1942; Hess & Schwartz, 1941) have been used most commonly. Both Hynes (1950) and Maitland (1964) have criticized the use of number in this context. Hynes (op. cit.) recommends employing a measurement of bulk based upon the points method for calculation of availability; this has been used by Maitland (1965).

An ' availability ' estimate enables calculation of ' availability factors ' (Allen, 1940), forage ratio (Hess & Rainwater, 1939), ' indices of electivity ' (Ivlev, 1961; Shorygin, 1939), or overlap between volume percentages (Frame, 1974). All four give a measure of the degree of selection of the prey items found in the diet. Strauss (1979) considered both the forage ratio (Hess & Rainwater, 1939) and Ivlev's index of electivity and demonstrated their inadequacies. He proposed a linear food selection index which largely overcomes these difficulties.

Consideration of both numerical and frequency occurrence percentages for one sample can give an indication of the homogeneity of feeding within the population. For instance, high values for both indicate that the population is utilizing the same food source whereas high numerical and low frequency occurrence percentages for a food category indicate that only certain fish within the population utilize this food source.

The calculation of diversity indices also serves to indicate the amount of specialization in feeding habits within a population (Frame, 1974; Sanders, 1968; Simpson, 1949), the relationship of mouth and body form to food specialization has been studied by Keast & Webb (1966). Similarity of diet has been assessed using a non-parametric rank correlation (Cadwallader, 1975).

Size selectivity may operate in the diet, i.e. two populations may utilize different sizes of the same prey item. Broadway & Moyle (1978) have used the mean volume of prey to assess size selectivity between year classes of fish.

METHODS OF REMOVING STOMACH CONTENTS FROM LIVE FISH

Situations exist where the killing of large numbers of fish for stomach contents analysis would seriously affect the populations concerned. Techniques have been devised which enable removal of stomach contents without harming the fish and among the simplest of these is removing stomach contents with forceps (Wales, 1962).

Pressure on the stomach region has been used to force contents out of a glass tube placed in the fish's mouth (White, 1930). Injection of water through the tube enables the stomach contents to be flushed if the water is then pumped out and suitable pieces of apparatus have been devised for this purpose (Robertson, 1945; Seaburg, 1957). The technique has been successfully employed in dietary studies (Johnson, 1977; Seaburg & Moyle, 1964). Andreasson (1971) simplified the apparatus and checked its efficiency by dissection of stomachs. Stomach flushing has also been used in studies of food conversion (Swenson & Smith, 1973), and digestive rate (Seaburg & Moyle, 1964).

One criticism of the stomach flushing technique is that it is difficult to apply to piscivorous fish (Jernejcic, 1969), a proposed solution is the use of emetics (Jernejcic, 1969; Markus, 1932). An emetic is a drug which induces vomiting, Jernejcic (op. cit.) lists a number of these and discusses their advantages. Alternatively a gastroscope may be employed (Dubets, 1954). This is a long metal cone which, when inserted into the fish's mouth, holds the stomach open enabling observation of the contents.

The stomach flushing technique may also be difficult to apply to small fishes. Techniques which circumvent this problem are: syringe flushing (Meehan & Miller, 1978) where food items are flushed from the stomach using water pressure from a syringe, and back flushing (Baker & Fraser, 1976), which involves flushing the total gut contents out of the mouth by injecting water into the intestine at the anus, using a syringe. Kuthalingham (1961) has proposed drawing stomach contents out by suction.

Of the methods listed the stomach flushing technique appears to be the most generally applicable. Its efficiency, i.e. the amount of contents flushed compared to the total present in the stomach, has been found to be high (Andreasson, 1971; Meehan & Miller, 1978), and the survival of fish after treatment has been good (Meehan & Miller, op. cit.), however, it appears that the efficiency of flushing is negatively correlated with fish size (Meehan & Miller, op. cit.).

IV. CONCLUSION

It is evident that no one method of stomach analysis gives a complete picture of dietary importance. In order to glean maximum information from the material, the prudent investigator should employ at least one method measuring the amount, and one measuring the bulk of food material present. Allowance must be made for differential digestion and, ideally, all measurements of bulk should be linked to fish or stomach capacity.

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