Chapter 17
Quantitative Description of the Diet

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17.1 INTRODUCTION

This chapter presents a summary of considerations and techniques necessary to plan and carry out an efficient study for quantitative description of the diet. It is absolutely essential that the goals of the diet study be clearly established before the details of the study are planned. The filing cabinets of biology are replete with "food habits" data. Although collected at great expense, these data add little to our knowledge of fish ecology because they were collected without a particular goal in mind. By carefully planning the goals of a diet study, it is possible both to produce data to answer specific questions and to plan an efficient study in which only useful data are collected. An efficiently planned study allows the researcher to focus the available resources on the important questions and, thus, to increase greatly the probability of the study's success. Appropriate techniques can be selected only after the goals are established.

17.2 TECHNIQUES FOR COLLECTING FISH

Of the many fish collection techniques, some are more useful than others for collecting specimens to be examined for gut contents. Some capture techniques result in loss of information as a result of regurgitation. Although a systematic study has not been made, various reports suggest that capture techniques that stress fish severely, such as rotenone treatment, electroshocking, gill netting, and trawling at depth, are most likely to cause regurgitation. In some cases, a gentler technique, such as seining, may cause less regurgitation. In other cases, a very sudden shock may be useful. One worker found that a single-pronged spear allowed fish to regurgitate, but a three-pronged spear stunned fish on contact and regurgitation was eliminated. Some fish are more likely than others to regurgitate. Piscivorous predators have large distendable esophaguses which make regurgitation fairly easy, and these fish frequently regurgitate. Fishes that feed on small prey, however, are much less likely to regurgitate. Investigators who plan to study the diet of a piscivore should keep this potential problem in mind. If preliminary collections over a 24-hour cycle yield mostly specimens with empty stomachs, a different collection technique should be tried.

Post-capture digestion may also result in loss of valuable dietary information. Gill nets and traps of various sorts may hold fish for long hours during which much of the diet can be digested beyond the point where identification is possible. Consequently, these capture techniques are most useful where catch rates are high and specimens can be removed from the gear soon after capture. Some post-capture digestion may be tolerable if gill nets or traps are the only effective means by which the target species can be collected.

17.3.3 Effects of Fish Size and Territoriality

Diets selected by fish vary according to size and sex. As fish grow larger, they often select larger prey. The change may be abrupt and associated with a change in habitat as when salmon smolts change from invertebrate diets in freshwater to fish diets at sea. In many cases, the transition is gradual, as with lake herring which change slowly from a diet of nauplii to a diet of adult copepods as they grow. If the change is abrupt, the goals of the study may be served by analysis of gut contents from fish divided into two size groups. When the diet changes more gradually, ten or more size groups may be required to document the change, and it may be necessary to expand the range of habitats sampled in order to obtain statistically significant numbers of individuals for all size groups.

Adult male fishes often establish and defend breeding territories that they rarely leave. They must depend on food resources within the territories, and, consequently, their diets may be considerably different from those of the females and subadult males. If brightly colored males are captured, their gut contents should be compared to those from other specimens. It may be necessary to modify the sampling program so that enough territorial males are collected to permit description of their diet.

17.3.4 Differential Digestion Rates

Stomach contents may not accurately reflect the diet of a fish for two reasons. First, some prey, such as tubificids (Kennedy 1969) or protozoa, may be digested rapidly and leave little recognizable trace in the digestive tract. The importance of these prey, therefore, may be underestimated or overlooked entirely. If such a bias is suspected, it may be useful to hold the fish in an aquarium, watch how they feed, and then collect samples of their food for comparison to gut contents. A second data bias can result from differential rates of digestion for various prey. Slowly digested prey may accumulate relative to rapidly digested prey and, thus, be over-represented in the gut (Mann and Orr 1969; Gannon 1976). This effect can be minimized if fish are collected at the peak of daily feeding intensity when all food items in the anterior gut have been ingested recently.

17.4 REMOVING, FIXING, AND PRESERVING GUT CONTENTS

17.4.1 Removing Gut Contents

Many workers have developed methods for removal of stomach contents from fish that are to be kept alive. Most methods employ a stomach pump to flush stomach contents from the fish with one or more volumes of water (Seaburg 1957; Giles 1980). Tests in which the stomachs were dissected after pumping indicate that this procedure is a highly effective method of removing prey from a fish stomach. Emetics have also been used to obtain stomach contents from live fish (Jernejcic 1969). Both of these methods are useful only with the more robust fishes such as the Percidae, Centrarchidae, and the many catfishes. Delicate fishes such as the Clupeidae and many Cyprinidae are unlikely to survive the experience. Although this approach requires construction of special apparatus, valuable fish are not destroyed, and, in many cases, it is faster than removal of gut contents by dissection.

Often it is preferable to remove gut contents by dissection. This allows the worker

A third potential difficulty of a diet study stems from fish in traps feeding on foods they would not normally eat. For example, catfish, which are not normally piscivorous, may feed on small fishes during the time they and the small fishes are trapped together. Because of the problems of post-capture digestion and atypical feeding, traps are of limited utility in diet studies.

17.3 SAMPLING STRATEGIES

There are many factors that potentially influence both the amount of food and the type of food found in the digestive tracts of fish. The effects of the diel cycle, seasonal changes, the size and territoriality of fish, and differential digestion rates must be considered if an efficient and accurate sampling program is to be planned.

17.3.1 Diel Effects

The behavior of most fishes is highly structured within the diel cycle. Diel changes in habitat, feeding intensity, and the diet itself must be considered. During nonfeeding hours, fish often seek shelter in low risk environments. Just prior to feeding, they move into habitats where suitable food is available. Some fish feed intensively during a single extended feeding period lasting six hours or longer. Others may feed intensively for only one or two hours, followed by low levels of feeding activity for several hours. Still other fish are known to feed intensively at dusk and dawn with little evidence of feeding at other hours. Although given patterns of diel feeding behavior are commonly associated with particular species, fishes can radically alter their diel cycle in response to changes in food availability or predator distribution (Bowen and Allanson 1982). In order to maximize the amount of information gained per fish collected, fish must be collected when their stomachs are fullest. Therefore, it is often useful to begin a study of diet with a 24-hour series of collections made at 2-hour intervals. This will yield data on both catch per effort and stomach fullness to help plan an efficient sampling program.

Diet may vary with time of day. Salmonids in large streams may feed on invertebrate drift during the night and small fish during the day. I once found a population of golden shiners that fed on periphyton at night, Cladocera at dusk and dawn, and on sessile invertebrates during the day. Comparison of stomach contents from a 24-hour series of collections is necessary to determine if the diet varies according to time of day. If no such variation is apparent, then other factors discussed above will determine the best time of day to sample. If diel variation is detected, it is important to sample at a constant level of effort throughout the feeding period to avoid biasing the diet data.

17.3.2 Seasonal Effects

Fishes are highly responsive to seasonal changes in food availability. Changes within trophic categories, for example, from mayflies to chironomids, are common as invertebrate populations mature and emerge. Changes from one trophic category to another are also know to occur. Bluegills may switch from a diet of invertebrates to a diet of algae as invertebrate numbers decline toward the end of summer (Kitchell and Windell 1970). Thus, to adequately describe the trophic resources utilized by a fish population, it is often necessary to sample at frequent intervals throughout the year.

to examine the intestine for fullness and to be confident that all prey are removed from the stomach or anterior gut segment. Data on sex and gonad maturity may be collected at the same time (*see* chapter 15). If data on intestinal contents are needed, dissection is essential.

Before dissection, kill the fish be severing the spinal column. For small fishes, scissors are adequate, but a knife may be necessary for larger fishes. Open the coelom to expose the viscera. Using blunt scissors, sever the esophagus, the last few millimeters of the intestine, and the mesentary at its dorsal point of attachment. This allows the visceral mass to be lifted out of the coelom and into a dissection pan for more careful manipulation. Separate the digestive tract from the rest of the viscera and divide it into segments as dictated by the needs of the study. Open each segment by slitting it lengthwise with fine scissors. For piscivorous fishes, prey items can be lifted directly from the stomach. For fish eating smaller prey, it is often useful to hold the slit segment with forceps over a petri dish or small beaker and then to wash the food items from the segment with tap water in a wash bottle. If quantitative recovery of gut contents is not required, the food may be extruded by sliding a blunt probe along the length of the segment. This may, however, also extrude the gut mucosa. Do not mistake this tissue as part of the diet.

17.4.2 Fixing and Preserving Gut Contents

Ten-percent formalin is fully adequate as a fixative (*see* chapter 14 for dilution method). Because it rapidly hardens prey tissues, partly digested prey are more likely to stay intact and, thus, are easier to identify. Before samples are examined in detail, remove excess formaldehyde by soaking the samples in several changes of water. After excess formaldehyde is removed, preserve the samples in a 45-70% aqueous solution of alcohol. Methanol, ethanol, and isopropanol are all satisfactory. Wear plastic gloves and work in a fume hood to minimize exposure to residual formaldehyde. Formaldehyde is suspected of being a carcinogen and can cause permanent damage to fingernail growth areas and sinus tissues.

The availability of field time and facilities usually determines when gut contents are removed and fixed. It is best to remove and fix gut samples immediately after capture. This minimizes post-capture digestion and avoids difficulties associated with dissection of hardened fish tissues (Borgeson 1963). When tens or hundreds of fish are captured at one time, however, it is often necessary to fix the gut contents *in situ* with the least investment of time possible. In warm climates, hold fish on ice if more than a few minutes will elapse before fixation. Fishes of 100-g live weight or less can be fixed whole. In order to halt post-capture digestion, slit the coelom or inject formaldehyde directly into the coelom (Emmett et al. 1982). For larger fish, it is usually more efficient to fix only the digestive tract.

The goals of the study will determine the extent to which individual samples must be kept separate and identified. When gut contents are removed in the field, they may be stored in small numbered vials or plastic bags, and concomitant data (length, weight, sex, etc.) may be recorded on data sheets. When intact digestive tracts are fixed, they may be stored in separate containers. Several digestive tract samples may be stored in a single container if they are wrapped individually in cheese cloth, each with a paper label written in pencil. For some studies it may be adequate to pool gut samples according to size groups of the fish. Although this results in loss of data on variation among individuals, it requires less handling and greatly simplifies subsequent analyses.

17.5 IDENTIFYING THE DIET

17.5.1 Identifying Partly Digested Prey

Identifying stomach contents is often made difficult by digestion. Even recently ingested food items may be ground by jaw or pharyngeal teeth to a point at which recognition is difficult. Consequently, it is usually necessary to identify food items with reference to some characteristic part of the organism that is resistant to digestion. For invertebrates, various parts of the exoskeleton, such as eye capsules, head shields, and tarsal claws, have been commonly used. Otoliths have been used to identify fish prey (Whitfield and Blaber 1978). Macrophytes often can be identified by a characteristic shape or sculpturing along the edge of the leaves. In contrast, algal cells are usually found intact in the anterior digestive tract, and identification of these presents no special problems.

17.5.2 Choosing the Level of Identification

Many fish biologists have invested huge amounts of time identifying at the species level. In a few cases this has yielded interesting data, but often the data are too complex for meaningful interpretation. Competing predators are rarely locked in a struggle for single-species prey resources. In the last ten years, those studies that have provided the greatest insights into the trophic ecology of fish have been those that identified prey at only the higher taxonomic levels, such as order or family, and that included data on prey size. Unless there is a specific need for identification to species, higher taxonomic levels of identification are adequate to produce the most useful data per unit of time invested.

17.6 QUANTITATIVE DESCRIPTION OF THE DIET

There are three simple approaches to quantitative description of the diet: frequency of occurrence, percent composition by number, and percent composition by weight. Each approach provides distinctly different information, and, consequently, it is necessary to discuss each one in some detail.

17.6.1 Frequency of Occurrence

Frequency of occurrence is the fastest approach to quantitative analysis of fish diets. The worker makes up a list of all likely food types and records the presence or absence of each food in each specimen collected. When all specimens have been examined, the proportion of the fish that contained one or more of a given food type is calculated as the frequency of occurrence for that food type. For example, if 18 out of a sample of 22 bluegills contained one or more chironomids, then the frequency of occurrence of chironomids in the diet would be 0.82 or 82%.

These results indicate the extent to which fish in the sample functioned as a single feeding unit. If nearly all fish contained the same set of prey types, this will be clearly documented with uniformly high frequencies of occurrence. Under some circumstances, individual fish concentrate on a single food type, and this will be reflected in low frequencies of occurrence for nearly all foods. A group of omnivorous fish, however, that share a common source of vegetable matter, such as filamentous algae, but specialize individually in selection of invertebrate prey will have high

frequency of occurrence values for most algae types and low values for most invertebrate types.

It is important to note what frequency of occurrence data do not show. High frequency of occurrence does not mean that a given food type is of nutritional importance to the consumer. It may be consumed with great regularity but in very small quantities. For example, a fish that feeds on benthic invertebrates may unavoidably ingest a small quantity of sedimented algae. Because these algal cells are small and tend to be evenly distributed throughout a water body, the frequency of occurrence for each algal type may be 100%. The frequency of occurrence for individual invertebrate prey, in contrast, may not excede 75%. This does not suggest that algae are more important than invertebrates in the consumer's diet. Frequency of occurrence data, therefore, describe the uniformity with which groups of fish select their diet but do not indicate the importance of the various types of food selected.

17.6.2 Percent Composition by Number

In this approach, the number of food items of each food type is determined for each fish examined. The percent composition by number is the number of items of a given food type expressed as a percentage of the total number of food items counted. After a preliminary examination of a few samples, it is often necessary to give some thought to the appropriate unit to be counted (Fig. 17.1). If the diet consists of invertebrate prey that are largely disarticulated by the pharyngeal apparatus, some characteristic fragment must be counted. To minimize counting time, it is best to choose some fragment that is found only once per prey. Not all foods, however, are well suited to a counting approach. Detrius and higher plants that are ingested bit-by-bit are not found in discrete units of uniform size, and, thus, counts of these particles have little meaning.

For fish that feed on large prey, it is possible to count all food items in the stomach. However, most fish feed on small prey, and their stomachs often contain such great numbers that counting all items directly is impractical. Under these circumstances, subsampling is necessary. Suspend the gut contents in a known volume of water using a beaker and a magnetic stirrer. When invertebrate prey are to be counted, a large-bore pipette (5-ml graduated pipette with the tip cut off) is used to transfer a known volume of the suspension to a petri dish for counting at the required magnification. When algal cells or other microscopic foods ($< 100\ \mu$ m maximum dimension) are to be counted, the subsample is a single water drop of known volume which is put on a slide and counted by the drop-transect method (Edmondson 1974). Adjust the volume of the suspension and/or the volume transferred so that 50 to 100 items are counted for each prey type of interest. Subsampling errors become significant if fewer than 50 are counted, but counts above 100 do little to reduce subsampling errors (Allanson and Kerrich 1961). The number of items counted for each food type can be multiplied by the suspension volume and divided by the transfer volume to estimate the total number of items of that food type in the gut sample.

The importance of bacteria in the diets of some fishes is becoming increasingly apparent (Moriarty 1976; Bowen 1979). Counting of bacteria requires an epiillumination microscope. Suspend the diet in particle free water and pass a small subsample through a 0.2-μ m pore-size membrane filter. Stain the bacteria trapped on the filter with a flurochrome; acradine orange is most commonly used. Under the microscope, the light beam from the epiillumination unit is focused on the membrane filter and causes the flurochrome in stained bacteria to fluoresce. Using this approach,

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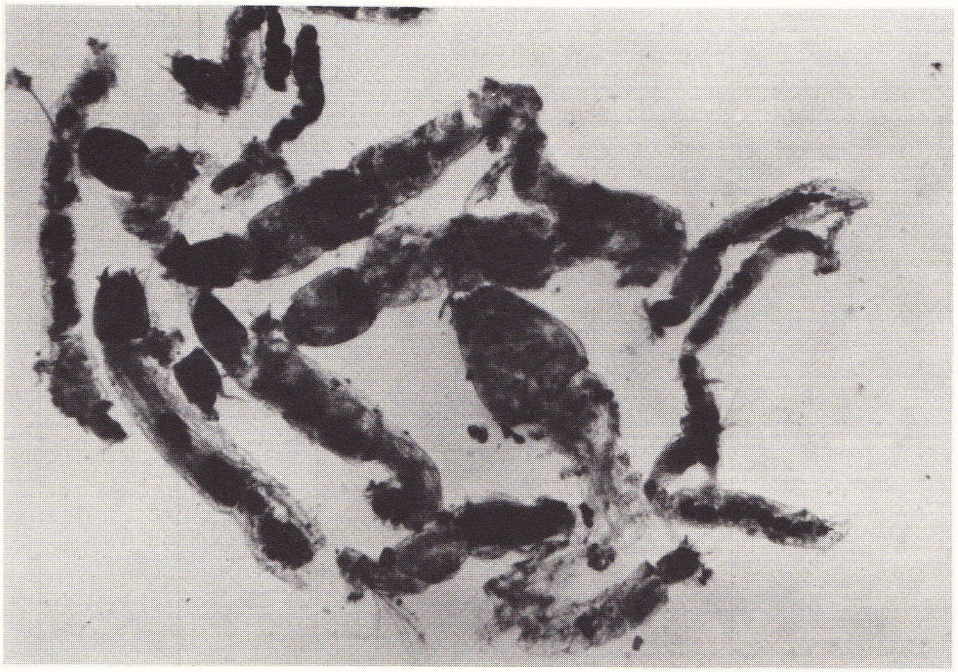

Figure 17.1. Fragments of chironomids teased from detritus in stomach contents of a small white sucker. Head capsules stay intact as softer tissues are digested and can be counted to estimate numbers consumed. Measurements of head capsule width can be used to reconstruct the weight of chironomid prey eaten.

bacteria can be distinguished quantitatively from detritus. For details of bacterial counting methods, *see* Zimmerman et al. (1978).

Unlike the frequency of occurrence approach, which provides a quantitative description only for the entire sample of fish, calculating percent composition by number describes the diet of an individual fish. To summarize results for the entire sample, calculate mean values. Remember that percentage data are not normally distributed and must be transformed for calculation of confidence intervals.

Percent composition by number data are of little value on their own, but they are useful as a step toward other calculations. The raw data from which percent composition by number are derived can be combined with estimates of feeding rate to assess the impact of predators on prey population dynamics. More commonly, percent compostion by number figures are combined with estimates of prey weight.

17.6.3 Percent Composition by Weight

In this approach to quantitative analysis of the diet, the weight of items in each food type is expressed as a percentage of the total weight of ingested food for an individual fish. If prey are large enough to be handled individually and are only slightly digested, they may be weighed directly. Both wet and dry weights have been used. Wet weight is obtained by gently blotting surface fluid from the item and weighing it (*see* chapter 15). Dry weight is obtained by drying the item to constant weight. Preweighed aluminum foil pans are useful for drying and can be purchased commercially or made easily in the laboratory (Fig. 17.2). Because these pans do not

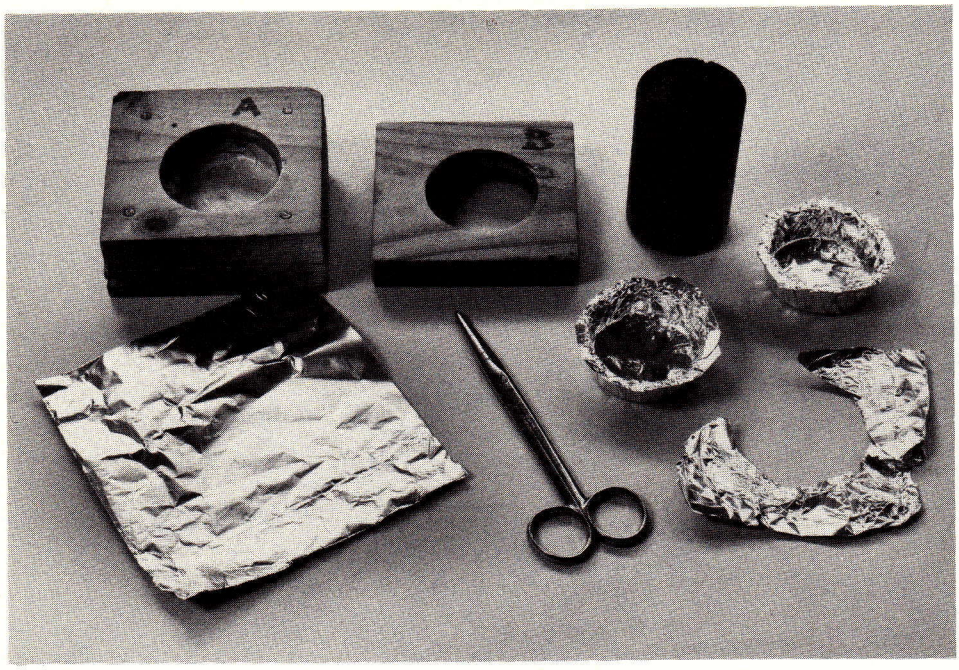

Figure 17.2. Foil pans can be made inexpensively using this simple press. A piece of foil is placed over the press base *(A)*, and then the top *(B)* is placed over the foil. The top is held lightly in place as the cylinder is used to press the foil into a dish shape. Then the top is held down firmly as the cylinder is pressed against the sides to form the top edge of the pan. Finally, the pan is trimmed with scissors. These pans hold 50 ml, but presses for pans of 0.1 - 100 ml volume work just as well. This press was made by Dudley Forsythe, Department of Zoology, Rhodes University.

absorb moisture and are light in weight, they add little weighing error. A wide range of drying temperatures has been recommended, but at 105 C drying is rapid and bacterial action is stopped. Dry weight is more precise than wet weight and should be used when a drying oven is available.

If prey are disarticulated or partly digested, it is necessary to estimate their weight at ingestion by reconstruction. In this procedure, some hard structure such as an operculum, vertebrae, or head capsule is measured and compared to a graph of hard structure size versus whole prey weight (Pearre 1980). The graph should be prepared using prey collected from the fish's feeding habitat. This type of estimate may be quite accurate for fish, but not for invertebrates. Some insect prey, especially chironomids, have vastly different weights with very similar head capsule sizes. In such cases and if there is no evidence that fish select prey according to size, it may be as accurate to sample the feeding habitat and use the average weight of a chironomid as the average weight of chironomid in the diet.

Because many invertebrates and most algae are too small to weigh directly, weight must be estimated from measurements made through a microscope. Although this approach is potentially labor-intensive, a microcomputer combined with a digitizer table (graphics tablet) can be used to reduce the time required and to increase the accuracy of measurement. I have used a camera lucida to trace the outlines of food particles from several microscope fields onto a single sheet of paper. The paper is then

put on the digitizer table and the length (long axis) and width (perpendicular to the long axis) are recorded for each particle. Some microscopes are equipped so that the depth of a particle (Z-axis) can be read from the focus knob by focusing first on the top, then on the bottom of the particle. This measurement can be recorded in the computer along with length and width. If depth is not measured, it may be reasonable to assume depth is some constant proportion of width. The volume of the food item is estimated by calculation of the volume of a geometric solid of similar size and shape. The shape approximation need not be complex since this source of error is small relative to subsampling error. Estimated wet volume is converted to dry weight as 1 mm^3 = 0.1 mg. The exact conversion varies among taxa, but this figure is precise enough for most studies (Cummins and Wuycheck 1971).

It is important to cross-check calculations for small particle diets to see if the results from reconstructed weight and indirect weight estimates are realistic. Weigh the whole sample (dry weight, corrected for subsampling), and compare that weight to the sum of estimated weights of all prey. Unless extensive digestion is expected, the sum of the individual prey weights should not exceed the total sample weight. In many cases when fish feed on benthic invertebrates, algae, or macrophytes, the sum of estimated prey weights may be much less than total sample weight. Inorganic sediment and organic detritus are usually responsible for this.

Biologists have tended to ignore material in diets that they cannot recognize as part of an organism. This is clearly a mistake since some fish can derive most or all of their nutritional needs from detritus (Bowen 1979, 1980). To distinguish between detritus and inorganic sediment, combust the sample in a muffle furnace to constant weight at 550 C. Times required to reach constant weight range from 30 minutes to 12 hours depending on the size and composition of the sample. Accuracy can be improved by cooling the samples in a desiccator prior to weighing. The weight loss on combustion provides a very close approximation to total organic weight (Dean and Gorham 1976). For the purpose of these calculations it may be reasonable to assume that organisms are 100% organic matter (with the exception of mollusks for which special calculations must be made). Organic weight in the sample that cannot be accounted for as prey weight must be present in the form of detritus. The weight of detritus may also be estimated directly from measurements made through the microscope as described above.

Percent composition by weight is the only one of the three widely used methods that begins to identify the food or foods important for the fish's nutrition. Although percent composition by number does describe the diet quantitatively, the weight differs for each food type, and, thus, no comparison of types is possible. Which is more important, 10,000 bacteria or 1 amphipod? Numbers alone do not provide an answer. Percent composition by weight quantifies food types in directly comparable weight units. With the obvious exception of mollusks for which special calculations of organic weight must be made, food value is roughly proportional to weight. Thus, percent composition by weight data do suggest the relative importance of individual food types in the nutrition of the fish.

17.6.4 Net Food Value

Biologists using the percent composition by weight approach have developed new techniques which greatly increase our ability to assess the value of different foods. Although the details are beyond the scope of this chapter, persons contemplating a study of fish diets must be aware of these developments to realistically evaluate percent

composition by weight data. These new approaches fall into two categories: those applied in the study of animal diets, and those applied in the study of vegetable and detritus diets. Although animal prey are very similar in their food value for consumers, the cost of acquiring individual prey may vary greatly. The net nutritional significance of a prey item depends not only on its weight, but also on how much time and energy it takes to search for, pursue, capture, and eat that prey. A cost-benefit concept has been applied by Werner (1974, 1977), Werner and Hall (1974, 1976), and Stein (1977) among others to account for the role of acquisition cost in diet selection by fishes. Consult these and subsequent work when you want to consider possible differences in the net food value per unit weight of different animal prey.

Food items that make up vegetable and detritus diets differ relatively little in acquistion costs but greatly in the extent to which they are assimilated. Quantities of protein and energy assimilated from each type of food in the diet must be determined before the quality of a particular food type can be assessed. For details of this approach *see* Moriarty and Moriarty (1973), Caulton (1978), Bowen (1979, 1980, 1981) and Buddington (1979).

17.7 DIET INDICES

Biologists have sometimes worried about biases in information provided by frequency of occurrence, percentage by number, and percentage by weight data. In the scientific literature there are statements that percentage by number overemphasizes the importance of smaller prey since they weigh so much less than larger prey, but that percentage by weight overemphasizes the importance of large prey because it takes more time to capture and eat a large number of small prey (Pinkas et al. 1971; George and Hadley 1979; Hyslop 1980). Because of this dissatisfaction with a single data approach, biologists have created several formulas that combine frequency of occurrence, percentage by number, and/or weight data into a hydrid index intended to compensate for the perceived biases of the individual indices. Although these indices may at first offer some intuitive appeal, there is no identifiable biological basis for their interpretation. The fault lies not with frequency of occurrence, percentage by number, or percentage by weight data, but with the investigator's failure to define clearly the objective of the analysis. For example, if the investigator wishes to determine the impact of the predator on a prey's population dynamics, then percentage by number will provide useful data without regard to the size of different prey types. If the investigator wishes to measure the contribution of prey to the predator's nutrition, then percentage by weight is fully adequate. A sample of 25 bass stomachs which contains a total of 5,000 Cladocera weighing 1 g and one fish weighing 99 g indicates that 99% of the bass population's gross energy comes from fish, in spite of the relative numbers of prey consumed. It may be that Cladocera are digested more rapidly than fish or that the single fish prey is not representative of the true diet because the sample size was too small. These problems are not biases attributable to percentage by weight data but to the sampling design. Use of indices that combine frequency of occurrence, percentage by number, and/or percentage by weight data does not solve these problems.

There is a second group of indices which has basis in scientific theory and may be of use in analysis of diet data if the limitations are kept well in mind. Electivity indices can be used to compare the diet selected by fish to the available resources in the feeding environment. The index value indicates the extent to which the observed diet differs from a diet selected at random. This concept was developed by Ivlev (1961), who

compared diets and resources for fish feeding in precisely controlled aquarium experiments. Electivity indices have been applied in field studies by a number of workers (*See* Strauss 1979). Application of the concept in field situations makes it necessary to determine accurately the relative abundances of all potential prey. Because of the patchy distribution of most prey, this is a formidable sampling problem (Strauss 1979, 1982). Once electivity has been established, however, it can provide invaluable clues to environmental factors that influence the nutrition of the fish.

Indices which quantify diet overlap are based on niche theory. This area of ecology is evolving rapidly, and at least ten different measures of diet overlap have been proposed. At present, opinions are divided as to which measure has the most desirable mathematical properties, the most statistical reliability, and the most biological relevance (Hurlbert 1978; Jumars 1980; Wallace 1981). Extensive diet overlap is not conclusive evidence for competition because the resources may not be in short supply. Measures of diet overlap may be useful if diets of two similar species are to be compared across a wide range of different water bodies. An inverse correlation between diet overlap and growth rate may suggest that competition for food resources limits growth in some waters. Alternative explanations should be considered as well.

The advantage of these indices is that they may reveal relationships in the data that are not otherwise apparent. The disadvantages are that they possess poorly understood statistical properties and that they shift attention away from the original data. Indices that remove the complexities of original data sometimes let us think that we know more than we do. For these reasons, indices of electivity and diet overlap must be used with full recognition of their limitations.

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