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Etymology of Ghoti

George Bernard Shaw (1856–1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

Fish gut content analysis: robust measures of diet composition

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Abstract

Trophic studies are fundamental components of our understanding of biology and ecology, from observing individual organisms to modelling ecosystem function. When measuring fish gut contents, we rely on collecting samples that represent snapshots in time. Many limitations in extrapolating from these snapshots are well understood. However, there seems to be a widespread belief that when quantifying the composition of gut contents, more detail always provides more information. We highlight some fundamental problems with the apparently more quantitative approaches (i.e. 'bulk' methods measuring biomass or volume of each prey type) and suggest that frequency of occurrence (%F) provides the most robust and interpretable measure of diet composition. The additional information provided by bulk methods contains unquantifiable and potentially significant error from a variety of sources. In our experience, the contents of most guts cannot be unambiguously separated into prey categories for quantification because of the presence of unidentifiable and inseparable partially digested material. Even where separation is possible, the composition of a gut at one point in time is affected by many unquantifiable factors unrelated to the actual composition of the diet. Conse-

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quently, bulk methods provide ambiguous interpretations from superficially quantitative models. Where research questions require more detail, these problems mean there is little alternative to time-consuming approaches like prey reconstruction. However, for the descriptions of dietary composition presented in many studies, % F provides robust data that overcome many of the limitations of the more detailed approaches and provides considerable logistical and economic benefits.

Keywords digestion, feeding habits, stomach contents, trophic ecology.

Introduction

Debate over how to best represent the composition of gut content samples has a long history in dietary studies of both fish (Hynes 1950; Pinkas *et al.* 1971; Cortes 1997) and terrestrial animals (e.g. McAtee 1912; Norris 1943). There are many methods for quantifying gut contents of fishes, ranging from simple presence/absence or frequency of occurrence (%F) of different prey categories (e.g. Abrantes *et al.* 2011) to estimates of the nutritional value of the originally ingested prey items (e.g. Hartman and Brandt 1995). For a detailed description of the available techniques, see reviews by Hynes (1950) and Hyslop (1980). The %F technique relies simply on the positive identification of some body part of the prey to provide accurate and precise data on the dietary composition. The relative importance of various prey types is then inferred from the proportion of total guts containing each prey type. Hyslop (1980) considered that %F provides only a crude qualitative indication of dietary importance because it lacks information on the relative bulk of each prey type. This point of view appears to have been widely influential, and the majority of the thousands of diet studies employ apparently more quantitative techniques such as measuring the contribution of each prey type by weight or volume (Table 1). Additionally, compound indices incorporating several measures including numbers, volume and/or weight have been proposed to provide a more balanced representation of dietary importance (Pinkas *et al.* 1971; Liao *et al.* 2001) and to provide standardized methods for reporting and comparing fish diets (e.g. Mohan and Sankaran 1988; Cortes 1997, 1998). The compound indices developed by fish biologists have also been promoted for use by terrestrial ecologists to overcome the biases of the particular emphasis of individual metrics of gut composition (Hart *et al.* 2002).

The theoretical applicability of the various techniques under a range of scenarios and for highlighting different aspects of trophic ecology has been discussed at length (e.g. Hyslop 1980; Cortes 1998; Hansson 1998), and we do not address those issues here. Instead, we focus on two underlying and fundamental problems with measures of gut composition by bulk (volume or weight) which became apparent when quantifying the gut contents of several thousand fishes spanning multiple trophic niches from coastal systems in north-eastern (Sheaves and Molony 2000; Wilson and Sheaves 2001; Baker and Sheaves 2005, 2009a,b; Sheaves *et al.* 2007) and south-western Australia (A. Buckland unpublished data). Firstly, in the vast majority of guts, it was not possible to physically separate different prey types with any level of accuracy due to partial digestion. Even if it was possible, there is a second, more broadly relevant issue: the detailed gut composition observed at one point in time is the result of a variety of unquantifiable factors that interact to prevent the observed composition from providing an accurate representation of the actual composition of the prey consumed. Although the review of Hyslop (1980) discusses several of the factors to varying degrees, the recommendations of Hyslop and subsequent application of bulk techniques in thousands of studies appear to give little further regard to these fundamental problems. In this paper, we aim to highlight these problems using examples from the literature and our own experience. For studies that require detailed quantification of the bulk of different prey types consumed, approaches such as estimating the original prey size from partial remains are appropriate (Scharf *et al.* 1997). However, for the descriptions of dietary composition presented and analysed in many studies, the frequency of occurrence of each prey type would provide the most robust and interpretable data.

Table 1 Summary of diet analysis from 100 of the most recent papers to cite Hyslop (1980) (from a total of 1499, Web of Science, accessed 10 July 2012).

	%F only	Bulk	Reconstructed bulk	Compound index	Implied precision ≤ 0.1	Pooled summary	Multivariate analysis
% of studies	2	82	3	43	–	–	–
% of those employing Bulk	–	–	3.7	52	79	46	61

%F only: studies that quantified diet composition by frequency of occurrence only. Bulk: studies that employed gravimetric, volumetric or points methods. Reconstructed bulk: studies which reconstructed original prey size from remains in the gut. Compound index: incorporated bulk measures (usually along with prey numbers and %F) into compound index to quantify diet composition. Implied precision ≤ 0.1: bulk data presented to one or more decimal places. Pooled summary: gut contents quantified by bulk but only pooled summary data presented. Multivariate analysis: bulk gut content data used in multivariate analyses. No data are presented for implied precision, pooled summary or multivariate analyses for the 18% of studies not employing bulk methods (used %F and/or enumerated prey), because these factors relate specifically to problems with the bulk methods.

Quantifying gut contents

In our experience, the separation of prey items in fish guts can rarely be carried out unambiguously and attempts to do so introduces unquantifiable errors to any measure of prey bulk. Loose tissue amongst partially digested prey remains in the stomach (Fig. 1) cannot be visually allocated to any prey category with absolute confidence, regardless of how prey categories are defined (Schafer *et al.* 2002). This is because it may be the remains of separate prey items no longer represented by identifiable parts, or an inseparable mixture of digested tissues from multiple prey items. Consequently, loose tissue allocated to any category other than 'unidentified' potentially adds error to each volume or weight value obtained, meaning the summarized dietary composition contains unmeasurable and potentially substantial error. The points method, whereby each prey category is allocated points in proportion to its visually estimated contribution to gut volume (Hyslop 1980), allows for the estimation of the volume of each prey category without the need to physically separate the gut contents. However, separation must be carried out visually, and even under simulated ideal conditions using discrete artificial prey items, estimates of composition using the points method are highly subjective (Marrero and Lopez-Rojas 1995).

The level of digestion of prey determines the difficulty in accurately separating prey types (Hyslop 1980), and this varies according to the type of prey and the time since ingestion (MacDonald *et al.* 1982; Legler *et al.* 2010), as well as the prey handling and feeding mode of the consumer, for example, grinding prey or biting it into pieces (Scharf *et al.* 1997). Many diet studies use gears, such as gill nets (e.g. Salini *et al.* 1990) and long lines (Barnett *et al.* 2010) that entangle or accumulate fish over an extended sampling period. This exacerbates the problem of separating prey types due to post-capture digestion of gut contents during the period between capture and retrieval of the gear (Rozas and LaSalle 1990; Haywood 1995).

The fishes we have examined in our dietary studies were mostly collected by techniques such as seine netting and angling, with captured fish placed immediately in an ice slurry to halt the digestion process and frozen as soon as possible. Despite this protocol, the study of Baker and Sheaves (2005) found <5% of individual guts contained intact, easily separable prey items with no free tissue (Table 2). Amongst the almost 1900 fishes summarized in Table 2, 72.4% of stomachs contained only one identifiable prey type along with unidentifiable loose tissue, an additional 19.2% contained two prey types and loose tissue (Fig. 1). Allocating this tissue amongst the one or two identifiable prey categories in these stomachs would have resulted in occurrences of unidentifiable prey more typical of those reported elsewhere. Whilst it is probable that this approach would often correctly classify loose tissue, for example, assuming that the loose tissue in Fig. 1b is part of the easily identifiable digested fish, this cannot be visually confirmed, so allocating it as such is not a rigorous method of quantifying dietary composition. Furthermore, physically separating unidentifi-

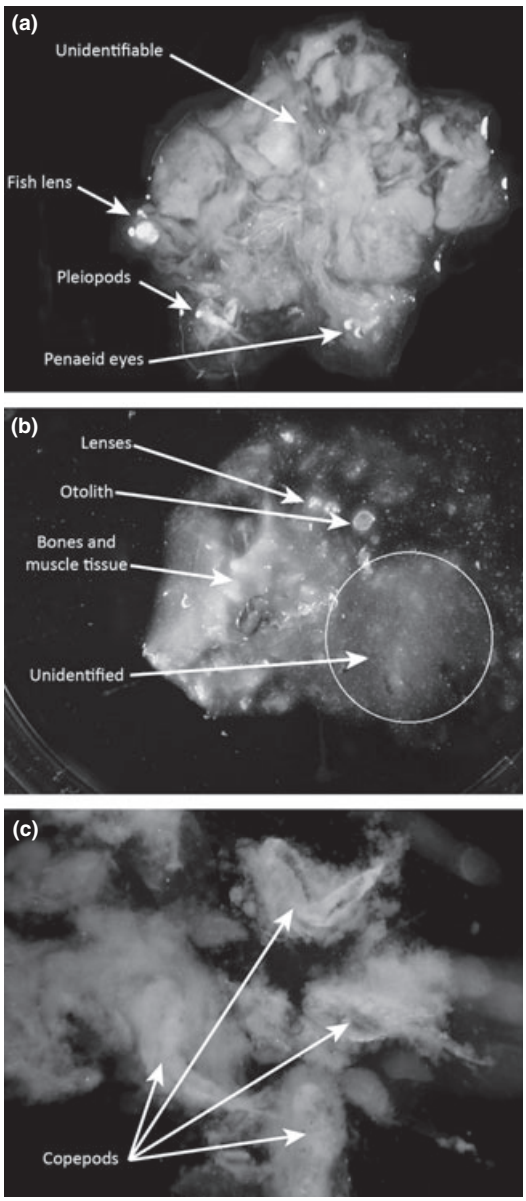

Figure 1 Typical prey remains from the stomachs of fishes examined by the authors. (a) fish and penaeid shrimp; (b) partially digested fish remains; (c) copepods; all with unidentifiable tissue.

able tissue from identifiable remains is highly subjective; what is fish and what is unidentifiable in Fig. 1b? Even in guts containing easily identifiable prey such as whole small crustaceans, individual items are regularly covered with a coating of mucous (Fig. 1c). Like other unidentifiable material, its origin is uncertain, and because it is usually not possible to physically separate the mucous from each prey item, the resulting measures of

Table 2 Percentage of stomachs (n = 1889) of tropical estuarine fishes containing different numbers of prey categories, with or without loose unidentifiable tissue that prevents the accurate separation of individual prey types for quantification by volume or weight.

	Number of identifiable prey categories						
Unidentifiable tissue	1	2	3	4	5	6	Total
Present	72.4	19.2	3.1	0.4	0.1	0.1	95.3
Absent	3.8	0.8	0.2	0	0	0	4.7

Data from Baker and Sheaves (2005), where prey categories and consumer identities are defined.

volume or weight may be significantly biased. The presence of unidentifiable and inseparable material in the guts of fishes is not a feature of particular trophic groups; our studies have examined fishes spanning the full spectrum of trophic roles and from both tropical and temperate waters.

Despite the practical problems of accurately separating prey types, gut composition data measured by volume or weight are regularly presented to one or more decimal places (Table 1), implying, in our experience, an unrealistic level of precision. Multiplying such values together to calculate indices of dietary composition (e.g. Pinkas *et al.* 1971) serves to magnify the already potentially significant errors associated with each parameter (Hyslop 1980; Tirasin and Jorgensen 1999), yet this is carried out in around half the studies employing bulk methods (Table 1). Biases in compound indices related to the taxonomic resolution of prey identification have been discussed (Hansson 1998; Cortes 1998); however, the underlying biases and unquantifiable errors inherent in the individual parameters included in these indices have received little consideration.

Interpreting dietary composition

Whilst the problems of separating prey categories represent a serious practical limitation of measuring diet composition using bulk methods, there are further underlying problems that apply more generally to quantifying sample composition. Even where it is possible to accurately separate prey items in a gut, the actual composition of a gut content at a single point in time is affected by a broad range of unquantifiable factors unrelated to

the actual composition of the diet consumed (MacDonald *et al.* 1982). The sample size of consumers, mechanical prey handling, differential digestion and evacuation rates of different prey types and volumes, and the order of ingestion, combine to provide bulk data that are ambiguous, contain unquantifiable error and are difficult to interpret (Hyslop 1980; Jobling 1981; MacDonald *et al.* 1982; Haywood 1995; Rindorf and Lewy 2004). The result is that a detailed measurement of the composition of a sample, beyond recording the presence of each category, will often provide little additional useful information relevant to the underlying ecological patterns we seek to understand (Royle and Nichols 2003). %F data, on the other hand, are precise and unambiguously interpretable because the values presented represent simply the proportion of individuals containing a particular positively identified prey type.

Unusual prey items in the gut of a single predator have the potential to greatly influence the data obtained by the bulk measures. For example, Salini *et al.* (1990) report that 37% of 214 *Arius proximus* (Ariidae) contained fish prey and that fish contributed 61.1% of the total dry weight of prey consumed by this species. Whilst the interpretation of the meaning of 37% occurrence is clear, that is that 79 of the 214 individuals had consumed fish, the meaning of 61.1% dry weight of fish prey is ambiguous. In fact, Salini *et al.* (1990) further explain that one individual *A. proximus* had consumed a single large fish prey which accounted for 47% of the total dry weight of prey consumed by the 214 individuals. Examples of such issues that confound interpretation of diets quantified by bulk are rarely reported or discussed, but are likely to be quite common.

At small sample sizes, descriptions of composition obtained by bulk (volume/weight) can diverge considerably from those provided by %F (e.g. Salini *et al.* 1990; Haywood *et al.* 1998). This is because of the increased influence of unusual prey items, digestion rate and the order of ingestion. For example, a small sample of fish may have equal occurrence of two prey types, but a much greater contribution by bulk of one prey because either (i) a greater bulk of that prey was consumed, (ii) that prey was consumed more recently, (iii) has been digested more slowly or (iv) is able to be identified over a greater range of digested states than the other. Summaries of dietary composition by bulk make no distinction between these scenarios, even though their meanings are quite different. This is exacerbated by the potential for a number of fish in one sample to have fed on a series of prey types in the same order (Tirasin and Jorgensen 1999), leading to a great overemphasis of the importance of the prey type consumed last or digested slowest. Furthermore, as digestion proceeds, the components that remain identifiable and potentially measureable in the gut for the longest tend to be those components that are indigestible or otherwise of limited nutritional value, for example mollusc shells (Hyslop 1980). These confounding factors have less influence on interpretations of %F data because individual prey items are recorded as present from the point of ingestion until the last identifiable prey component is gone, whilst the bulk of a prey item continuously changes throughout the digestion process.

In larger samples, with broad spatio-temporal distribution, the effects of digestion rate and order of ingestion are less influential on dietary compositions quantified by bulk because it is unlikely that there would be any consistent order of ingestion of particular prey types through space and time. Published data indicate that at large sample sizes (≥ 100), quantifying the diet by either bulk or by %F usually provides similar representations of dietary contributions (Fig. 2). For example, the key ontogenetic shift in the diet of the flathead *Platycephalus fuscus* (Platycephalidae) from feeding heavily on gammarid amphipods at small sizes to

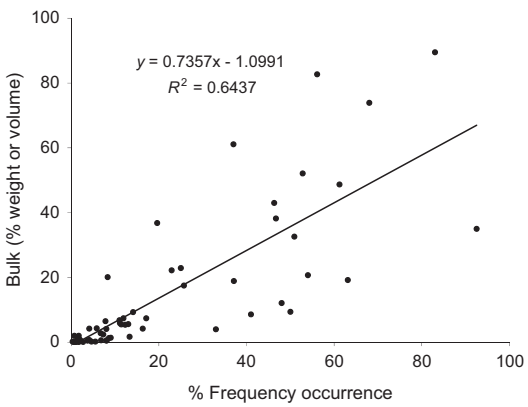

Figure 2 Published contributions of prey items measured by both% frequency of occurrence (%F) and by bulk (either %volume or weight). Includes data on nektonic prey, for species with a sample size ≥ 100, from Salini *et al.* (1990, 1998), Schafer *et al.* (2002), Brancini and Perez (2005) and Xue *et al.* (2005).

fish at larger sizes (Baker and Sheaves 2005) is highlighted by both %F and when diet composition was quantified by estimating the contribution by volume (Fig. 3). However, all of the potential ambiguities in the bulk values remain, thus making the more complicated methods redundant (Hynes 1950; MacDonald and Green 1983). Should the two approaches presented in Fig. 3 have yielded conflicting results as they would do at some smaller sample size, only the %F data could be interpreted with confidence. An alternate way to consider this is that when sample sizes are sufficiently large to obtain reliable and robust interpretations, most of the information on diet composition is captured by %F (Fig. 3), because the greater the bulk of any prey that is consumed, the more likely it is to occur in the gut of any particular individual (Royle and Nichols 2003).

Conclusions

We recognize the theoretical benefits of detailed information on the composition of a fish's diet, but the objectives of many of the studies based on diets quantified by bulk methods could be more validly met by employing %F, in our opinion the most robust and interpretable approach. For some questions such as quantifying nutritional support or the predation impact of consumers, simple presence–absence data will not provide adequate information on diet composition. In these instances, reconstruction of the original prey items using remains that have a known size relationship to whole prey provides the most accurate measure of the size or bulk of each prey type consumed (e.g. Hartman and Brandt 1995; Scharf *et al.* 1997; Buckel *et al.* 1999). This method is time consuming and not commonly employed (Table 1), but

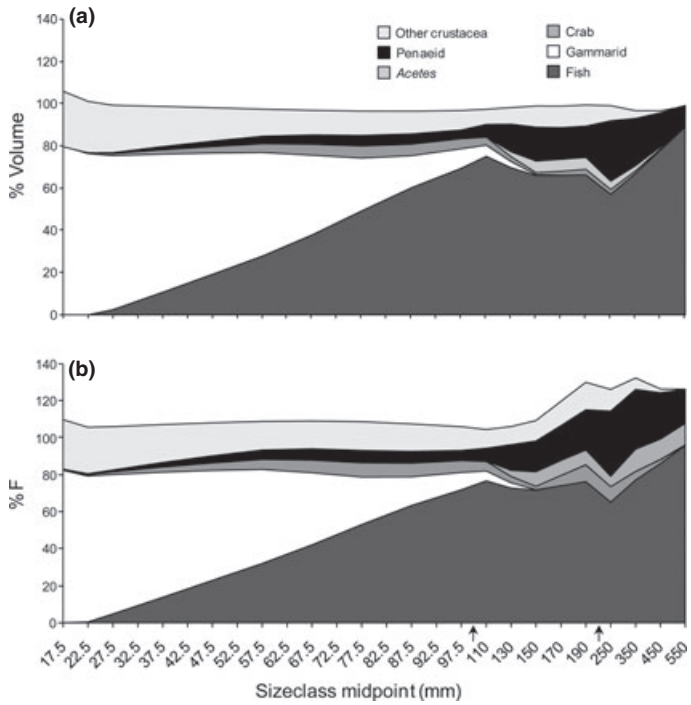

Figure 3 Ontogenetic dietary models for *Platycephalus fuscus* (Platycephalidae) (n = 357) from tropical estuaries in north-eastern Australia (from Baker and Sheaves 2005), based on: (a) visually estimated % contribution of each prey type by volume, assuming loose unidentifiable tissue belonged to identifiable prey categories in the gut and (b) frequency of occurrence or presence/absence of each prey type in each gut. Prey categories in legend from top to bottom, left to right, match stacked categories from top to bottom, most clearly seen at 130 mm on x-axis. All data were lowess smoothed using smoothing factor 0.7. The upper limit of the (unsmoothed) frequency of occurrence figure represents the mean number of prey types per individual gut through ontogeny, whilst that of the (unsmoothed) volume model is constrained to 100%. Note the size class widths along x-axis change, indicated by the arrows below the x-axis in b), being 5 mm classes to 100 mmTL, 20 mm for 100–200 mmTL and 100 mm classes from 200 to 600 mmTL.

where it is deemed important to accurately determine the bulk of different prey types, this provides the most robust approach to quantifying the true composition of the diet. Reconstructing original prey size from measurable parts in the gut is based on the assumption that the prey was consumed whole; however, this assumption can be stated clearly and tested against observations of the freshest prey of that type regularly found in the guts.

Around half of the studies employing bulk methods only present data and analyses based on some measure of the general composition of the diet, and more than half of recent studies go on to perform complex multivariate analyses on these data (Table 1). In all cases, it is important to recognize the fundamental practical limitations of the apparently more detailed methods for quantifying gut content composition and to give careful consideration to how the detailed contents of a fish's gut, ingested in some unknown order at variable and unknown points in time, actually relates to the composition of the diet as it was ingested by the consumer. The %F approach at worst provides only a minor loss of information relative to more intensive and superficially detailed methods, and at best provides the only robust and interpretable models. It can also be executed with far less effort, and hence cost, than more detailed methods.

In an early review of fish gut content analysis, Hynes (1950) hinted at the problems of false accuracy in several of the methods, but only specifically discussed the problem of counting the number of prey items. Hynes points out that enumerating prey is realistically only an estimate of prey numbers because of the breakage of items into pieces. The advantage of 'simpler' methods such as frequency of occurrence is that they *'avoid the unwarranted impression of accuracy which results from the use of counts…which has led some authors into basing a great deal of mathematical analysis on data which would appear to be fundamentally uncertain'* (Hynes 1950). The concerns we raise here, decades after the reviews of Hynes (1950) and Hyslop (1980), are not about the theoretical value of the information provided by volume or weight indices, rather it is about the level of accuracy implied in thousands of studies from data that are in practice 'fundamentally uncertain'.

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