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Standardising fish stomach content analysis: The importance of prey condition

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ABSTRACT

Comparisons of fish trophic data are limited by the range of methods used to quantify dietary composition, with scientists yet to agree on a standard approach to stomach content analysis. This study examined how prey type and condition of stomach contents influenced identification of prey and the ability to estimate dietary importance by methodologies based on volume, weight, number and frequency of occurrence. A total of 154 stomachs were examined from six trophically diverse, temperate fish species. The condition of prey i.e. entirety, digestion state, and presence of mucus were recorded for each stomach, and the taxonomic level to which prey could be identified to assessed. The influence of prey condition on the application of each metric was then assessed. Descriptions based on prey volume or weight were significantly affected by differences in prey condition. In contrast, the simple presence/absence or frequency of occurrence approach (%F) provided a rapid, unambiguous and reliable account of diet composition and was not affected by the condition of prey. It was the only approach able to quantify the full spectrum of prey types in a consistent manner, making it the most practical metric. Variable prey condition also highlighted uncertainties in prey identification. We recommend routine reporting of how prey condition influences identification, the specific approaches used, and any assumptions made in identifying prey. In addition, %F data should be reported as a nested hierarchy of taxonomic levels which allows these data to be readily standardised across studies and used in meta-analyses.

1. Introduction

From elucidating the biology of a single species (Sarre et al., 2000; Graham et al., 2007) to understanding trophic flows and the functioning of ecosystems (Winemiller and Polis, 1996; Andrea and Ojeda, 2001; Cox et al., 2002), the benefits of investigating and describing diet are far reaching. In fish research, defining trophic habits/levels has long relied on the direct quantification of stomach contents (Hynes, 1950; Hyslop, 1980). However, this has not always provided data that can be directly compared across a range of studies (Cortés, 1997). The taxonomic level to which prey are identified, and the metric used to quantify dietary composition (e.g. volume, count; Table 1) can vary among studies, with the different methodologies used to quantify diets not directly comparable with data from other approaches (Berg, 1979; Hyslop, 1980; Hansson, 1998). Comparing trophic data over broad spatial and temporal scales provides insights rarely possible within the constraints of individual studies (Jackson et al., 2001; Elliott et al., 2007). Consequently, the value of studies that cannot be compared across regions, time periods and changes in environmental conditions is limited. Although standardising dietary analyses has been advocated in the past (Pinkas, 1971; Cortés, 1997), consensus has not been reached on a standard methodology (Baker et al., 2014).

Metrics used to quantify prey contribution to diet have primarily been reviewed based on their ability to represent prey importance i.e. the overall value of a prey item to the consumer (e.g. Hyslop, 1980; Cortés, 1997). However, some studies have shown that all metrics provide similar accounts of prey importance and dietary composition at large samples sizes (Hynes, 1950; Baker et al., 2014). As such, the ability of each metric to represent general prey importance has proved to be an inappropriate foundation upon which to establish a standard. Reviewing metrics in this way also reveals little about the reliability of final values/data delivered by these metrics, a factor crucial for studies aiming to draw meaningful and valid conclusions from cross study comparisons of dietary data. A recent review by Baker et al. (2014) suggested that a standard measure of prey quantity is better defined when metrics are reviewed in light of the prey conditions commonly

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Table 1
Summary of the main metrics used to describe the dietary composition of fish. Final prey contribution presented as mean percentage (final column).

Metric	Type	Description	
Frequency of occurrence	Presence/Absence	Proportion of individuals containing a particular prey type	%F
Numerical	Count	Number of items of a prey type as proportion of total number of prey items	%N
Volumetric: Points	Bulk	Visual estimate of relative volume by allocating points to each prey type (points out of 10 or stomach fullness value, also out of 10)	$\%V_P$
Volumetric: Grid	Bulk	Area of each prey type when prey squashed to uniform depth	$\%V_G$
Volumetric: Displacement	Bulk	Volume of water displaced by each prey type	$\%V_D$
Gravimetric: Weight	Bulk	Wet or dry weight of each prey type	%W

Note: Detailed descriptions of each metric can be found in Hynes (1950) and Hyslop (1980).

found at the time of analysing stomach contents. Describing problems encountered while "*quantifying the gut contents of several thousand fishes*" they concluded that the presence of inseparable, unidentifiable and partial prey introduced considerable error to estimates based on mass or volume, while frequency of occurrence (%F) was the least affected, providing unambiguous, consistent results. Previous reviews have acknowledged the potential effects of prey condition, particularly fragmented and digested prey, on the results of dietary studies (e.g. Hynes, 1950; Windell and Bowen, 1978). However few have attempted to directly assess the influence of prey condition on diet metrics and thus the suitability of different metrics (including those they recommend) to quantify diet when prey condition is poor. Instead the onus was mostly placed to the investigator to make an assessment of prey condition e.g. "*allowance must be made for differential digestion*" (Hyslop, 1980). The findings of Baker et al. (2014) suggest that the impact of poor prey conditions on dietary studies is widespread, however, direct evaluation against all metrics is lacking and the implications for non-nektivore trophic groups less clear.

The presence of partial, digested and/or unidentifiable prey also creates uncertainty in the taxonomic level to which prey can be identified. The taxonomic resolution to which prey are identified varies considerably among studies (e.g. Elliott, 1967; Baker and Sheaves, 2005; Saunders et al., 2012) and is influenced by a number of factors, including, the objectives of the particular study, the taxonomic knowledge of the prey species, the condition of the prey, and the approaches employed by investigators to identify prey. In many instances, the identities of prey are reported to fine taxonomic resolutions that, in our experience, would not be possible to achieve for all prey items based on visual observation alone. In such cases it appears that investigators are relying on information additional to that available from the stomach contents alone, for example using prior knowledge of the prey assemblage (Mauchline and Gordon, 1985; Gray et al., 2015), or assuming identity based on similar positively identified prey (Hynes, 1950). Few studies provide more than a statement to the effect that '*prey were identified to the lowest taxonomic level possible*'. Some studies do discuss how prey condition influenced identification (e.g. Balcombe et al., 2005), but rarely in enough detail to assess the reliability of any particular taxonomic resolution presented. The inconsistency in classification level makes it difficult to compare studies, which may be further compounded by unreported assumptions in prey identification.

To determine the most suitable standard approach for quantifying dietary composition, this study investigated the influence of stomach content condition on the ability to identify and quantify dietary components using the most commonly employed dietary metrics. Building on the conclusions of Baker et al. (2014) we adopted the following approach: (1) establish the condition of stomach contents for six trophically diverse, temperate estuarine fish fauna, (2) determine how often prey are identified from partial and/or digested remains and, how this influenced the taxonomic resolution in which prey could be classified and, (3) determine the influence of prey type and condition on the application of six different diet metrics.

2. Materials and methods

2.1. Consumers for dietary analysis

Stomach content analyses were performed on an assemblage of estuarine fishes collected from the Swan-Canning Estuary, Perth, Western Australia in 2011 and 2012. The consumers examined covered a range of feeding guilds, including a sparid *Acanthopagrus butcheri* (benthic generalist), an atherinid *Leptatherina wallacei* (pelagic feeder), a mugilid *Mugil cephalus* (detritivore), a platycephalid *Platycephalus endrachtensis* (nektivore), a gobiid *Pseudogobius olorum* (benthic omnivore) and a paralichthyid *Pseudorhombus jenynsii* (benthic carnivore) (Table 2). Most fish were collected from nearshore waters of the middle Swan Estuary using a 41.5 m seine (20 mm mesh in the wings, 9 mm in the cod-end), in the austral spring (Sep-Nov) 2011. To account for ontogenetic diet shifts and any diel cycles in feeding patterns, sampling was conducted at dawn, midday and dusk and individuals in two contrasting size classes of each species (i.e. small and large) were kept for

Table 2
The mean size (total length, mm), size range and number of fish examined in each of the six species of fish collected at different times of day from the Swan-Canning Estuary, Western Australia, in 2011 and 2012. A total of 30 fish were collected for each species, except for *Pseudorhombus jenynsii* (21) and *Platycephalus endrachtensis* (13).

Species	Category (mm)	Mean Range	Dawn	Midday	Dusk	TOTAL
Acanthopagrus butcheri	Small ≤ 135	115 (97–131)	5	5	5	15
	Large ≥ 180	213 (182–300)	5	5	5	15
Leptatherina wallacei	Small ≤ 45	39 (34–44)	5	5	5	15
	Large ≥ 50	54 (50–59)	5	5	5	15
Mugil cephalus	Small ≤ 90	67 (53–88)	5	5	5	15
	Large ≥ 120	143 (122–165)	5	5	5	15
Pseudogobius olorum	Small ≤ 30	26 (23–29)	5	5	5	15
	Large ≥ 35	44 (36–53)	5	5	5	15
Pseudorhombus jenynsii	Small ≤ 115	88 (45–115)	5	4	2	11
	Large ≥ 120	153 (122–205)	5	5	0	10
Platycephalus endrachtensis	Small ≤ 175	142 (66–174)	3	7	0	10
	Large ≥ 225	324 (225–391)	0	0	3	3
Total						154