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

analysis (Table 2). The aim was to collect a total of 30 fish for each species (15 small and 15 large) and 5 individuals from each time of day.

Additional samples were collected in Autumn 2011 and 2012 (April to May) to supplement the sample size of *P. endrachtensis* and *P. jenyntii* (see total n in Table 2). These fish were collected from the lower Swan-Canning Estuary where seasonal changes in salinity, dissolved oxygen and temperature are small between autumn and spring and thus unlikely to drive seasonal variations in diet or impact the outcomes of this study (Prince et al., 1982; Loneragan et al., 1989; Gaughan et al., 1990; Swan River Trust, 2013). To halt stomach content decomposition, all fish were euthanised immediately after capture in an ice-water slurry, before being packed in ice and transported to the laboratory for freezing.

2.2. Prey condition

The condition of each item in the stomach contents was assessed and described so that its influence on identification and quantification of prey could be assessed. Prey were only grouped into separate prey items if they were of the same broad prey type (e.g. fish), entirety (i.e. if the prey body was whole or partial) and prey state (see Appendix A Table A1) (as well as assigned the same taxonomic level, Section 2.3). For example, multiple amphipod fragments of the same prey state found within a single fish stomach would be grouped as a single prey item for this analysis. Mucus (clear to cloudy, sticky fluid of unknown origin), detritus (particulate organic material of consistent composition (mostly a brown mush) and often with benthic diatoms present), and unidentifiable organic matter (e.g. digested tissue) were grouped separately where possible but not recorded for prey entirety or state (with exception of unidentified matter which by definition is prey state 7—see below).

The state of each prey item reflected effects of digestion, feeding style, mechanical handling of prey upon ingestion, and prey type on condition. Prey state and entirety were considered separately because some consumers bite prey into pieces before ingestion, and therefore undigested, but fragmented body parts, may be present in the stomach. Previous experience with fish stomach content conditions was used to develop prey state categories for the prey types of interest. Detailed descriptions of prey states ranged from 1; representing minimally damaged (and most likely freshly ingested) prey items, to stage 6 (mainly fragmented and barely recognisable); with stage 7 indicating material that was no longer identifiable (Appendix A Table A1).

The prey state and entirety of each prey item and the presence of unidentifiable matter, detritus or mucus were recorded for each stomach. To describe the general condition in which prey were found, prey items were analysed within broad prey categories, with the proportion of fish stomachs containing a prey item in each condition (prey state and entirety) summarised for each major prey type. The major prey categories, polychaete; amphipod; bivalve; prawn; fish (teleost); and insect (terrestrial), were chosen to represent items consumed frequently by many fish species and a range of prey morphologies, with different probable rates of digestion (e.g. soft bodied polychaetes in contrast to hard shelled bivalves).

To examine variability in prey condition and determine if there are circumstances in which all prey are found in equivalent conditions, the effect of fish species, diel period and fish size on prey state (i.e. the 7 categories) was investigated using a multivariate classification and regression tree (mvCART) (De'Ath, 2002). Classification and regression trees work by successively splitting the data into homogenous groups that minimise the total variation in the response variable (in this case, prey state). Trees are presented graphically, with splits at the top of the tree more important than those at the bottom and the relative lengths of the vertical lines associated with each split indicating how much of the variability in the dataset is explained by the associated split (De'Ath, 2002). In the present study, each 'leaf' of the tree represented the proportion of fish stomachs with a prey item present in one of the 7

prey states and the importance of each explanatory variable (i.e. fish species, diel period or fish size) to prey state determined by its position on the tree. Ten-fold cross validation was used to estimate the prediction error for trees of different sizes and the tree with the lowest cross validation error selected as the final model. As detritus and mucus were not assigned a prey state value, they did not contribute to the mvCART dataset. Prey composition for each fish species (%F) were used to interpret the patterns revealed from the mvCART analysis. Note: The selection of a full tree for the final model, small sample sizes, and the absence of a major prey group from the analysis, necessitate that the mvCART presented in this study be interpreted cautiously. The intent of this analysis was to evaluate for effects of diel period within the given dataset, with results not intended to be widely applicable or reflective of broader patterns in fish feeding.

2.3. Prey identification

One objective of this study was to assess the taxonomic detail in which prey can be independently classified (e.g. to family or species) based solely on the morphological characteristics evident from the prey in the stomach. Therefore, no prior knowledge of the prey assemblage was used for identification purposes. For example, while *Ostorhinchus rueppellii* is the most commonly (and for most locations, only) apogonid species found in the Swan-Canning Estuary, for this study any apogonid otoliths found free, and with obvious signs of digestion would still be deemed identifiable only to the family level. Each prey item was assigned to one of four taxonomic categories; species, genus, family or above family and the features used for making positive identifications to each taxonomic level recorded. Separated body parts were assumed to belong to the same ingested prey item when each segment was in a similar condition, and not beyond prey state 3 (Appendix A).

The proportion of fish stomachs with a prey item assigned to each taxonomic category was calculated for each of the broad prey groups: polychaete, amphipod, bivalve, prawn, fish, and insect; and the typical condition of prey was described for each taxonomic category. Larval/juvenile bivalves were excluded from this analysis because they were never identified with finer taxonomic resolution. Data were pooled by prey type across all stomachs examined. Although the trophic identity of the consumer is likely to also influence prey identification due to different prey handling and feeding modes (Garrison and Link, 2000), insufficient samples were available to explore the relationship between taxonomic resolution achievable and consumer type directly. This is because we deliberately chose consumers to represent a range of trophic niches, and therefore consumer type and prey type were confounded.

2.4. Metrics for quantifying prey

Prey were measured or estimated using one Gravimetric method (wet weight), three Volumetric methods – points, grid, and displacement, and the numeric method to provide measures of prey quantity. Quantities were estimated as per the points method before the more direct volumetric metrics, to eliminate potential bias determining points, once more precise volumes were known. The frequency of occurrence method involved quantifying the proportion of fish stomachs with a prey type present; giving a total of six prey measures used (Table 1).

For the gravimetric approach, the wet weight of prey was measured for all components of each prey category. Some studies exclude the indigestible hard parts (e.g. bivalve shell, otoliths) from weight calculations as these parts are not considered to be nutritionally valuable and thus may bias outcomes of prey importance (Hyslop, 1980; Potier et al., 2007). However, indigestible hard parts were often the only identifiable components representing a prey item/type in a stomach, so they were included in all weight measures. All prey groups were quantified by each metric for each individual stomach.

2.5. Evaluating metric performance: method application and reliability of outcomes

To evaluate metric performance, the influence of prey condition, differences in the morphological characteristics of prey types, and the distribution of prey amongst individual stomachs on the application and interpretation of dietary composition by different metrics was investigated. The time and effort required to quantify prey (measured qualitatively), applicability of the method across all prey types, and potential for technician influence (i.e. any action where technician choice can influence the final value of prey quantity measured), were also recorded. This allowed the different metrics to be compared based on their overall performance. Initially, evaluations of the dietary metrics were performed for a total of 57 stomachs: 10 for each of *A. butcheri*, *L. wallacei*, *M. cephalus*, and *P. olorum*; 9 for *P. endrachtensis*; and 8 for *P. jenkinsii*. This initial evaluation highlighted some serious limitations with several of the metrics that meant it was simply not possible to derive meaningful values for all metrics from all stomachs. As a result, the comparison among metrics was restricted to the initial 57 stomachs and a subset of metrics.

To demonstrate the influence of prey condition on the account of diet provided by different metrics, the mean contribution of different prey items to the total diet of *A. butcheri* and *P. jenkinsii* were compared using %F, %V (points) and %W. It was not possible to make this comparison for other species because a large proportion of their diet could not be quantified using all metrics, either due to problems physically separating different prey components and/or difficulties in quantifying microscopic prey items. Similarly, issues with measuring the volume of some prey types via the grid or displacement methods meant that prey volume was represented by %V (points) only; with findings from the evaluation of %V (points) diet outcomes also applicable to %V (grid and displacement). Because some common prey types could not be counted without having to assign an arbitrary value (e.g. for plant material, bits of shell fragments), the relative contribution of each prey item to the total number of all prey in the stomachs of each fish %N was not evaluated. However, it was still possible to make observations on the reliability of diet descriptions based on prey counts for some prey types.

3. Results

3.1. Condition of prey

Prey entirety varied considerably among the broad prey categories, ranging from 7% of stomachs with whole prey for fish to 91% of stomachs containing at least one whole insect and 63% with fragmented insects (Fig. 1). Note that the sum of whole and partial prey in Fig. 1 can exceed 100% because some stomachs contained both groups in the same broad category. Each of the broad prey categories was found in a range of prey states (at least 4 of the 6 states). Few fish and polychaetes, the two categories with soft fleshy exteriors, were found whole and most were in more advanced stages of decomposition (Fig. 1). Few of any prey type were found in state 1, i.e. with little sign of damage. However, the other prey categories all have hard exteriors and were more frequently found whole and in less digested prey states than fish and polychaetes. The proportion of whole prey tended to decline and partial prey to increase, as the prey state increased (Fig. 2).

The mvCART presented in this study should be interpreted cautiously, particularly the tertiary splits in the tree based on small sample sizes. The mvCART analysis indicated that consumer species was the most important factor determining prey state, and this may be correlated, in part, with the prey type most commonly consumed (Fig. 3, Table 3). For example, diatom and copepod prey are small in size, which allows them to largely avoid mastication during ingestion and increases the percent of whole items recorded. The frequent consumption of these prey types, particularly by *M. cephalus* and *P. olorum*, corresponded to a high proportion of stomachs with prey items found in

states 1 and/or 2 for these species. Alternatively, a high proportion of stomachs with prey in early states of digestion and fragmentation could also indicate continuous feeding. Irrespective of differences in prey type consumed, all fish species were found to have prey present in a number of different prey states (indicated by the spread of stomachs across multiple prey states in the bar chart below each leaf, Fig. 3). Diel period only influenced the state of prey found in the stomachs of *M. cephalus*, with stomachs separated into two sub-groups – individuals caught at midday only contained prey that were in states 1, 2 or 3, while individuals collected at dawn and dusk did not have any prey present in state 1. Note that detritus, the prey type most frequently consumed by *M. cephalus* (97%, Table 3), was not graded for entirety or prey state and therefore not accounted for in the mvCART analysis. Unidentifiable organic matter (prey state 7) was present in $\geq 50\%$ of the stomachs from *A. butcheri*, *L. wallacei*, *P. endrachtensis*, *P. olorum* and 33% of *P. jenkinsii*; further distinguishing the condition of these species' stomach contents from that of *M. cephalus*.

3.2. Taxonomy of prey

Across the six broad prey categories, only a small proportion of prey could be identified to species or genus (max. 42% and 36% respectively), and between 17 and 60% of prey were identified to much broader taxonomic levels (i.e. above family) (Fig. 4). More bivalve prey could be identified to species (42%) than any other prey type followed by fish (39%), prawns (31%) and amphipods (29%). Insects were the most difficult to identify to species, with only 4% of insects identifiable to species. However, many insect prey could be identified to genus (36%). Polychaetes could be identified to species or genus in only 20% of stomachs and only 20% of the remainder could be identified to family.

The taxonomic resolution possible varied among and within prey types (Fig. 4, Table 4). Although fish and polychaete prey were recorded in similar prey states (Fig. 1), they differed greatly in the level of identification achievable (Fig. 4), with $> 50\%$ of polychaete prey identifiable only above family level, while $> 50\%$ of fish prey were identified to genus or species because otoliths allowed fish to be identified over a broader range of prey states (Table 4). Like fish, $> 50\%$ of amphipods could be identified to genus or species, however this was because the majority of amphipods were found whole and/or in earlier states of digestion and fragmentation (prey states 1–3). In contrast, while insects were found in similar prey states to amphipods, few could be identified to species (4%), as the identification and separation of this taxonomically diverse group into genera and species generally required the presence more intricate body parts (Table 4). For some prey types, the level of identification also varied among genera. For example, small bivalves were less likely to be masticated than large bivalves and thus easier to identify.

3.3. Influence of stomach contents on the application of diet metrics

There was no practical way to physically separate stomach contents into individual prey categories for quantification where mucus (which varied greatly in thickness and volume and caused prey to prey adhesion in $> 61\%$ of stomachs; e.g. Fig. 5a), unidentifiable organic matter (Fig. 5b), and/or large quantities of small prey items (e.g. diatoms; Fig. 5c) were present. As a result, it was difficult to quantify the mass and volume of prey in 84% of fish examined, with calculations of prey bulk directly biased by the presence of other prey and/or mucus in samples, or potentially biased through the misallocation of unidentifiable components to particular prey groups. Additionally, water needed to be added to 81% of fish stomachs to offset rapid evaporation and drying-out of prey during the attempted separation process, creating potential for further unquantifiable changes to prey weight and volume (measured via the displacement approach, with the grid and points approach less affected). The %F approach was not affected by any of the

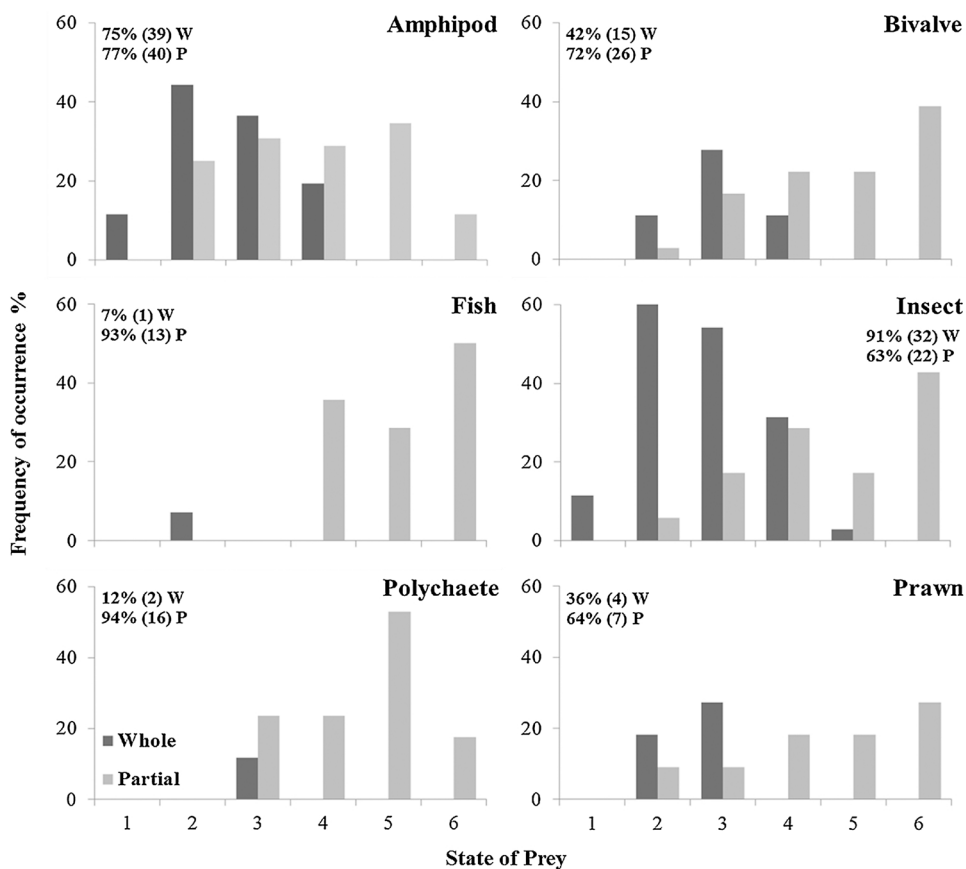


Fig. 1. The proportion of fish stomachs containing whole (W, dark grey) and partial (P, light grey) prey items in various prey states (1–6) for six broad prey categories. State of prey items defined in Appendix A Table A1 ranges from 1 = minimal damage to 6 = highly digested and/or fragmented. Dark grey bars represent prey items that were found whole, light grey bars represent partial prey items. Prawn prey may be of penaeid or caridean shrimp origin. Frequency of fish found with whole (W) or part (P) prey items presented top left (right for insects) for each broad prey type and number of fish found with whole or partial prey in brackets.

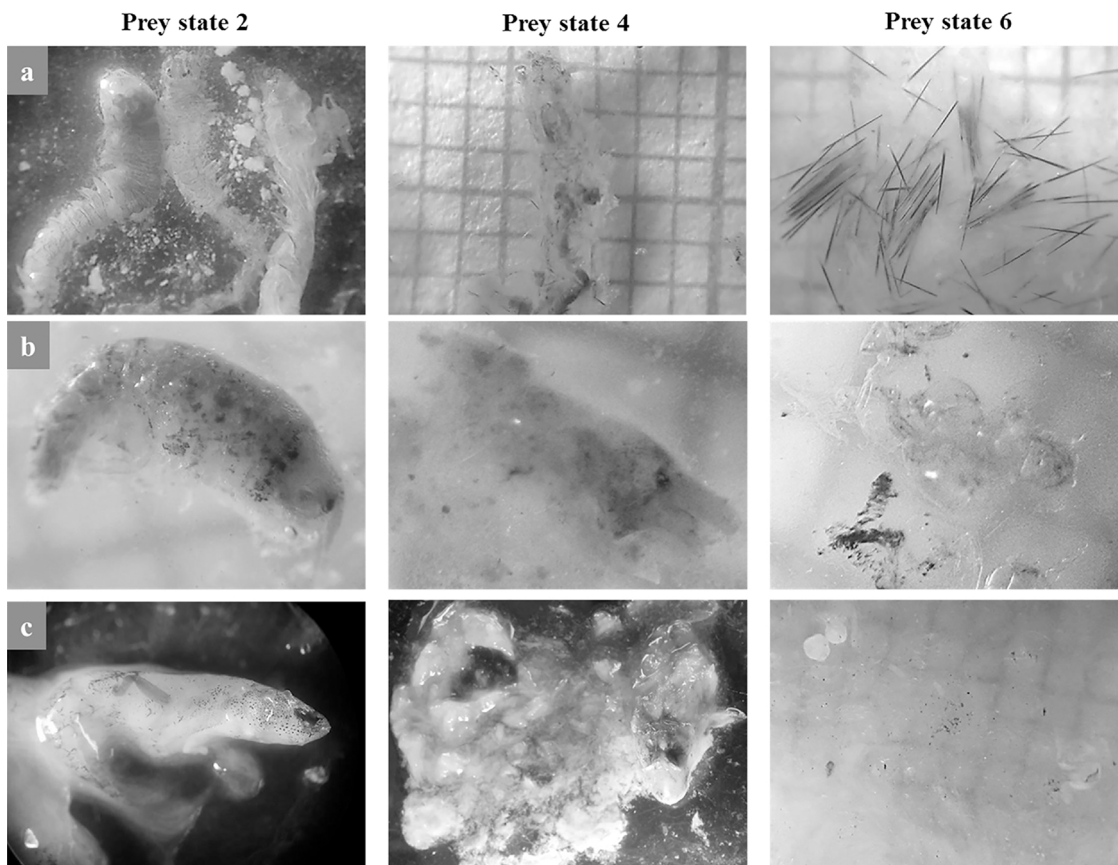


Fig. 2. Examples of changes in prey state (Appendix A Table A1) during digestion in fish stomachs for a) polychaete, b) amphipod and, c) fish prey. Prey states range from least (1) to highest digestion and fragmentation (6).

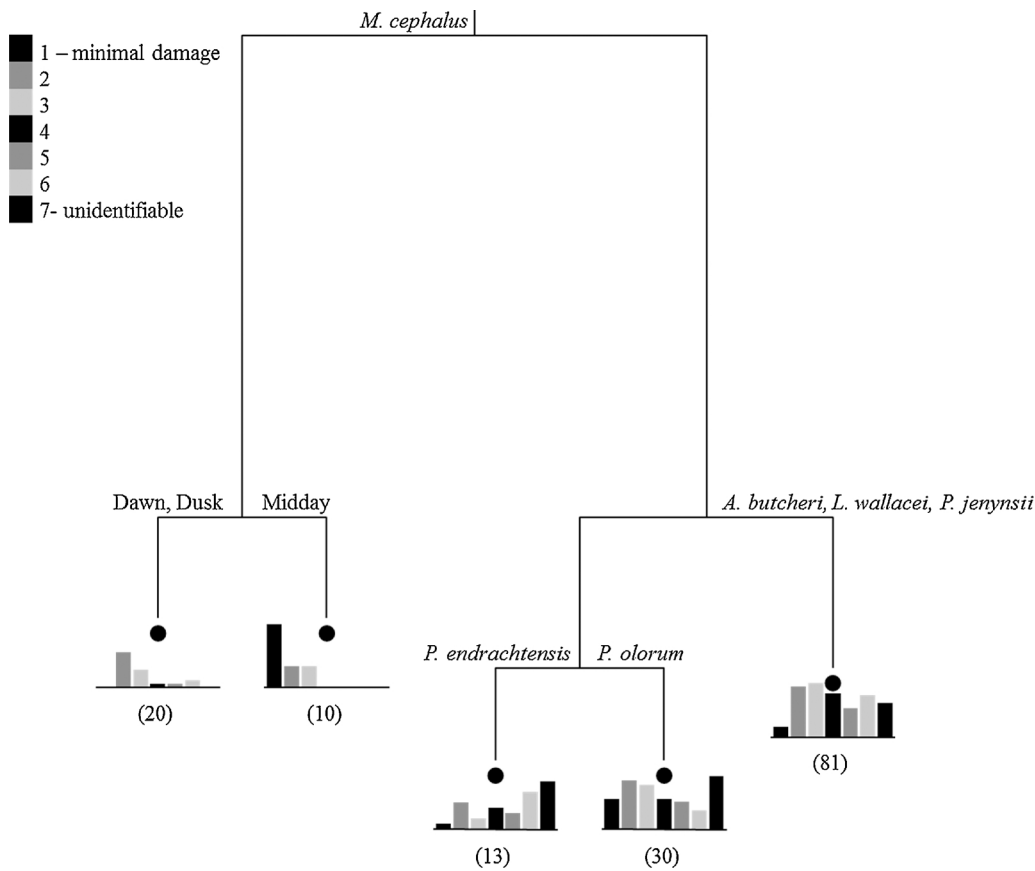


Fig. 3. Multivariate classification and regression tree investigating the influence of consumer fish species, fish size and diel period on the state of prey found in fish stomachs. Text above branches indicates the factor responsible for the split (i.e. species or diel period). The frequency of occurrence of stomachs with prey present in each prey state (bar chart) and sample size (number of stomachs in parentheses) are given below each leaf. Prey states in the bar chart from left to right match those in the legend from top to bottom. Prey states are described in detail in Appendix A Table A1. Selection of the final tree models was conducted using 10-fold cross validation, with the tree with the minimum cross validation error presented (De’Ath, 2002).

above issues and provided an unambiguous interpretation of diet (Fig. 6).

The numeric method was the second most rapid approach in application (with the %F approach the most rapid), but it lacked precision where prey types could not be counted (e.g. plants) or where prey were fragmented and/or masticated (Table 5). For example, due to the number of empty and separated shell halves found, it was difficult to quantify the number of small bivalves found in a stomach (Fig. 5f).

Similarly, masticated pieces of larger bivalve prey (e.g. Fig. 5d) could equally belong to one or many individuals. Some prey types could be quantified from fragments (e.g. polychaete jaws, amphipod heads), if a distinct, identifiable part of the body was present (e.g. Fig. 5g) and consistently used for count. For this reason, the numeric approach was able to provide a less ambiguous account of diet than gravimetric and volumetric methods, which were significantly influenced by differences in prey state and entirety (see Section 3.3.1). However, this method

Table 3

The percent frequency of occurrence of prey types for six fish species, with prey items occurring in > 50% of individuals in bold. Crustacea = unidentifiable crustacean; Decapod = unidentifiable decapod; HermitC = hermit crab, Unidentifiable = unidentifiable organic matter.

Prey item	Fish species and number of stomachs examined					
	<i>A. butcheri</i>	<i>L. wallacei</i>	<i>M. cephalus</i>	<i>P. endrachtensis</i>	<i>P. jenynsii</i>	<i>P. olorum</i>
n	30	30	30	13	21	30
Polychaete	40	–	–	–	5	13
Bivalve	83	–	–	8	–	33
Copepod	43	27	13	–	–	70
Amphipod	63	30	–	15	38	47
Isopod	7	23	–	–	–	3
Ostracod	–	–	3	–	–	40
HermitC	–	–	–	–	48	–
Decapod	–	–	–	–	24	3
Crustacea	7	10	–	–	33	10
Fish	3	–	–	62	24	–
Prawn	3	–	–	38	24	–
Insect	30	87	–	–	–	–
Spider	–	13	–	–	–	–
Plant	40	10	13	8	–	40
Diatom	20	10	77	–	–	57
Detritus	17	–	97	–	–	7
Mucus	53	67	13	85	52	23
Unidentifiable	57	50	–	69	33	77

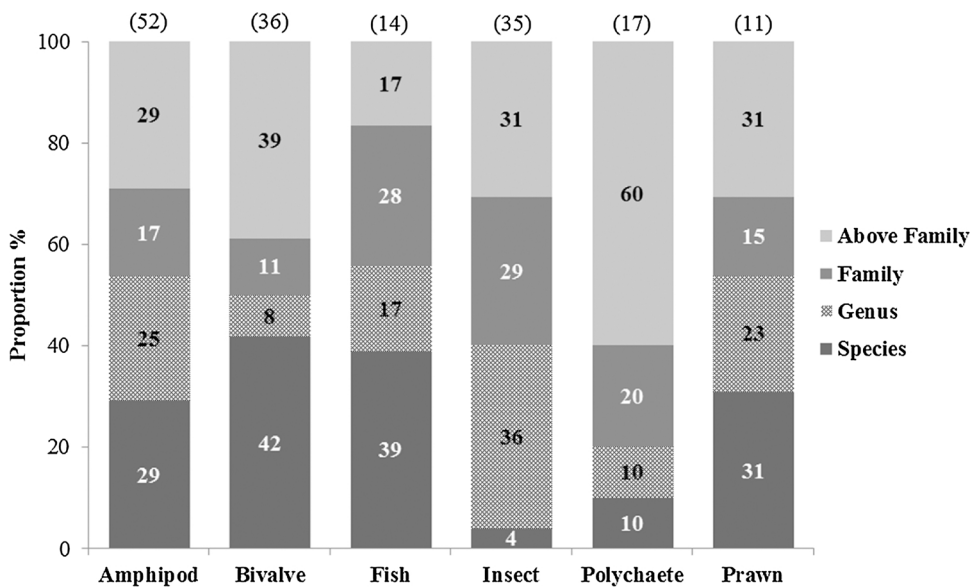


Fig. 4. Proportion of fish stomachs with a prey item present for each major prey type that were identifiable to one of four different taxonomic levels. Results for each taxonomic level stacked in bar as per legend i.e. bottom (species) to top (above family). Typical condition of prey assigned to each taxonomic level is described in Table 4. Prawns identified to species were represented by penaeids, prawn prey falling into the 'above family' category may be of penaeid or caridean shrimp origin. Number of fish stomachs with major prey types present represented in brackets above each stacked bar.

failed when only an alternative body part was present, for example the body (when counting heads) (e.g. Fig. 5h) or more commonly for polychaetes, the chaetae (Fig. 2a, state 6); parts that indicate their presence but not the number of individuals consumed.

Because of the need to separate individual items carefully and/or the use of analytical instruments to quantify prey bulk, gravimetric and volumetric methods required more time to measure and record results for each prey item. They were also susceptible to technician error because of the difficulty in separating and allocating stomach content components to particular prey groups. Furthermore, the mass and volume of some smaller and microscopic prey items were difficult to quantify, requiring high-resolution or multiple instruments to quantify prey at finer scales. Prey volume was estimated visually by the points approach and therefore depended solely on the experience and judgment of the technician (which has been shown to be a source of significant variation in the reporting of diet, Marrero and Lopez-Rojas (1995)).

3.3.1. Consequences for interpretation of diet composition

The mean volume (%V) or mass (%W) of prey was based on a mixture of variably digested whole and partial prey (e.g. Fig. 5b,d,e) or only on indigestible parts of prey, such as bivalve shells or hermit crab carapaces (Figs. 5f, 6a,b). However, these factors cannot be assessed from the final presentation of diet data (i.e. prey values and graphical presentation of diet) and the extent to which they bias quantified diet composition remains unclear. For example, when the diet of *P. jenynsii* is calculated, penaeid prawns contribute more by bulk than fish, despite being present in the same number of stomachs (Fig. 6b). This is because fish prey bulk was mainly represented by otoliths and small fragments of bone and tissue, while prawn bulk was based primarily on whole prey (e.g. Fig. 5e). Similarly, the apparent importance of the same broad prey type varied between fish species and specific prey taxa. For example, polychaete prey consumed by *P. jenynsii* were represented primarily by chaetae, while the majority of polychaete bulk in the diet of *A. butcheri* was calcified polychaete tubes. Summaries of prey contributions by weight or volume make no distinction between these prey states, and because of the variable influence of less-digestible components, neither measure accurately reflects the contribution of nutritional material (Fig. 6a,b).

Measures of prey number and/or bulk were also affected by occasional increases in the consumption of a prey type that typically was consumed in low quantities. For example, algae was the most important prey by weight in the diet of *A. butcheri* (Fig. 6a), despite being

consumed by only 2 out of the 9 individuals, with 1 individual consuming 99.9% of the total algae weight. Similarly, while copepods were consumed by 5 of the 9 *A. butcheri*, they were generally not consumed in large numbers (26 copepods between 4 fish). However, the consumption of 278 copepods by one individual greatly increased the importance of copepods by volume and weight. It is not possible to identify these issues in the summary data presented in most studies, unless some measure of variation in the measure is also presented.

4. Discussion

Comparisons across studies in different geographic locations and in different time periods have the power to identify patterns, develop hypotheses, and elucidate knowledge gaps (Jackson et al., 2001; Lotze et al., 2006; Elliott et al., 2007). Cross-study comparisons also provide the basis for developing ecosystem models that can be used to estimate indicators of ecosystem state and evaluate different environmental and management scenarios (e.g. Lozano-Montes et al., 2011; Lozano-Montes et al., 2013). Central to ecosystem functioning, comparisons of fish trophic data offer significant improvements in our understanding of the environment (Winemiller and Polis, 1996; Ullah et al., 2012) but are limited by the lack of dietary data available in one standard form (Berg, 1979; Cortés, 1997). Widely cited reviews of diet methodologies and studies (e.g. Hynes, 1950; Hyslop, 1980) have failed to standardise dietary analyses mostly because they a) recommend multiple or different approaches and b) state that stomach content condition ultimately dictates which method is appropriate for the quantification and (to a lesser extent) identification of prey but never directly investigate how condition influences the results of different methodologies. Motivated by these knowledge gaps and the findings of Baker et al. (2014), this study examined how the condition of stomach contents and type of prey influence the applicability of different methodologies to determine whether it was possible to develop a standardised approach. An approach which produced reliable data for use in statistical comparisons was a primary focus of this study. In the past some methods have been matched to specific consumer types and diet. However, as food web studies become more common and valued (Babcock and Pikitch, 2004; Pikitch et al., 2004; Smith et al., 2011), method suitability for studies involving many consumer and prey types is also discussed.

4.1. Condition of prey

The physical attributes of prey present and intact at the time of

Table 4
Typical conditions underpinning the allocation of prey items (found in fish stomachs) to different taxonomic levels of identification.

	Amphipod	Bivalve	Fish
Species	Whole, intact specimen. Minor damage to inconsequential features only.	At least one valve intact, with minimal wear or damage.	Otoliths encased in otic capsule. Otolith characteristics distinct between species of the same genus.
Genus	Intact head and pereon; with appendages, particularly gnathopods and antenna.	One valve whole but heavily degraded. Or, shell crushed but most held together by tissue. If loose fragments, combined presence of colour, pattern, notch shape and thickness may be used.	Otolith/s in good condition; little signs of wear, mostly encased or just free. And/or, parts of body and fins intact. Otolith characteristics similar between species of the same genus
Family	Head in good condition; most features recognisable. Identification allocated via comparison to whole reference specimen.	A few loose fragments only demonstrating some colour and pattern; and sometimes shape.	Free otolith/s, intact with obvious signs of smoothing and wear. Or, segment/s of body only with fins, indicating shape and colour. Skeletal parts only.
Above Family	Segments of pereon and pleon. Commonly exoskeleton fragments only.	Small fragments of shell, lacking evidence that would suggest gastropod or polychaete origin e.g. operculum, chaetae.	
		Polychaete	Prawn
Species	Whole, intact specimen.	Head and upper trunk intact with minimal wear or damage.	Undamaged carapace (head) with colour, rostrum, antennae, maxilla and pereopods intact.
Genus	Head and thorax in reasonable condition (abdomen absent).	Head features recognisable e.g. shape, tentacles, complete jaw system. And/or relevant body features e.g. branchiae, intact parapodia	Carapace in good condition with minor damage to colour, rostrum, antennae etc.
Family	Or, whole specimen with obvious all-over damage, wear and appendages missing.	Chaetae with another distinct classifiable body part e.g. jaws, operculum, calcareous tube	Carapace falling apart but rostrum mostly intact. Or, intact tail segment
Above Family	Sections of body, exoskeleton and free appendages (often damaged) e.g. wings, antennae, legs	Chaetae	Sections of exoskeleton, pleopods and/or tail segments present

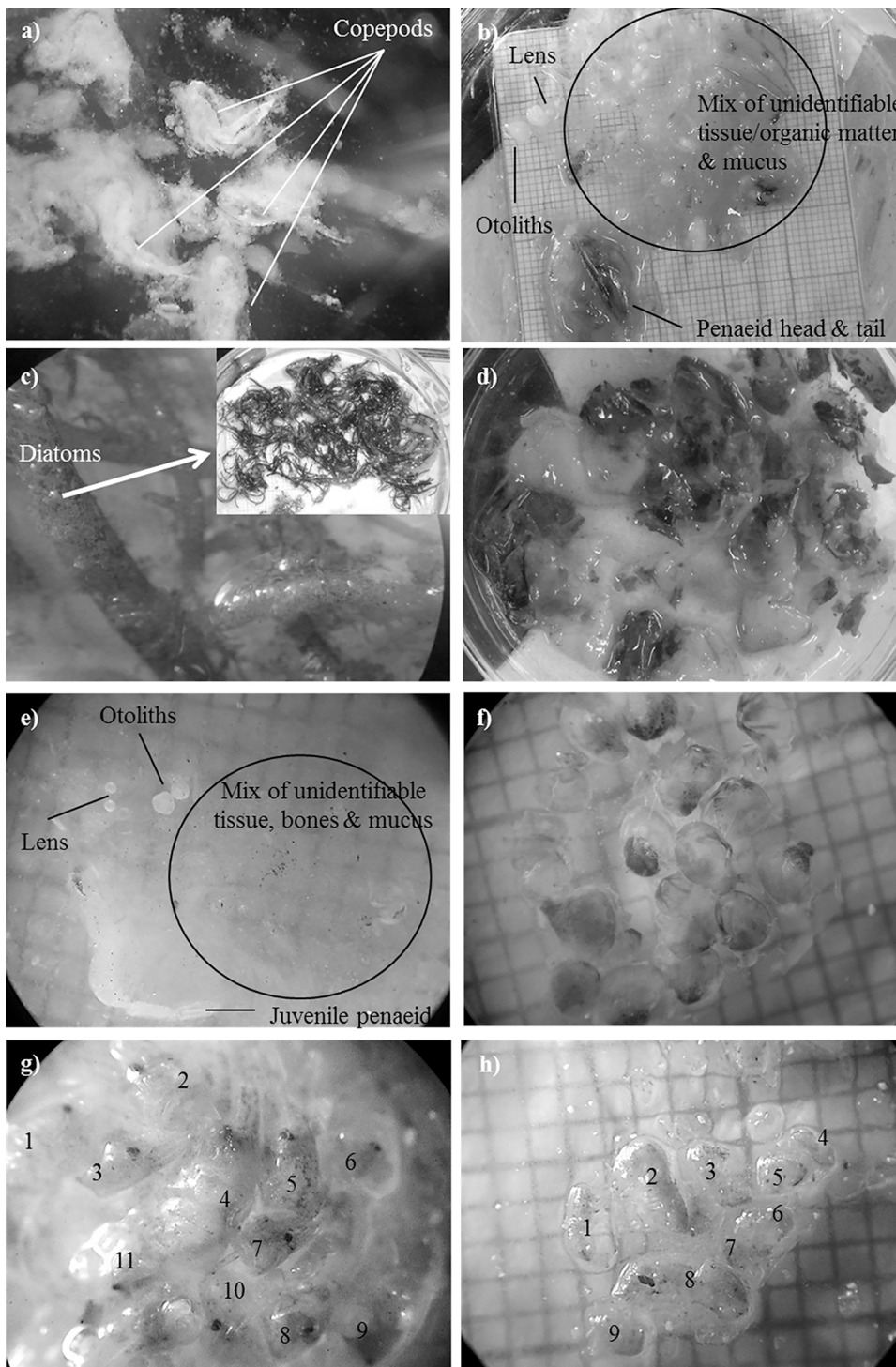


Fig. 5. Condition of stomach contents commonly encountered in fish dietary analysis. a) mucus coating copepod prey, b) contents dominated by unidentifiable tissue/organic matter (of no obvious origin), c) diatoms stuck to algae, *Gracilaria sp.*, d) masticated bivalve remains amongst unidentifiable tissue, e) variable condition of prey present in one stomach, f) empty and separated shell halves of a small bivalve species, g & h) sections of amphipod prey found in one fish stomach.

stomach content analysis are dictated by a complex web of processes including degree of mastication, order of ingestion, digestion rate, water temperature, and capture and storage methods (Swenson and Smith, 1973; Macdonald et al., 1982; Rindorf and Lewy, 2004). In this study, prey condition (entirety and state) varied widely between fish consumers, within and among stomachs, and with prey type. In addition, unidentifiable organic matter was a significant component of stomach contents (present in 33–77% of individuals) and its presence was largely independent of consumer species or the identity of prey types consumed. This meant that only a small proportion of the diet for six trophically diverse estuarine fish species could be described and quantified based on intact prey. The presence of unidentifiable material

can be reduced and the condition of prey improved in some situations, such as when fish feed only on similar prey type, or sampling is completed at peak feeding times (Robert et al., 2009). However, this study found no circumstances wherein all prey items from any given sample could be found in equivalent conditions, and it is likely that this is typical of most dietary studies (e.g. Prince et al., 1982; Scharf et al., 1997; Barnes et al., 2011), given the difficulty for controlling many of the factors driving prey condition (Baker et al., 2014). Any method that aims to produce a repeatable and unambiguous description of diet must therefore not be influenced by variation in prey condition or the presence of unidentified prey.

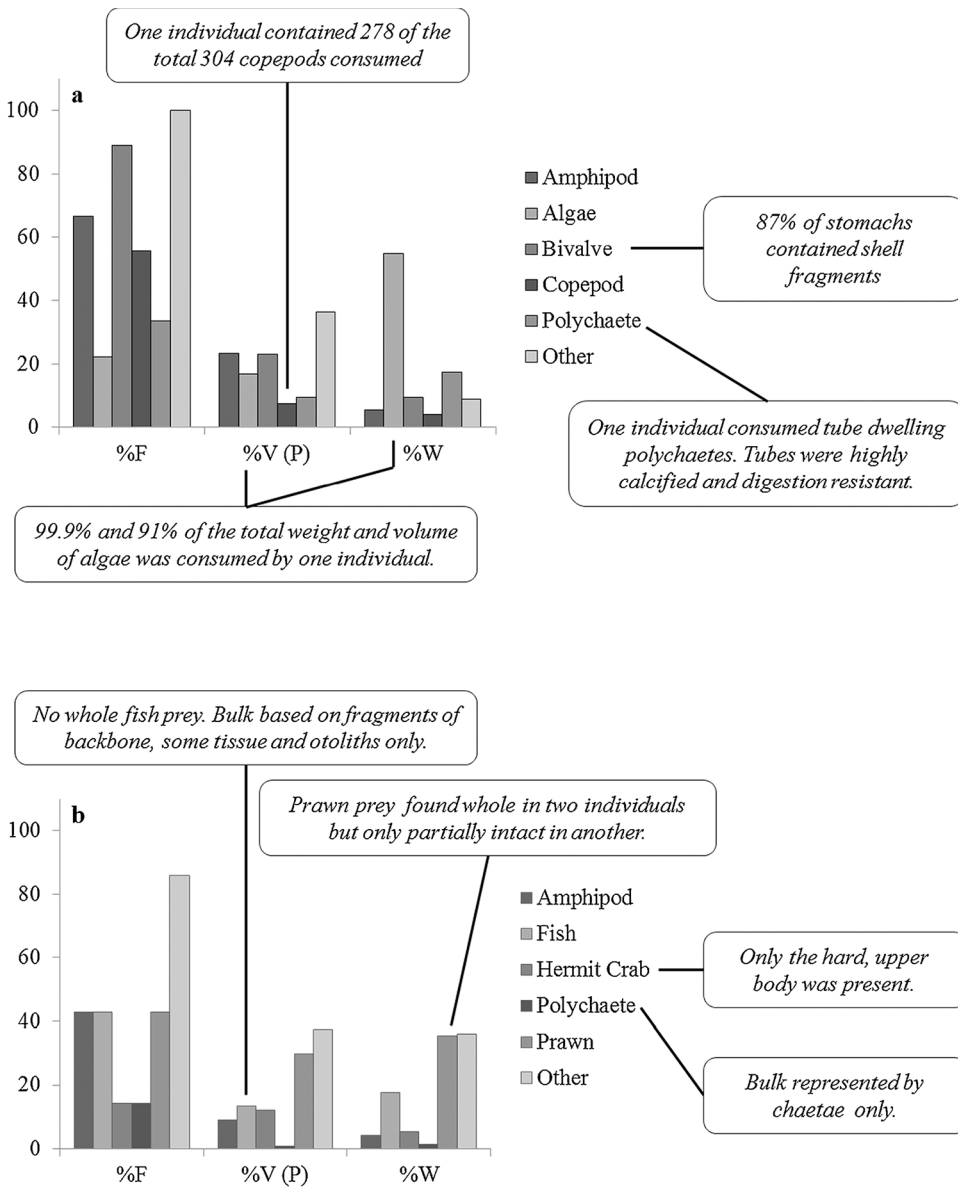


Fig. 6. Demonstration of ambiguity that can occur when interpreting the dietary compositions of fish measured by volume or weight, using stomach contents of *A. butcheri* (a) and *P. jenynsii* (b) for examples (sample size totals 9 and 7 respectively). Conversation bubbles highlight conditions influencing %V and %W.

4.2. Measures of prey quantity

Few prey were found intact or in equivalent conditions of entirety or digestion (Fig. 1), and so dietary descriptions based on prey volume or weight (bulk) (measured as per the most commonly used methods, see Table 1, Baker et al. (2014)) reflected differences in prey condition at the time of analysis, making it difficult to draw conclusions on the nutritional importance of prey to diet (Hyslop, 1980). The outcomes from using these measures of “prey bulk” were biased towards difficult to digest, freshly ingested, whole and bulky prey items, even if rarely consumed. For example, a whole prawn has a much greater influence on measures of volume and weight than a fish otolith (which was often the only portion of the fish found in the stomach). While quantitatively comparing the bulk of these two prey would provide an inaccurate representation of their nutritional and relative importance to the consumers’ diet, this is exactly the sort of data that bulk measures generated from the majority of stomachs examined. Descriptions of dietary composition from different metrics tend to converge when large numbers (≥ 100) of fish stomachs are analysed (Hynes, 1950; Baker et al., 2014), so the influence that prey condition has on final dietary outcomes appears to lessen with increased sample size. However, the

underlying practical problems of quantifying prey bulk remain, and the reputation that bulk methods provide the most accurate representation of prey importance (Ahlbeck et al., 2012) are therefore unjustified. The convergence of metrics at larger sample sizes implies that the simplest and fastest metric to quantify, i.e. percent frequency of occurrence (%F) for each identifiable prey type in a stomach, captures most of the information on dietary composition and importance, with minimal influence of non-quantifiable confounding factors. Thus, for studies aiming to provide a basis for comparison with other studies or to evaluate change over time, %F values are less ambiguous and sensitive to confounding issues than more “quantitative” measures of prey importance.

Recognising that differential digestion of prey greatly influences measures of prey bulk, attempts have been made to minimise this error, e.g. through the extrapolation of bulk from the mean bulk of whole/intact prey or from prey reconstruction (Hyslop, 1980; Alonso et al., 2002; Overton et al., 2009). However, extrapolation relies on higher occurrences of intact prey than found here, and both methods make the assumption that prey were initially consumed whole (Baker et al., 2014). More importantly, these methods cannot be extended to prey items such as plants and detritus. These latter two prey categories were

Table 5

Summary of the overall performance of different dietary approaches when quantifying the diet of six trophically diverse fish fauna. Time required to record diet represented by relative rank i.e. most rapid approach (1) to the most labouring and thus time-consuming approach (6). Confounded; refers to dietary outcomes that were biased by variable prey condition (entirety, state), and/or ambiguous separation of stomach contents. (Contents of table further explained in text).

Method	Criteria:			
	Practicality and repeatability	Manage multiple prey types	Time and effort	Final interpretation of diet
Frequency of occurrence	Simple	Equally and without difficulty	1 Identify prey only	Reporting of prey importance Transparent and unambiguous
Displacement	Lack of precision in prey/content separation	Difficult with microscopic to small prey	6 Identify and separate prey Quantification = involved	Confounded
Grid	Lack of precision in prey/content separation	Difficult with prey of variable size and morphology	4 Identify and separate prey Quantification = moderate	Confounded
Points	Lack of precision in prey/content separation	Difficult with prey representing < 1% of total contents	3 Identify and minor separation Quantification = estimation	Confounded
Gravimetric	Lack of precision in prey/content separation	Difficult with microscopic to small prey	4 Identify and separate prey Quantification = moderate	Confounded
Numerical	Complicated when prey not whole	Poorly quantifies masticated prey and plants	2 Identify prey Quantification = count only	Confounded

found in the stomachs of all except one (*P. jenynsii*) of the six species investigated in the current study and are the main dietary items for detritivores (*M. cephalus*) and herbivores (e.g. adult *Sarpa salpa*, Havelange et al. (1997)). It is important that these components are represented when estimating trophic flows within systems. Such prey can rarely be counted in any meaningful way either, making it difficult for the numeric approach to quantify diets where plant material or detritus was consumed. Some studies substitute counts with an arbitrary number (e.g. a one for all uncountable prey, Abdurahiman et al. (2010)) or an estimate (Kido et al., 1993), however this is not an accurate representation of prey quantity and the results from this approach are questionable; likely to significantly under-represent some prey types. In the absence of prey types that cannot be counted, and when counts are made conservatively for fragmented prey (e.g. Branco et al., 1997; Hoover et al., 2007), the present study found the numeric approach to provide much more unambiguous data than the bulk approaches, in contrast to the views of others (e.g. Prince et al., 1982; Schafer et al., 2002).

Quantifying diet solely on the positive identification of a prey item (Hyslop, 1980), the %F approach was the simplest of all methods reviewed, and was the essential first step of all other metrics. While previously criticised for being overly simplistic (Berg, 1979), our study, like that of Baker et al. (2014), found that the %F had many positive attributes that make it more robust to a range of confounding issues, particularly in light of the condition of fish stomach contents. It was the only approach able to quantify a range of different prey types in an equivalent manner, and produce an account of diet composition that was both unambiguous (i.e. proportion of individuals containing a particular type of prey) and least biased by the condition of prey at the time of analysis. Furthermore, %F was not impacted by an inability to unambiguously separate prey from each other or the presence of unidentifiable material and/or mucus. Therefore, this study concludes that %F provides the most reliable option for quantifying fish diets, particularly for providing a consistent measure that makes it possible to compare diets across different studies.

For studies requiring information on prey mass e.g. to determine the calorific importance of prey or for mass transfer models, methods such as prey reconstruction (Hartman and Brandt, 1995; Scharf et al., 1997) provide the most reliable option to quantify diet; with %F providing ancillary data. Where such methods cannot be used e.g. due to budget constraints or because modern dietary data is being compared to data

which is only available as %V or %W, studies should proceed carefully (acknowledging the limitations of such data and the condition in which prey were found), use large sample sizes (to reduce the influence of variable prey condition) and also report %F data which will be inevitably collected as part of such analyses. The merging of %F data with that from other metrics, as is done with the 'indices of dietary importance' approach (e.g. IRI, Pinkas (1971)) however, is not recommended; with errors associated with each metric only likely to be amplified when merged (Hyslop, 1980; Baker et al., 2014) and outcomes easily biased by differences in the taxonomic resolution of prey (Hansson, 1998).

4.3. Challenges for %F as the standard for quantifying diet composition

While %F overcomes many issues to provide a robust measure of diet, errors in the reporting of diet, e.g. overemphasising the importance of rare/uncommon prey (Berg, 1979) are still possible when diet is quantified based on a limited number of fish stomachs. Increasing sample sizes not only reduces the influence such factors have on final dietary outcomes but also improves the ability to capture, and account for, any variability in fish feeding behaviour; providing a more reliable representation of diet overall (Winemiller, 1990; Ferry and Cailliet, 1996). However, collecting and processing a large number of stomach samples requires a larger commitment of time, money and labour. Fortunately, %F is rapid, logistically simple (Hyslop, 1980) and thus cost effective, making it easier to process more samples with limited resources. Where small sample sizes are unavoidable errors will at least be transparent in the final presentation of diet (where diet is presented as %F and sample size has been specified), however the limitations of such data to adequately represent diet should be acknowledged and outcomes treated with caution. Alternatively, traditional stomach content analyses can also be paired with other reliable and more informative methods such as stable isotope and fatty acid analysis (Phillips et al., 2001; Davis et al., 2012). This can help validate trophic relationships elucidated through stomach content analyses (Clarke et al., 2005) as well as offer new information on trophic flows and sources of primary productivity (Dalsgaard et al., 2003; Melville and Connolly, 2003; Abrantes et al., 2014).

In addition to sample size, any biases in the detection and identification (see Section 4.4) of prey will influence the final description of dietary composition. The dietary importance of different prey items is

well known to be influenced by their retention rate in the stomach (Hyslop, 1980; Sutela and Huusko, 2000; Doupé and Knott, 2010). Because the visual detection of prey in stomachs often favours prey with digestion resistant features (Macdonald et al., 1982), and a large proportion of prey found is unidentifiable (this study, Grutter, 1997; Schooley et al., 2008), there is strong potential for the importance of prey to be misrepresented; (i.e. concealed, underestimated or over-emphasised) (Macdonald et al., 1982; Doupé and Knott, 2010). For example, Scholz et al. (1991) found that when fish stomachs were examined using visual analysis only, (hard bodied) harpacticoids were preferred over (entirely fleshy) nematode prey. However, examination of prey antigens in stomachs (present even after visible traces of prey have gone) revealed that nematodes may be significantly more important to diet. Where estimates are made by visual analysis only, final accounts of prey importance should be treated cautiously and highlight the need for complementary approaches to stomach content analyses. As in the antigen example above, DNA analysis can detect and identify prey in stomachs where visual inspection could detect none (Jarman et al., 2002; Symondson, 2002). This technique could significantly improve the quality and accuracy of dietary outcomes obtained using % F, which only requires the identification of prey to quantify diet. However, DNA analysis is more commonly applied to megafauna research (e.g. Dunn et al., 2010), where smaller sample sizes and a correlation between prey types and existing molecular databases presumably make this resource intensive tool more accessible (Symondson, 2002). While it is accepted that stomach content analysis will never produce an exact picture of diet, the improvements such techniques could offer to current food web understanding (Carreon-Martinez et al., 2011; Berry et al., 2015) warrant consideration.

4.4. Taxonomic resolution of prey items

In light of the complex range of factors driving prey identification, e.g. prey condition, consumer and prey type, taxonomic diversity of prey, method choice (Mauchline and Gordon, 1986; Sampey et al., 2007; Legler et al., 2010), the only practical way to standardise prey identification to facilitate comparisons among studies would be to identify prey at broad taxonomic levels that are reliably achievable regardless of the particular factors confronting any individual study. However, such an approach potentially loses some resolution to detect significant differences or changes in trophic structure, which will often be the objective for making such comparisons in the first place. Therefore, we recommend a two-stage/step approach. Firstly, comparisons of dietary data would be better facilitated through clearer descriptions of the method used, including descriptions of the condition of the prey and how prey were identified from fragments, with some description of the uncertainty in identification for each prey item. For example a qualitative statement on prey condition and its influence on identification method e.g. “most cephalopods were largely digested and identified by their remaining hard parts (beaks, lenses, and gladii)”, followed by detail on the identification catalogues/guides used to identify prey from ‘hard parts’ (Karakulak et al., 2009). Similarly studies could detail when they have sampled the prey assemblage available to consumers at the time of stomach content analysis

Appendix A

(Kanandjembo, 1998; Kanandjembo et al., 2001), as this may improve confidence in prey identified with finer resolution. More detailed methodologies would also allow studies to identify any methodological differences that may confound comparisons of diet e.g. differences in investigator expertise. Secondly, comparisons of dietary data would further be facilitated if changes were made to the way prey identities are reported. Specifically, the contribution of prey could be presented for all taxonomic levels in a nested hierarchy and published as supplementary information (for an example, see Appendix B Table B1). One limitation of %F data is that it is not possible for other researchers to retrospectively calculate %F contributions for broader taxonomic levels by pooling published values, because more than one item within a broader category can be present in a single gut (note 2, Appendix B Table B1). Such an approach would make dietary data more widely accessible and allow future studies to determine the most robust level of resolution for a particular study. It would also be invaluable when the taxonomy of prey changes.

5. Conclusion and recommendations

While this study has come to some definite conclusions for how dietary data can be standardised, simple changes in the way research is reported could also enhance the effectiveness and reliability of meta-analyses of dietary data. Irrespective of the quantification method used, all dietary studies collect presence/absence data by default, which means that percent frequency of occurrence data can be extracted from any data set and made available. Similarly, prey recorded and presented to species level only can also be reported at broader taxonomic levels. Given this, we encourage the use of appendices to provide comprehensive information on the dietary analyses, including data for any important factors (e.g. size, location, season) that shape diet composition (e.g. Appendix B Table B1). We also recommend that methodological approaches are described more clearly and with great detail, particularly the condition of prey items and their taxonomic affinities.

It is important to note that all of the recommendations made here are impractical for past studies where data is unavailable for re-analysis and no further methodological information can be gained e.g. as in historical records. The value in the information these records provide often outweighs the implications of comparing data of reduced reliability (Jackson et al., 2001). As such, we are not suggesting that researchers should avoid using existing historic data for comparisons, but believe that researchers need to fully consider the potential limitations and reliability of these data based on the findings from the current study. For future studies of stomach contents, we believe that recording the percentage frequency of occurrence and details of prey condition and taxonomic affinities in appendices will facilitate more robust comparisons between studies and in turn advance our understanding of trophic ecology.

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Table A1
States of prey as determined directly through stomach content analysis. Categories 1 - 6 describe the condition of each major prey part and may apply to whole prey or the part of prey present at the time of content analysis. Most whole prey become partial remnants by state 4.

Major category of prey	
Bivalve	
STATE OF PREY	<p>1 Characteristics intact and clear.</p> <p>2 At least one shell valve intact. Shell shape, structure, colour and pattern distinct. Most internal tissues intact and attached to valve/s.</p> <p>3 Reduction of internal tissues present. Valve/s intact. Shell shape, structure, colour and pattern distinct. Or, shell all crushed but most attached to tissue.</p> <p>4 Unattached valve/s present only. Shell thinning; features fading. Little to no internal tissues present. Or, mostly separated and thinning large shell fragments</p> <p>5 Shell fragments only. Colour and pattern fading. Size, shape and structure of valve may be distinguishable.</p> <p>6 Small, thin, broken shell fragments only. Shell valve shape and pattern not clear, some colour may be visible.</p> <p>7 Unidentifiable</p>
Amphipod	
STATE OF PREY	<p>1 Characteristics intact and clear.</p> <p>2 Head intact. Exoskeleton beginning to soften & loosen from tissue on pereon and pleon. Some appendages may be absent or broken.</p> <p>3 Head and pleon soft but intact. Pereon soft, losing shape. Exoskeleton thinning, peeling in spots. More appendages absent or broken, including antennae.</p> <p>4 Head and pleon losing shape; head features distorting. Pereon and pleosome segments breaking apart. Most appendages broken or absent. Antennae may be absent or broken.</p> <p>5 Head, pereon, pleon represented by segments or fragments only. Some internal tissues present.</p> <p>6 Fragments of exoskeleton and appendages, with little or no internal tissues.</p> <p>7 Unidentifiable</p>
Fish	
STATE OF PREY	<p>1 Characteristics intact and clear.</p> <p>2 Head, body, fins intact. Minor deterioration or absence of skin and/or filament.</p> <p>3 Head soft but easily identifiable with eyes intact. Skin and/or fins falling apart or may be absent. Flesh attached to backbone.</p> <p>4 Head breaking apart; losing structure and flesh falling away. Eye lens may free but otoliths remain encased. Flesh falling off backbone.</p> <p>5 Otolith/s free. Eye lens breaking apart. Tissues and bone fragmented.</p> <p>6 Free otolith/s and/or loose bone.</p> <p>7 Unidentifiable</p>
Major category of prey	
Insect	
STATE OF PREY	<p>1 Characteristics intact and clear.</p> <p>2 Head, thorax, abdomen mostly intact. Colour, pattern distinct. (If present) wings attached to thorax, crumpled but intact. Some legs, antennae may be broken, free from body segment.</p> <p>3 Head, thorax soft and losing shape. Exoskeleton thinning. Abdomen beginning to break apart. Wings attached, soft and thinning. Legs, antennae broken, free or absent.</p> <p>4 Head just identifiable, falling apart. Legs, antennae broken, free or absent. Substantial loss of tissue and structure from thorax, abdomen. Wings breaking apart, loosening from thorax.</p> <p>5 Head, thorax, abdomen distorted and broken into pieces. Wings broken, parts free or absent from thorax. Colour and pattern may still be visible on some fragments.</p> <p>6 Fragments of legs, antennae and/or exoskeleton. Some tissue may remain attached to exoskeleton fragments.</p> <p>7 Unidentifiable</p>
Polychaete	
STATE OF PREY	<p>1 Characteristics intact and clear.</p> <p>2 Flesh opaque. Head intact. Cuticle & /or flesh digested in parts of body. Segmentation of body clear. Parapodia intact.</p> <p>3 Head intact but losing shape. Body soft but worm shape distinct; parts of segments may be missing. Colour fading. Parapodia just visible with most chaetae attached.</p> <p>4 Head just recognisable; features distorted and/or missing. Worm shape visible. Some internal tissues present. Parapodia not recognisable, many chaetae free. If present, jaws encased and in position.</p> <p>5 Head absent or reduced to cuticle only. Body mainly fragments of cuticle and chaetae only. If present, jaws free within or outside body.</p> <p>6 Chaetae and/or jaws only. Fragments of calcareous tube only, for tube dwelling species.</p> <p>7 Unidentifiable</p>
Prawn	
STATE OF PREY	<p>1 Characteristics intact and clear.</p> <p>2 Carapace intact. Exoskeleton beginning to soften & loosen from abdomen. Tissue opaque. Some appendages may be absent or broken.</p> <p>3 Carapace soft and beginning to disintegrate. Exoskeleton falling away from abdomen, tissue soft. Telson and urosome intact. More appendages absent or broken, including antennae.</p> <p>4 Carapace falling apart. Rostrum may be absent or broken. Antenna mostly absent. Abdomen falling apart, exoskeleton absent in places and tissue lost.</p> <p>5 Carapace not identifiable. Eyes free. Telson and urosome present but damaged. Sections of exoskeleton and tissue.</p> <p>6 Fragments of exoskeleton and appendages, with little or no internal tissues.</p> <p>7 Unidentifiable</p>

Appendix B

Table B1

Example of how studies could present dietary data in order to facilitate comparisons with data from other studies. (Table contents are hypothetical).

<i>P. jenynsii</i> (n = 100)						
PREY	Class	Order	Family	Genus	Species	%F
FISH		Perciformes				72
			Apogonidae	<i>Ostorhinchus</i>	<i>rueppellii</i>	15
			Gobiidae			32
				<i>Favonigobius</i>		10
					<i>F. lateralis</i>	6
					<i>F. lentiginosus</i>	2
				<i>Pseudogobius</i>		16
					<i>P. olorum</i>	13
					<i>P. poecilosoma</i>	5

Note:

- 1.%F values are hierarchically nested e.g. the %F value given for the genus *Favonigobius* includes stomachs where prey were identified to species (i.e. *F. lateralis* and *F. lentiginosus*), as well as prey that were only identifiable to the genus level. Similarly, %F values for 'Fish' include any stomach where fish, identifiable at any taxonomic level, and including unidentifiable fish prey, were present.
2. The *Pseudogobius* example demonstrates why %F values presented at the species level cannot be reliably recalculated to obtain the %F values at broader taxonomic levels. In this example, 2 fish consumed both *P. olorum* and *P. poecilosoma* and thus simply combining the dietary contribution of *P. olorum* and *P. poecilosoma* would over-represent the contribution of *Pseudogobius* (the genus) to diet. As such, %F values need to be independently calculated (and presented) for each taxonomic level.
3. As all Apogonidae prey were identifiable to the species level, the same %F value (i.e. 15%) applies at all taxonomic levels i.e. 15% of *P. jenynsii* individuals consumed Apogonidae; or 15% of *P. jenynsii* individuals consumed *Ostorhinchus* sp.; or 15% of *P. jenynsii* individuals consumed *O. rueppellii*.
4. In many studies dietary composition is reported across different categories e.g. fish size, sampling location, season etc. These categories represent important drivers of dietary composition and reporting of such data is encouraged within the format of this table e.g. by adding columns or additional tables. Sample sizes should be recorded for all calculations of diet composition, as this will allow other studies to pool diet across different categories (e.g. to obtain overall diet composition) where required.

References

- Abdurahiman, K., Nayak, T., Zacharia, P., Mohamed, K., 2010. Trophic organisation and predator-prey interactions among commercially exploited demersal finfishes in the coastal waters of the southeastern Arabian Sea. *Estuar. Coast. Mar. Sci.* 87 (4), 601–610. <http://dx.doi.org/10.1016/j.ecss.2010.03.002>.
- Abrantes, K.G., Barnett, A., Bouillon, S., 2014. Stable isotope-based community metrics as a tool to identify patterns in food web structure in east African estuaries. *Funct. Ecol.* 28 (1), 270–282. <http://dx.doi.org/10.1111/1365-2435.12155>.
- Ahlbeck, I., Hansson, S., Hjerne, O., 2012. Evaluating fish diet analysis methods by individual-based modelling. *Can. J. Fish. Aquat. Sci.* 69 (7), 1184–1201. <http://dx.doi.org/10.1139/f2012-051>.
- Alonso, M.K., Crespo, E.A., García, N.A., Pedraza, S.N., Mariotti, P.A., Mora, N.J., 2002. Fishery and ontogenetic driven changes in the diet of the spiny dogfish, *Squalus acanthias*, in Patagonian waters, Argentina. *Environ. Biol. Fishes* 63 (2), 193–202. <http://dx.doi.org/10.1023/A:1014229432375>.
- Andrea, A., Ojeda, F.P., 2001. Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. *Mar. Ecol. Prog. Ser.* 217, 81–91. (Retrieved from). <http://www.int-res.com/abstracts/meps/v217/p81-91/>.
- Babcock, E.A., Pikitch, E.K., 2004. Can we reach agreement on a standardized approach to ecosystem-based fishery management? *Bull. Mar. Sci.* 74 (3), 685–692.
- Baker, R., Sheaves, M., 2005. Redefining the piscivore assemblage of shallow estuarine nursery habitats. *Mar. Ecol. Prog. Ser.* 291, 197–213. <http://dx.doi.org/10.3354/meps291197>.
- Baker, R., Buckland, A., Sheaves, M., 2014. Fish gut content analysis: robust measures of diet composition. *Fish Fish.* 15 (1), 170–177. <http://dx.doi.org/10.1111/faf.12026>.
- Balcombe, S.R., Bunn, S., McKenzie-Smith, F.J., Davies, P., 2005. Variability of fish diets between dry and flood periods in an arid zone floodplain river. *J. Fish Biol.* 67 (6), 1552–1567. <http://dx.doi.org/10.1111/j.1095-8649.2005.00858.x>.
- Barnes, L.M., Leclerc, M., Gray, C.A., Williamson, J.E., 2011. Dietary niche differentiation of five sympatric species of Platycephalidae. *Environ. Biol. Fishes* 90 (4), 429–441. <http://dx.doi.org/10.1007/s10641-010-9752-4>.
- Berg, J., 1979. Discussion of methods of investigating the food of fishes, with reference to a preliminary study of the prey of *Gobioculus flavescens* (Gobiidae). *Mar. Biol.* 50 (3), 263–273. <http://dx.doi.org/10.1007/bf00394208>.
- Berry, O., Bulman, C., Bunce, M., Coghlan, M., Murray, D.C., Ward, R.D., 2015. Comparison of morphological and DNA metabarcoding analyses of diets in exploited marine fishes. *Mar. Ecol. Prog. Ser.* 540, 167–181. <http://dx.doi.org/10.3354/meps11524>.
- Branco, C.W.C., Aguiaro, T., Esteves, F.A., Caramaschi, E.P., 1997. Food sources of the teleost eucinostomus argenteus in two coastal lagoons of Brazil. *Stud. Neotrop. Fauna Environ.* 32 (1), 33–40. <http://dx.doi.org/10.1076/snfe.32.1.33.13463>.
- Carreon-Martinez, L., Johnson, T., Ludsins, S., Heath, D.D., 2011. Utilization of stomach content DNA to determine diet diversity in piscivorous fishes. *J. Fish Biol.* 78 (4), 1170–1182. <http://dx.doi.org/10.1111/j.1095-8649.2011.02925.x>.
- Clarke, L.R., Videgar, D.T., Bennett, D.H., 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. *Ecol. Freshwater Fish* 14 (3), 267–277. <http://dx.doi.org/10.1111/j.1600-0633.2005.00103.x>.
- Cortés, E., 1997. A critical review of methods of studying fish feeding based on analysis of stomach contents: application to elasmobranch fishes. *Can. J. Fish. Aquat. Sci.* 54 (3), 726–738. <http://dx.doi.org/10.1139/f96-316>.
- Cox, S.P., Essington, T.E., Kitchell, J.F., Martell, S.J.D., Walters, C.J., Boggs, C., Kaplan, I., 2002. Reconstructing ecosystem dynamics in the central Pacific Ocean, 1952–1998. II. A preliminary assessment of the trophic impacts of fishing and effects on tuna dynamics. *Can. J. Fish. Aquat. Sci.* 59 (11), 1736–1747. <http://dx.doi.org/10.1139/f02-138>.
- Dalsgaard, J., John, M.S., Kattner, G., Müller-Navarra, D., Hagen, W., 2003. Fatty acid trophic markers in the pelagic marine environment. *Adv. Mar. Biol.* 46, 225–340.
- Davis, A.M., Blanchette, M.L., Pusey, B.J., Jardine, T.D., Pearson, R.G., 2012. Gut content and stable isotope analyses provide complementary understanding of ontogenetic dietary shifts and trophic relationships among fishes in a tropical river. *Freshwater Biol.* 57 (10), 2156–2172. <http://dx.doi.org/10.1111/j.1365-2427.2012.02858.x>.
- De'Ath, G., 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology* 83 (4), 1105–1117. [http://dx.doi.org/10.1890/0012-9658\(2002\)083\[1105:MRTANT\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2002)083[1105:MRTANT]2.0.CO;2).
- Doupé, R., Knott, M., 2010. Rapid digestion of fish prey by the highly invasive 'detritivore' *Oreochromis mossambicus*. *J. Fish Biol.* 76 (4), 1019–1024. <http://dx.doi.org/10.1111/j.1095-8649.2009.02531.x>.
- Dunn, M.R., Szabo, A., McVeagh, M.S., Smith, P.J., 2010. The diet of deepwater sharks and the benefits of using DNA identification of prey. *Deep Sea Res. Part I* 57 (7), 923–930. <http://dx.doi.org/10.1016/j.dsr.2010.02.006>.
- Elliott, M., Whitfield, A.K., Potter, I.C., Blaber, S.J.M., Cyrus, D.P., Nordlie, F.G., Harrison, T.D., 2007. The guild approach to categorizing estuarine fish assemblages: a global review. *Fish Fish.* 8 (3), 241–268. <http://dx.doi.org/10.1111/j.1467-2679.2007.00253.x>.
- Elliott, J., 1967. The food of trout (*Salmo trutta*) in a Dartmoor stream. *J. Appl. Ecol.* 59–71. <http://dx.doi.org/10.2307/2401409>.
- Ferry, L., Cailliet, G., 1996. Sample Size and Data Analysis: Are We Characterizing and Comparing Diet Properly.
- Garrison, L.P., Link, J.S., 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. *Mar. Ecol. Prog. Ser.* 202, 231–240. <http://dx.doi.org/10.3354/meps202231>.
- Gaughan, D., Neira, F., Beckey, L., Potter, I., 1990. Composition, seasonality and distribution of the ichthyoplankton in the lower Swan Estuary, south-western Australia. *Mar. Freshwater Res.* 41 (4), 529–543. <http://dx.doi.org/10.1071/MF9900529>.
- Graham, B.S., Grubbs, D., Holland, K., Popp, B.N., 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Mar. Biol.* 150 (4), 647–658. <http://dx.doi.org/10.1007/s00227-006-0360-y>.
- Gray, B.P., Norcross, B.L., Blanchard, A.L., Beaudreau, A.H., Seitz, A.C., 2015. Variability in the summer diets of juvenile polar cod (*Boreogadus saida*) in the northeastern Chukchi and western Beaufort Seas. *Polar Biol.* 1–12. <http://dx.doi.org/10.1007/>

- s00300-015-1796-7.
- Grutter, A.S., 1997. Spatiotemporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. *Copeia* 346–355. <http://dx.doi.org/10.2307/1447754>.
- Hansson, S., 1998. Methods of studying fish feeding: a comment. *Can. J. Fish. Aquat. Sci.* 55 (12), 2706–2707. <http://dx.doi.org/10.1139/f98-158>.
- Hartman, K.J., Brandt, S.B., 1995. Trophic resource partitioning, diets, and growth of sympatric estuarine predators. *Trans. Am. Fish. Soc.* 124 (4), 520–537.
- Havelange, S., Lepoint, G., Dauby, P., Bouqueneau, J.M., 1997. Feeding of the sparid fish *Sarpa salpa* in a seagrass ecosystem: diet and carbon flux. *Mar. Ecol.* 18 (4), 289–297. <http://dx.doi.org/10.1111/j.1439-0485.1997.tb00443.x>.
- Hoover, J.J., George, S.G., Killgore, K.J., 2007. Diet of shovelnose sturgeon and pallid sturgeon in the free-flowing Mississippi River. *J. Appl. Ichthyol.* 23 (4), 494–499. <http://dx.doi.org/10.1111/j.1439-0426.2007.00893.x>.
- Hynes, H., 1950. The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.* 36–58. <http://dx.doi.org/10.2307/1570>.
- Hyslop, E., 1980. Stomach contents analysis—a review of methods and their application. *J. Fish Biol.* 17 (4), 411–429. <http://dx.doi.org/10.1111/j.1095-8649.1980.tb02775.x>.
- Jackson, J.B., Kirby, M.X., Berger, W.H., Bjorndal, K.A., Botsford, L.W., Bourque, B.J., Estes, J.A., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293 (5530), 629–637. <http://dx.doi.org/10.1126/science.1059199>.
- Jarman, S., Gales, N., Tierney, M., Gill, P., Elliott, N., 2002. A DNA-based method for identification of krill species and its application to analysing the diet of marine vertebrate predators. *Mol. Ecol.* 11 (12), 2679–2690. <http://dx.doi.org/10.1046/j.1365-294X.2002.01641.x>.
- Kanandjumbo, A., Platell, M., Potter, I., 2001. The benthic macroinvertebrate community of the upper reaches of an Australian estuary that undergoes marked seasonal changes in hydrology. *Hydro. Processes* 15 (13), 2481–2501. <http://dx.doi.org/10.1002/hyp.296>.
- Kanandjumbo, A.-R.N., 1998. Fish and Macrobenthic Faunas of the Upper Swan Estuary: Interrelationships and Possible Influence of a Dinoflagellatae Bloom. Murdoch University.
- Karakulak, F., Salman, A., Oray, I., 2009. Diet composition of bluefin tuna (*Thunnus thynnus* L. 1758) in the eastern mediterranean sea, Turkey. *J. App. Ichthyol.* 25 (6), 757–761.
- Kido, M.H., Ha, P., Kinzie III, R.A., 1993. Insect introductions and diet changes in an endemic Hawaiian amphidromous goby, *Awaous stamineus* (Pisces: gobiidae). *Pac. Sci.* 47, 43–50.
- Legler, N.D., Johnson, T.B., Heath, D.D., Ludsins, S.A., 2010. Water temperature and prey size effects on the rate of digestion of larval and early juvenile fish. *Trans. Am. Fish. Soc.* 139 (3), 868–875. <http://dx.doi.org/10.1577/T09-212.1>.
- Loneragan, N., Potter, I., Lenanton, R., 1989. Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. *Mar. Biol.* 103 (4), 461–479. <http://dx.doi.org/10.1007/BF00399578>.
- Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Jackson, J.B., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312 (5781), 1806–1809. <http://dx.doi.org/10.1126/science.1128035>.
- Lozano-Montes, H.M., Loneragan, N.R., Babcock, R.C., Jackson, K., 2011. Using trophic flows and ecosystem structure to model the effects of fishing in the Jurien Bay Marine Park, temperate Western Australia. *Mar. Freshwater Res.* 62 (5), 421–431. <http://dx.doi.org/10.1071/MF09154>.
- Lozano-Montes, H., Loneragan, N.R., Babcock, R., Caputi, N., 2013. Evaluating the ecosystem effects of variation in recruitment and fishing effort in the western rock lobster fishery. *Fish. Res.* 145, 128–135. <http://dx.doi.org/10.1016/j.fishres.2013.01.009>.
- Macdonald, J.S., Waiwood, K.G., Green, R.H., 1982. Rates of digestion of different prey in atlantic cod (*Gadus morhua*), ocean pout (*Macrozoarces americanus*), winter flounder (*Pseudopleuronectes americanus*), and american plaice (*Hippoglossoides platessoides*). *Can. J. Fish. Aquat. Sci.* 39 (5), 651–659. <http://dx.doi.org/10.1139/f82-094>.
- Marrero, C., Lopez-Rojas, H., 1995. Quantitative evaluation of the point method for fish stomach contents analysis. *J. Fish Biol.* 47 (5), 914–916.
- Mauchline, J., Gordon, J., 1985. Trophic diversity in deep-sea fish. *J. Fish Biol.* 26 (5), 527–535.
- Mauchline, J., Gordon, J., 1986. Foraging strategies of deep-sea fish. *Mar. Ecol. Prog. Ser.* 27 (3), 227–238.
- Melville, A.J., Connolly, R.M., 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. *Oecologia* 136 (4), 499–507. <http://dx.doi.org/10.1007/s00442-003-1302-8>.
- Overton, A.S., Margraf, F.J., May, E.B., 2009. Spatial and temporal patterns in the diet of striped bass in Chesapeake Bay. *Trans. Am. Fish. Soc.* 138 (4), 915–926. <http://dx.doi.org/10.1577/T07-261.1>.
- Phillips, K.L., Jackson, G.D., Nichols, P.D., 2001. Predation on myctophids by the squid *Moroteuthis ingens* around Macquarie and Heard Islands: stomach contents and fatty acid analyses. *Mar. Ecol. Prog. Ser.* 215, 179–189.
- Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Sainsbury, K.J., 2004. Ecosystem-based fishery management. *Science* 305 (5682), 346–347. <http://dx.doi.org/10.1126/science.1098222>.
- Pinkas, L., 1971. Food habits study. *Fish Bull.* 152 (5), 10.
- Potier, M., Marsac, F., Chérel, Y., Lucas, V., Sabatié, R., Maury, O., Ménard, F., 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. *Fish. Res.* 83 (1), 60–72. <http://dx.doi.org/10.1016/j.fishres.2006.08.020>.
- Prince, J., Potter, I., Lenanton, R., Loneragan, N., 1982. Segregation and feeding of atherinid species (Teleostei) in south-western Australian estuaries. *Mar. Freshwater Res.* 33 (5), 865–880.
- Rindorf, A., Lewy, P., 2004. Bias in estimating food consumption of fish by stomach-content analysis. *Can. J. Fish. Aquat. Sci.* 61 (12), 2487–2498. <http://dx.doi.org/10.1139/f04-200>.
- Robert, D., Castonguay, M., Fortier, L., 2009. Effects of preferred prey density and temperature on feeding success and recent growth in larval mackerel of the southern Gulf of St. Lawrence. *Mar. Ecol. Prog. Ser.* 377, 227–237. <http://dx.doi.org/10.3354/meps07833>.
- Sampey, A., McKinnon, A., Meekan, M., McCormick, M., 2007. Glimpse into guts: overview of the feeding of larvae of tropical shorefishes. *Mar. Ecol. Prog. Ser.* 339, 243–257. <http://dx.doi.org/10.3354/meps339243>.
- Sarre, G., Platell, M., Potter, I., 2000. Do the dietary compositions of *Acanthopagrus butcheri* in four estuaries and a coastal lake vary with body size and season and within and amongst these water bodies? *J. Fish Biol.* 56 (1), 103–122. <http://dx.doi.org/10.1111/j.1095-8649.2000.tb02089.x>.
- Saunders, R.J., Fowler, A.J., Gillanders, B.M., 2012. The use of food resources by 0+ snapper, *Chrysophrys auratus*, from northern Spencer Gulf, South Australia. *Mar. Freshwater Res.* 63 (8), 680–686. <http://dx.doi.org/10.1071/MF11266>.
- Schafer, L., Platell, M., Valesini, F., Potter, I., 2002. Comparisons between the influence of habitat type, season and body size on the dietary compositions of fish species in nearshore marine waters. *J. Exp. Mar. Biol. Ecol.* 278 (1), 67–92. [http://dx.doi.org/10.1016/S0022-0981\(02\)00337-4](http://dx.doi.org/10.1016/S0022-0981(02)00337-4).
- Scharf, F.S., Buckel, J.A., Juanes, F., Conover, D.O., 1997. Estimating piscine prey size from partial remains: testing for shifts in foraging mode by juvenile bluefish? *Environ. Biol. Fishes* 49 (3), 377–388.
- Scholz, D., Matthews, L., Feller, R., 1991. Detecting selective digestion of meiobenthic prey by juvenile spot *Leiostomus xanthurus* (Pisces) using immunoassays. *Mar. Ecol. Prog. Ser.* Oldendorf 72 (1), 59–67.
- Schooley, J.D., Karam, A.P., Kesner, B.R., Marsh, P.C., Pacey, C.A., Thornbrugh, D.J., 2008. Detection of larval remains after consumption by fishes. *Trans. Am. Fish. Soc.* 137 (4), 1044–1049. <http://dx.doi.org/10.1577/T07-169.1>.
- Smith, A.D.M., Brown, C.J., Bulman, C.M., Fulton, E.A., Johnson, P., Kaplan, I.C., Tam, J., 2011. Impacts of fishing low-trophic level species on marine ecosystems. *Science* 333 (6046), 1147–1150. <http://dx.doi.org/10.1126/science.1209395>.
- Sutela, T., Huusko, A., 2000. Varying resistance of zooplankton prey to digestion: implications for quantifying larval fish diets. *Trans. Am. Fish. Soc.* 129 (2), 545–551. [http://dx.doi.org/10.1577/1548-8659\(2000\)129<0545:VROZPT>2.0.CO;2](http://dx.doi.org/10.1577/1548-8659(2000)129<0545:VROZPT>2.0.CO;2).
- Swan River Trust, 2013. Swan River Vertical Plots. Available at <https://swanrivertrust.dpaw.wa.gov.au/> (Accessed 2013).
- Swenson, W.A., Smith, L.L., 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum*). *J. Fish. Res. Board Can.* 30 (9), 1327–1336. <http://dx.doi.org/10.1139/f73-213>.
- Symondson, W., 2002. Molecular identification of prey in predator diets. *Mol. Ecol.* 11 (4), 627–641. <http://dx.doi.org/10.1046/j.1365-294X.2002.01471.x>.
- Ullah, M.H., Rashed-Un-Nabi, M., Al-Mamun, M.A., 2012. Trophic model of the coastal ecosystem of the Bay of Bengal using mass balance Ecopath model. *Ecol. Modell.* 225, 82–94. <http://dx.doi.org/10.1016/j.ecolmodel.2011.11.013>.
- Windell, J., Bowen, S., 1978. Methods for study of fish diets based on analysis of stomach contents. *Methods for Assessment of Fish Production in Fresh Waters*. Blackwell Scientific Publication, Oxford (pp. 219–226).
- Winemiller, K.O., Polis, G.A., 1996. Food webs: what can they tell us about the world? In: Polis, G.A., Winemiller, K.O. (Eds.), *Food Webs: Integration of Patterns & Dynamics*. Springer US, Boston, MA, pp. 1–22.
- Winemiller, K.O., 1990. Spatial and temporal variation in tropical fish trophic networks? *Ecol. Monogr.* 60 (3), 331–367.