

# Trophic guild concept: factors affecting within-guild consistency for tropical estuarine fish

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**ABSTRACT:** The trophic guild concept has proved useful in distilling the diverse feeding interactions displayed by fish in temperate estuaries into a standardised subset that simplifies the application of trophic information to management. However, the high species richness displayed by tropical flora and fauna introduces the potential for feeding diversity within presumed guilds, potentially reducing the value of the standard guild concept. We evaluated within-guild consistency for a group of tropical estuarine fish species comprising a presumably coherent trophic zoobenthivore feeding guild (i.e. fish that feed primarily on zoobenthic prey) within 10 estuarine systems in tropical northeastern Australia. The zoobenthivore assemblage did not form a single coherent trophic group, rather the different components of the zoobenthivore guild responded to the broad spectrum of available prey in distinctly different ways. Some species displayed quite general diets while others fed principally on particular types of zoobenthic prey. The distinct prey specialisations often lead to different members of the presumed guild participating in different food chain pathways within the estuarine food web. As a result, substantial and important trophic differences would be masked if these disparate components were aggregated into a single trophic guild. While simplifications can be valuable, and often necessary, in data-poor situations, the complexity uncovered in this study emphasises that caution is required in applying a broad simplified scheme such as the guild concept to specific situations. Caution must be used when applying a guild approach that imports interpretation from other species and/or locations and should be explicitly recognised as an interim position until more specific data can be acquired.

**KEY WORDS:** Trophic guild · Tropical estuary · Ecosystem · Management · Food webs

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## INTRODUCTION

Trophic guilds are often used to simplify the understanding of trophic ecology by reducing the many complex feeding interactions that exist between fish and their prey into manageable groups that represent the major components of trophic pathways (Hawkins & Macmahon 1989, Garrison & Link 2000, Vander Zanden & Vadeboncoeur 2002, Blondel 2003, Coll et al. 2006a,b). Species grouped within the same guild are assumed to ‘...exploit the same class of environmental resources in similar ways...’ (Root 1967, p. 335) and have similar roles in the food web

(Yodzis 1996, Elliott et al. 2007, Lassalle et al. 2012). For this reason, guilds are considered valuable for use in ecosystem modelling (Metcalf et al. 2008) and for facilitating broad-scale comparisons between communities that span many biogeographic regions (Elliott et al. 2007).

Work by Elliott et al. (2007) (and updated by Potter et al. 2015) has been fundamental in bringing together a disparate body of literature on the guilds of fishes in estuarine systems to develop a standard set of guild categories that promote consistency and can be universally applied. These authors present this new guild structure as a framework to test and build

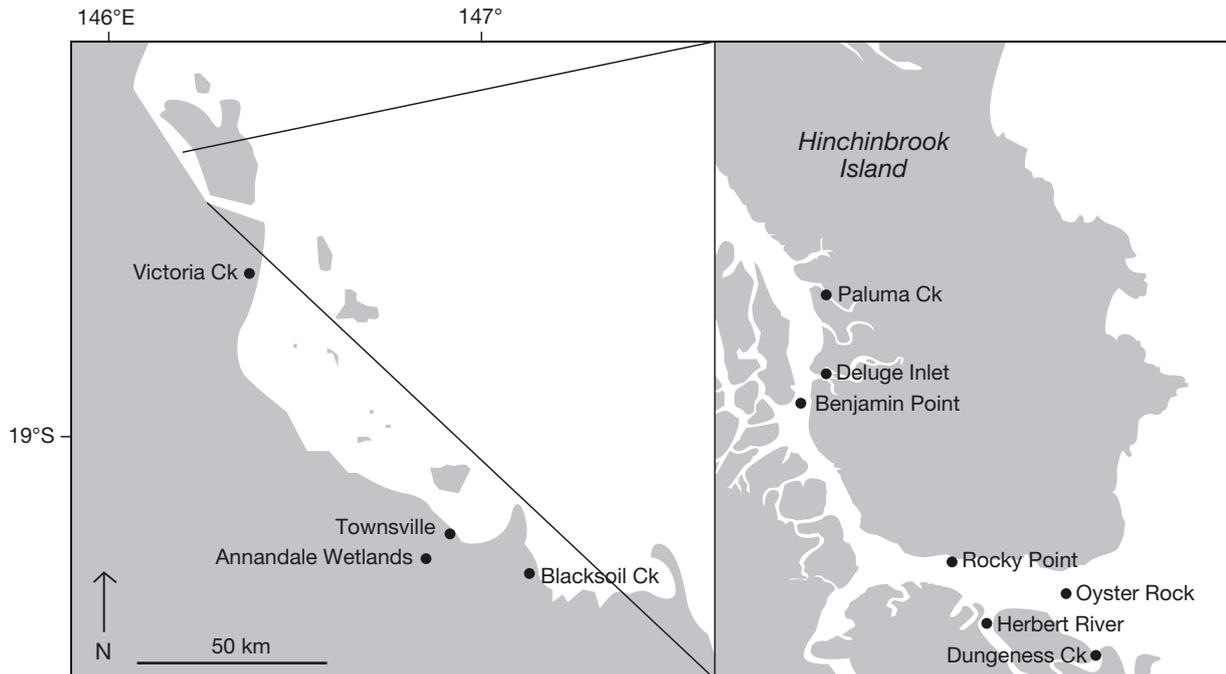


Fig. 1. Northeast Queensland, Australia, showing location of estuarine sites sampled. Ck: creek

upon as more detailed fish ecology studies are performed and new and alternative data are provided (Elliott et al. 2007). One area poorly understood at the time of the guild review concerned the food webs of tropical estuarine ecosystems, with information on the trophic ecology of fishes in this region generally lacking (Abrantes et al. 2015). The increase in species richness seen for most groups of tropical flora and fauna (Fischer 1961, Hawkins et al. 2003, Albaret et al. 2004) introduces much greater potential for feeding diversity within a presumed trophic guild than is the case in temperate systems (Elliott & Whitfield 2011). Consequently, the aggregation of species into trophic guilds needs to be carefully validated to ensure the presumed guild structure faithfully represents functional trophic relationships. Furthermore, the cause of any within-guild variability needs to be understood in detail. This will ensure that any future modifications of the guild structure, i.e. generalisations of trophic relationships, do not occur at the expense of detail relevant to the useful application of the guild concept.

The aim of this study was to evaluate whether the assumption of within-guild consistency is warranted for a group of tropical estuarine fish species comprising a presumably coherent trophic 'guild'. The focus was on fish that feed on zoobenthic prey because the diversity of both zoobenthos feeding fish and of their prey (Zahorcsak et al. 2000, Dittmann 2001) provides the possibility of variation in trophic interactions,

and because some members of this group are already known to display considerable dietary plasticity (Sheaves et al. 2014a). Elliott et al.'s (2007) guild model was used as a framework to investigate the consistency of guild approaches across broad spatial scales and specifically to investigate whether the feeding relationships of tropical estuarine fish fit with the proposed global guild model.

## MATERIALS AND METHODS

### Study Sites

Fish were collected from 10 sites along the northeastern coast of tropical Queensland, Australia (Fig. 1). Seven sites were located in the Hinchinbrook Channel (18° 23.26' S, 146° 08.07' E), a 44 km long tidal channel that comprises a diversity of smaller creeks and inlets, many of which are in pristine or near-pristine condition (Sheaves et al. 2014b). Hinchinbrook Channel and Victoria Creek are situated in the wet tropics, where some level of freshwater inflow is common throughout the year. In contrast, the remaining southern sites, the Annandale Wetlands (a marine wetland connected to the Ross River) and Blacksoil Creek, are located in the 'dry tropics' region and generally only experience freshwater inflow during a brief summer wet season. Tides in both regions are semi-diurnal, with a range of about 3.8 m

(Australian Hydrographic Service). All study sites featured extensive mangrove forests and intertidal sand and mud flats.

### Sampling design

Sampling primarily targeted 4 fish genera which have previously been reported to feed on benthic prey: *Pomadasys*, *Sillago*, *Acanthopagrus* and *Gerres*. To determine the stability of the feeding guild over a range of different conditions, fish were collected from all benthic habitat types available, and for both the wet season (April) and dry season (June–August) of 2010, as well as the wet season (March–April) of 2014 (see Table 1). To improve sample sizes, fish were sampled over multiple months for the 2010 dry season and 2014 wet season. Fyke nets, seine nets, cast nets and hook-and-line techniques were employed; with different gears matched to the habitat type it could most efficiently sample. Different gears unavoidably have different sampling biases and so collect different species compositions, which may have resulted in different representation of fish species in different habitats. However, this is assumed to have had minimal impact on the study because it was focused on the diets of the species that were collected. Other gear-related biases were accounted for during gut content analysis (e.g. excluding bait, freshly ingested prey likely to be the result of net-feeding). Fish were sampled across different habitat types, regions and seasons, to highlight the range of variations in diet that can occur. Sampling aimed to capture (1) fish known to have entered mangrove forests, (2) a sequence of samples outside the mangrove forests across the tidal cycle, (3) fish that utilised shallow sandbanks, (4) fish from areas of complex structure, and (5) a variety of fish species and sizes.

### Capture methods

A fyke net (18 mm mesh, 20 m wings, 2 m drop) was set along the mangrove edge during high tide. The wings were strategically placed so as to direct fish that had been in the mangrove forest into the catch box. Cast nets (18 mm mesh, 4.29 m diameter) were used throughout the tidal cycle in areas adjacent to the fyke nets, while shallow sandy habitats were sampled using a pocket beach seine (12 mm mesh, 30 m long, and 1.5 m drop). Fish from areas with complex structure (e.g. rocky outcrops) could not be sampled with these netting methods, so they

were targeted using hook-and-line. Line fishing also targeted larger size classes of fish which are often poorly represented in net samples (Sheaves & Johnston 2009). Bait could be easily differentiated from natural food items during gut content analysis as lines were baited with squid body tissue devoid of fins, skin, heads and internal organs and prawn bodies devoid of shells and heads.

### Trophic data

Fish were immediately euthanized in an ice-water slurry to prevent post capture digestion or regurgitation and frozen as soon as possible. Dietary analysis focused on stomach content because much of the material contained within the intestine was unidentifiable, with only the most resilient material remaining. Prey were identified to the lowest possible taxonomic resolution and diet composition summarised by the presence of prey categories. More complex measures, such as total number or volume of each prey type, were not used because the difficulty in identifying all prey individuals (e.g. due to varying stages of digestion) makes such data unreliable (Baker et al. 2014).

Prey were reduced to 16 categories for inclusion in dietary analysis (see Table 2). Material that was unidentifiable, of a non-trophic nature, or that could only be identified into broad categories that overlapped with other defined prey types (e.g. crustaceans) were excluded. Few fish had consumed detritus or sediment. Because this material could be derived from a wide range of potential sources and therefore provided no definitive information, it was excluded from analyses. Where trophically coherent, taxa that occurred in insufficient numbers were grouped into a broader prey category with other taxa of similar trophic position and function e.g. microcrustaceans (see Table 2).

### Statistical Analyses

The widely used guild classification of Elliott et al. (2007) was used as the starting point for trophic guild definition. As a trophic functional group has only previously been assigned for 2 of the fish species examined (Elliott et al. 2007) and can change with location, the overall diet of each species was first examined to ensure that their classification as zoobenthivores was warranted. Although assigned to the miscellaneous/opportunist group by Elliott et al. (2007), *Terapon jarbua* consumed more prey from the zoobenthic cate-





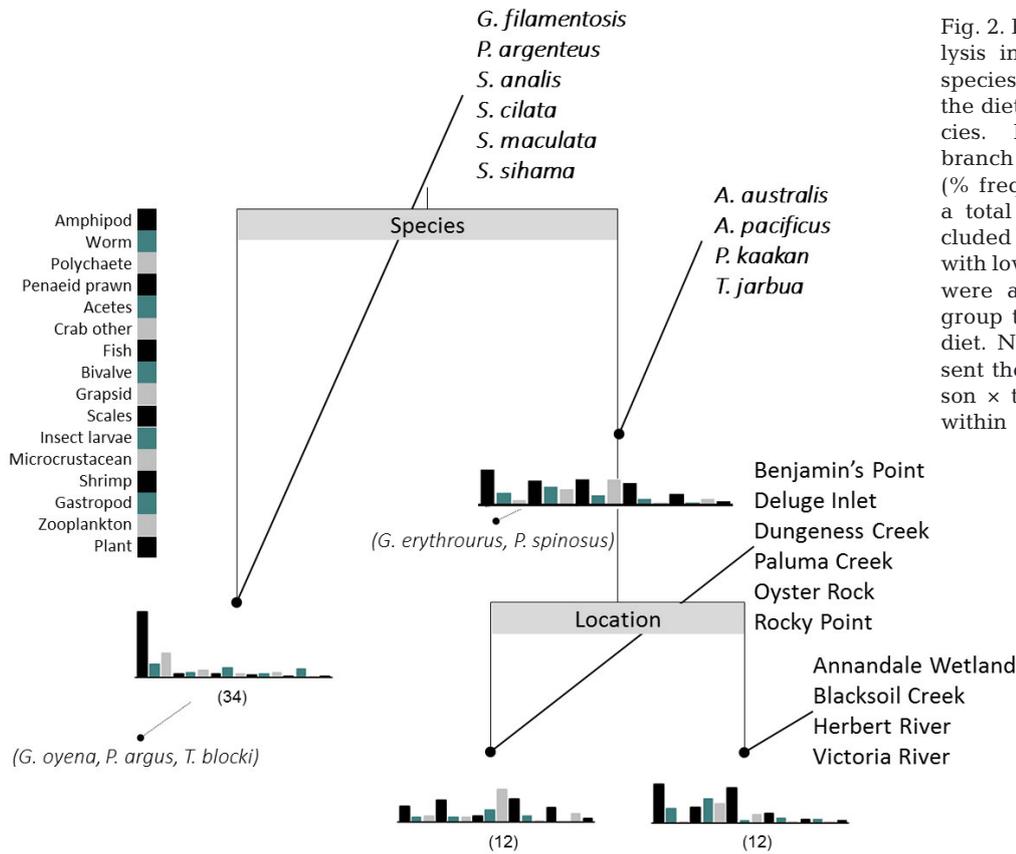


Fig. 2. Results of an mvCART analysis investigating the effects of species, season and location on the diet of zoobenthivore fish species. Histograms below each branch represent diet composition (% frequency). Only species with a total abundance >20 were included in the analysis. Species with low sample sizes (in brackets) were arbitrarily assigned to the group that best represented their diet. Numbers in brackets represent the number of species × season × trip combinations included within a branch. See Table 1 for full species names

**Co-occurring species**

Diet composition varied amongst co-occurring species, with the mvCART separating *A. pacificus* from *G. filamentosus* and *Sillago sihama* (Fig. 3). *A. pacificus* consumed many prey types with high frequency, while the diets of *G. filamentosus* and *S. sihama* were dominated by amphipods, worms and polychaetes. The diet of *A. pacificus* varied among locations. Bivalves, amphipods, *Acetes* and worms featured heavily in the diets of individuals caught in the lower Hinchinbrook sites of Rocky Point, Oyster Rock and the Herbert River. Diet composition of fish collected from all other locations was dominated by grapsid crabs. No seasonal effect on diet was detected.

**DISCUSSION**

Although all the species investigated would be classified as 'zoobenthivores' under Elliott et al.'s (2007) guild approach, the 'zoobenthivore' assemblage sampled from tropical northeastern Australian estuaries did not form a single coherent trophic group. A statistical approach that allowed dietary data to objectively define where similarities in diet occurred (mvCART)

revealed that 2 distinct trophic groups existed. These groups of 'zoobenthivores' responded to zoobenthic prey in different ways, contrary to what would be expected from species of the same guild (Root 1967). One group, comprising fish with relatively small mouths and/or specialised protrusible and sucking jaws e.g. Gerridae (Cyrus & Blaber 1983), fed heavily on amphipod prey and rarely consumed prey that was not small zoobenthic and/or infaunal. The other group comprised species with large mouths, pharyngeal jaws or crushing teeth e.g. Sparidae (Vandewalle et al. 1995), and consumed a large range of prey types at similar frequencies, including more mobile prey types such as crabs and fish. Despite the dichotomy within the assumed guild, similarities within and differences between the 2 groups do align with the nature of their prey and their morphology as consumers, or their ecotrophomorphology (Wootton 1990), a relationship Elliott et al.'s (2007) guild approach aims to represent. This suggests that for this tropical estuarine situation, the proposed guild model is a poor fit, providing little insight into the functional relationships between fish and their prey. It also highlights that while 'grouping fishes according to common broad food categories' (Elliott et al. 2007, p. 257) may be necessary to facilitate comparisons across large biogeographical scales,

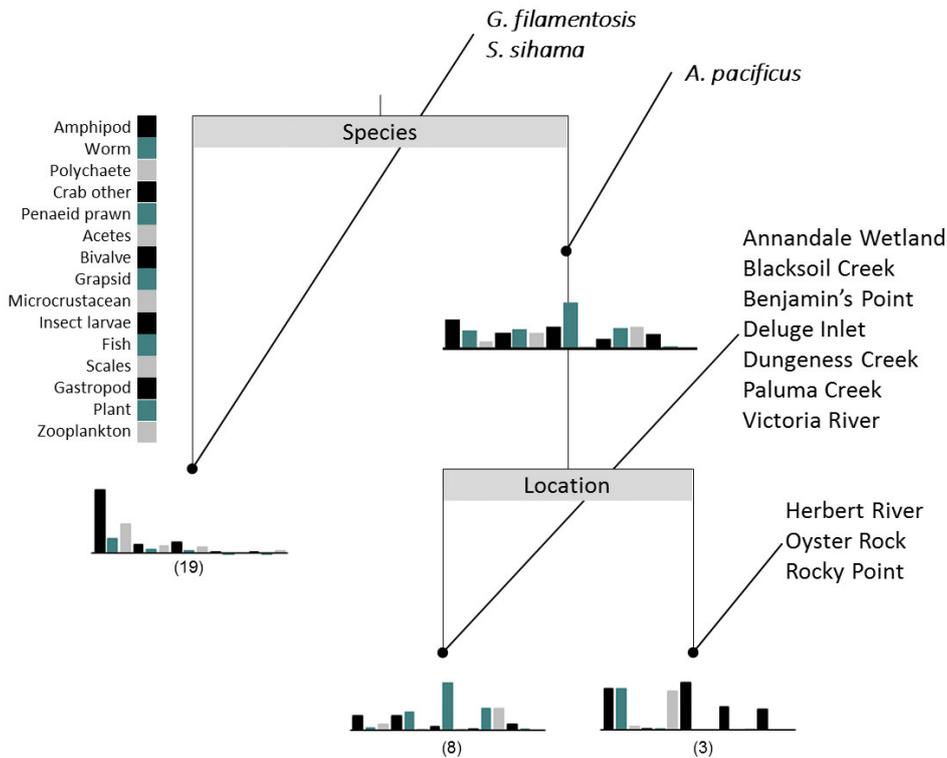


Fig. 3. Results of an mvCART analysis investigating the effects of species, season and location on the diet of co-occurring zoobenthivore fish species. Histograms below each branch represent diet composition (% frequency). See Table 1 for full species names, and Fig. 2 for further details

the trophic relationships such broad guild categories can characterise (and thus explore across regions) may be limited.

Variability in the feeding strategies employed by each trophic group identified would be masked under the standard guild definition. These feeding strategies can have very different implications for both the species that adopt them, and for food webs and ecosystem function. For example, generalists such as *Acanthopagrus pacificus* can engage in many diverse interactions with the ecosystem, operating at different trophic levels, in multiple food chains and in multiple food webs (Abrantes & Sheaves 2009, Igulu et al. 2013, Sheaves et al. 2013). Such species are likely to be more resilient to ecosystem change (Pérez-España & Arreguín-Sánchez, 1999, Elliott & Quintino 2007, Hadwen et al. 2007) and play a pivotal role in the transport of nutrients between a broad range of estuarine habitats (Sheaves et al. 2013). The success and behaviour of specialist amphipod feeders however, is likely to be predictably dictated by the abundance of their preferred prey (Hajisamae et al. 2006, Parsons & Robinson 2007, Terraube et al. 2011). This makes them more vulnerable to change in the prey assemblage (Cole et al. 2008, Wilson et al. 2008), but also increases their influence in determining amphipod abundance (Bøhn & Amundsen 2001). With conservation of processes and function imperative to eco-

system sustainability (Bellwood et al. 2004, Sheaves et al. 2015), the inability to differentiate important predator-prey relationships reduces the suitability of the guild approach as a management tool at regional and local levels.

The separation of *Pomadasys argenteus* and *P. kaakan* into different trophic groups was contrary to findings of a previous North Queensland study, which found the diets of these 2 species to be relatively similar (Sheaves & Molony 2000). More specifically, in that study the diet of *P. argenteus* was broader and included a higher consumption of large crustacean prey e.g. penaeids, a pattern that has also been reflected in the diets of *P. argenteus* from other regions (Nanjo et al. 2008, Kulbicki et al. 2009). This difference is likely to relate to ontogenetic differences in diet, with relatively small (most <150 mm) *P. argenteus* examined in this study. Interestingly, *P. kaakan* individuals examined were also small, suggesting that ontogeny may influence the diet of these 2 congeners in different ways, and that factors other than ecotrophomorphology and resource similarity influenced diet composition. Furthermore, because the ways in which generalist and specialist feeders interact with their environment are very different, the ontogenetic point at which specialist amphipod feeding stops and more generalist feeding begins for *P. argenteus* needs to be understood if the ecological impacts of all size classes are to be ac-

counted for. This demonstrates that trophic detail cannot be assumed transferable across a genus (or higher) and emphasises the importance of comprehensive ecological studies for all species, something encouraged by Elliott et al. (2007), with guilds expected to be improved as new information arises.

### Causes of diet variability between fish of the same guild

The purpose of the guild approach is to aggregate 'fish species that utilise similar food resources' and by doing so reflect the ecotrophomorphology of estuarine fishes (Schafer et al. 2002; Elliott et al. 2007, p. 254). However, under the current definition, zoobenthivores are essentially fish that feed on any prey living in the benthic zone (Froese & Pauly 2004). This casts a wide net, with 14 major prey types from 14 different families of benthos consumed in this study alone. More importantly, it captures a diversity of prey morphologies with differing feeding behaviours and capacity for movement; ranging from small, infaunal, detritivorous polychaetes (e.g. *Nereis diversicolor*, Kristensen & Mikkelsen 2003) to large, hard-bodied, swimming penaeids that feed on both zooplankton and zoobenthos (Wassenberg & Hill 1987, Stoner & Zimmerman 1988, Christensen 1996). Further adding to this complexity is the range of habitat types in which the benthic zone is present e.g. sandflats, mudflats, seagrass, mangrove forest, deep subtidal areas, and the subsequent effect this is likely to have on the composition and structure of benthic prey assemblages present (Coles et al. 1992, Edgar et al. 1994, Heck et al. 1995, Breitburg et al. 1997, Sheaves et al. 2005, Sheaves et al. 2016). Consequently, the extent to which the zoobenthic resource is 'similar' is unclear and, whether driven by individual preference, physical or morphological limitations, the different components of the 'zoobenthivore guild' respond to this broad spectrum of prey in distinctly different ways.

There is also an absence of a clear and consistent method for the initial process of assigning prey into groups, and this has the potential to undermine the accuracy of guild classification. Broad prey groups form the foundation of trophic guild categories (Elliott et al. 2007), yet they can be poorly defined and allow prey to occur in more than one group. For example, as a 'shrimp' *Acetes sibogae australis* would usually be categorised as zoobenthos (Froese & Pauly 2004); however, because it is pelagic/planktonic by nature (Ball et al. 1986) it can also be categorised as zooplankton (Froese & Pauly 2004). Such

ambiguity hampers consistency in the way prey and thus their consumers are classified into guilds across studies (i.e. fish consuming *A. sibogae australis* could be considered either zooplanktivores or zoobenthivores) and, as such, the integrity of outcomes of global comparisons of guild structure could be compromised. Adding to this ambiguity is exclusion from the zoobenthivore group of fish that feed (some exclusively e.g. *Psammogobius biocellatus*, Baker & Sheaves 2005) on benthic fish, despite the direct association of these benthic fish prey with benthic habitats. Although not explicitly stated (Elliott et al. 2007), this is presumably because fish prey bear the least similarity to other zoobenthos. However, it could be argued that whether this feeding behaviour (i.e. consuming benthic-associated fish prey) is associated with piscivory or with feeding from the benthic habitats depends on the question of interest. For instance, if the aim was to determine which regions had more fish dependent on the benthic zone, a guild which captures all benthic feeders (irrespective of morphological similarities in prey) may be more appropriate. Hence, guild categorisations developed to address particular questions are likely to be more appropriate than categorisations based on a single theoretical idea of what makes a resource similar.

Groupings of prey different to those in the standard guild concept can result if categorisation is based on the patterns of prey found in actual fish diets. In this study, *A. sibogae australis*, a small pelagic shrimp, was most commonly consumed with other types of more benthic-associated shrimps (e.g. palaemonids), penaeid prawns and crabs; indicating that fish tend to consume *A. sibogae australis* along with other 'shrimp' type prey, irrespective of their position in the water column. However, simply labelling shrimp, prawns and crabs as zoobenthos does not really align with fish feeding behaviour either. Although not permanently pelagic like *A. sibogae australis*, these prey are, for the most part, larger and more mobile than many other zoobenthic prey (e.g. infaunal bivalves), and the zoobenthic fish capable of eating them were limited to the larger species examined i.e. *Aconthopagrus australis*, *A. pacificus*, *P. kaakan* and *Terapon jarbua*. Interestingly, these prey are also prominent in the diets of fish species more commonly labelled as piscivores (e.g. *Scomberoides commersonianus*, Salini et al. 1990), suggesting that many fish species differentiate larger mobile crustaceans from other prey types and that a better understanding of estuarine trophic ecology may be achieved if these prey were grouped differently. Where other regional studies have similarly allowed dietary data to objectively

define trophic groups, alternative guild structures were also found (Wilson & Sheaves 2001, Hajisamae & Ibrahim 2008, Reum & Essington 2008, Davis et al 2011). Thus, with more independent and comprehensive guild studies conducted at regional scales, guild categories that better represent global patterns of fish feeding relationships may be achievable.

Elliott et al. (2007, p. 263) encourage 'rigorous treatment' of the current guild categories and have suggested their own modifications that may be implemented once there is sufficient data to support such changes. One proposal is a refinement of the zoobenthivore guild to reflect the different feeding modes and mechanisms required for fish to feed on prey that live either within, on or above the benthos i.e. zoobenthivore- infauna, epifauna and hyperbenthos guilds (Elliott et al. 2007). However, this is unlikely to be a generally applicable model because there are prey that utilise more than one of the benthic zones (i.e. within, on, above) (Beumer 1978, Ambrose 1984, Walters 1988, Dittman 2000), just as there are fish that consume prey from all benthic zones (present study, Wise et al. 1994, Sarre et al. 2000, Faye et al 2012, Nagelkerken et al 2015). Furthermore, with most estuarine fish occupying shallow-water habitats (Johnston & Sheaves 2008), and therefore readily encountering prey from all of these zones, the likelihood of finding fish that only/mostly consume prey from one of these levels also seems low. Our study suggests that categorisation based on ecotrophomorphology in the broader sense e.g. mouth size and degree of specialisation, may improve the ability of the guild approach to summarise estuarine ecosystems in a comparable and informative way. However, distinct and consistent differences in the diet of morphologically similar species (e.g. relatives) (present study, Hyndes et al. 1997) indicate that there are other factors dictating diet composition that also need consideration. One important relationship the guild structure does overlook is that between habitat type and the prey available to be consumed. This detail can be critically important to management, as sources of nutrients/energy can change between habitats, as can details of food web structure. Consequently, the way in which we reduce feeding relationships into standardised guilds may ultimately depend on the type of relationship we want to represent and explore.

### Conclusions

It has long been recognised that aggregation of species into trophic categories can influence appar-

ent food web properties (Hall & Raffaelli 1991). Despite this, managing real-world ecosystems, where there is always a deficit of information, means aggregations such as the guild scheme proposed by Elliott and Dewailly (1995) are necessary. Environmental managers require tools that simplify complex ecosystem processes into 'tractable' components, producing standards that can be applied over a broad range of systems, situations and geographic regions. As a theoretical construct the guild concept delivers on these requirements, providing a generalisation of food web structure that has proven useful in research (Elliott & Dewailly 1995). However, it needs to be emphasised that Elliott et al.'s (2007) proposed guilds were never intended to be prescriptive endpoints but rather that their value relates to '...their contribution in searching for differences in biogeographical areas and at the same time similarities in estuarine fish assemblage structure irrespective of that global position.' and in their ability to highlight areas of research that require further study (Elliott et al. 2007, p. 263). This is a large scale vision. For other research and management objectives, particularly at regional or local levels, the guild approach needs to be employed with caution because, as emphasised by Elliott et al. (2007), it represents a broadly focussed framework that requires fine-tuning for different situations as additional information becomes available. Creating guilds that are practical on a global scale requires merging and concealing many of the intricate relationships and processes that ultimately drive food web function. Consequently, treating a broadly developed guild structure too literally devalues the intent of Elliott et al. (2007) and risks overlooking important local detail. Such detail is crucial to the effective management of estuaries, and therefore the global guild approach should not be substituted for comprehensive species-specific ecological studies and independent investigations of estuarine trophic guilds at the regional level. So, while simplifications can be valuable and often necessary in data-poor situations (Pilling et al. 2009), caution must be used when applying a guild approach that imports interpretation from other species and/or locations, and should be explicitly recognised as an interim position until more specific data can be acquired. The potential for inaccuracy demonstrated in the current study underlines that this second step can not be overlooked and should always be seen as necessary. This is not to say that finer and finer division of trophic groups is necessary. In fact there is a point where finer resolution adds little functional benefit in either understanding or in the ability to manage the eco-

system. However, without recognising the potential limitations of the guild approach, it is neither possible to determine the point at which finer scale division is appropriate, nor to understand the extent to which the broad guild structure represents a useful tool.

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