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# Predator and prey interactions of fishes of a tropical Western Australia river revealed by dietary and stable isotope analyses

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Stomach content analyses of fishes occurring in the Fitzroy River, Western Australia, were used to investigate seasonal and ontogenetic changes in the diets and feeding relationships of the most abundant teleost and elasmobranch species. Concurrent analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope ratios was also used to determine which food resources were energetically important to each species (assimilated) and included less common fishes for which few dietary samples were attained. The use of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope and stomach content analysis indicated that differences often exist between the food types consumed and those that are energetically important to a species. Dietary analysis suggested that aquatic insects, and to a lesser extent filamentous algae, were important food sources for many of the species present. While stable isotope analysis also suggested that insects are important prey, both insects and algae did not appear to be as important as direct energy sources. In contrast, prey types that persist throughout the year (e.g. fish, molluscs and *Macrobrachium spinipes*) may be more important sources of energy than dietary data revealed. For example, isotope analysis suggested that fish are an important energy source for a large number of species including several which have been considered to be strict algivores/detritivores. Dietary overlap between species was found to be the highest during the wet season, when prey availability was presumably also high, decreased in the early dry season as fishes became more specialised in their feeding and increased again in the late dry when food became very limited.

**KEYWORDS:** ontogeny, stomach content analysis, isotope analysis, food web

## INTRODUCTION

Seasonality is recognised as a major factor affecting the diets and trophic relationships of riverine fishes via its effects on habitat availability, migration patterns, assemblage structure and prey availability (Zaret & Rand 1971; Angermeier and Karr 1983; Ross *et al.* 1985; Sumpton & Greenwood 1990; Winemiller & Jepson 1998). This influence is particularly relevant in highly seasonal systems such as tropical (monsoonal) rivers where the magnitude of flood events is important in determining their biological compositions (Bunn & Arthington 2002) and underpins river ecosystem function (Puckridge *et al.* 1998).

Fish communities of tropical Australian rivers are unique and have been shown to differ from those of Asia, Africa and South America (Unmack 2001; Allen *et al.* 2002). In the latter, terrestrially derived plant material and detritus are significant direct food sources for numerous species and these in turn support an abundant and diverse piscivorous fauna (Lowe-McConnell 1987). In contrast, dietary studies of fishes in tropical Australian rivers indicate that few species exclusively occupy the top and bottom trophic levels, with omnivorous species that consume a broad range of food types from multiple trophic levels being prevalent (see for example Arthington 1992; Pusey *et al.* 1995, 2000; Bishop *et al.* 2001; Morgan *et al.* 2004a; Davis *et al.* 2010). However, relatively few dietary studies of tropical Australian

riverine fishes have investigated changes in diet over time, in response to seasonal variation or ontogenetic change. Despite some recent exceptions, including the study of Raynor *et al.* (2010) who investigated temporal food web dynamics and those of Davis *et al.* (2011, 2012, 2013) who investigated ontogenetic dietary changes in Australian Terapontids, the description of many Australian species as being 'generalists' or 'omnivorous' remains, which may be partly attributed to the limited understanding of how diets vary over time in those species. Seasonality, for example, is known to greatly influence the prey availability of tropical food webs and as such dietary overlap (Lowe-McConnell 1987; Prejs and Prejs 1987; Winemiller 1989). As discussed by Matthews (1988), increases in dietary overlap can occur when food becomes very limited, however, it can also occur as a result of an abundance of prey sources. In consideration of this, dietary studies based on a single sampling event or in one season for example, would not detect changes in the prey available or the utilisation of that prey by a particular species.

The analysis of a fish's diet through quantification of stomach contents provides a 'snapshot' of the food recently consumed (Pinnegar & Polunin 1999). To obtain an accurate depiction of the overall diet of a species utilising this method numerous samples are required and classification of a species feeding habit (e.g. as a detritivore, insectivore or piscivore) can only be ascertained when diets are inspected over time or at least seasonally (Jepson & Winemiller 2002). Difficulties also often exist when attempting to classify fishes with broad

diets, those which feed at multiple trophic levels (i.e. omnivores) or those that feed opportunistically (Yoshioka & Wada 1994; Jepson & Winemiller 2002). These difficulties may be compounded by the reality that the presence of a food item in a stomach does not necessarily indicate that it is energetically important to that species (or assimilated) and that differences in digestion rates of different food types can lead to the over or under-representation of those prey types in the diet (Forsberg *et al.* 1993; Vander Zanden *et al.* 1997; Pinnegar & Polunin 1999; Melville & Connolly 2003).

In contrast to stomach content analyses, the stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotope ratios of a consumer can aid in the depiction of the organic source (primary producer of the system) and trophic position of the consumer, respectively, by determining those foods actually assimilated into tissues (DeNiro & Epstein 1981; Fry & Sherr 1984; Peterson & Fry 1987; Yoshioka & Wada 1994; Post 2002). Thus, in cases where dietary analysis reveals a broad range of food types, stable isotope analysis may be employed to investigate the assimilation of ingested food items, assist in the clarification of trophic interactions occurring between consumers, and trace variations of a species diet in response to, for example, seasonal food abundances and ontogenetic changes (Bunn & Boon 1993; Cocheret de la Morinière *et al.* 2003).

The paucity of detailed information on the dietary interactions of tropical freshwater fish communities in Australia and the inapplicability of foreign studies to a region that has a highly endemic ichthyofauna (Allen *et al.* 2002) generated this study's aims. These were to describe and compare the seasonal diets and feeding relationships of the different size classes of the most abundant teleost and elasmobranch species found in freshwaters of a large tropical river system of northern Australia using both stomach content and stable isotope analyses. The use of both techniques allowed dietary changes of fishes captured in low abundance (including *Pristis pristis* which is protected in Australia under the *Environment Protection and Biodiversity Conservation Act* 1999) to be investigated and also provided the basis for comparing the effectiveness of each technique in identifying the most important prey to the fish species present. These data were also used to investigate whether herbivores/detritivores and piscivores are under-represented in tropical Australian systems and provide a basis for comparisons to the criteria described by Lowe-McConnell (1987) for tropical systems of Asia, Africa and South America. Following Matthews (1998), we subsequently test the hypotheses that there is likely to be higher magnitudes of dietary overlap between species when prey availability is high (in this case the monsoonal wet season), that it will become reduced in the early dry season as resources begin to contract and the diets of each species becomes more specialised, and will increase when resources become very limited (in the late dry season).

## MATERIALS AND METHODS

### Sampling locality, seasonality and methods of collection

The Fitzroy River is one of the largest unregulated rivers

in northern Australia, draining almost 90 000 km<sup>2</sup>, and receives ~90% of its annual rainfall during the wet season (between November and March) (Anon 1993; Ruprecht & Rogers 1998). Fish were collected from the Fitzroy River in June 2003, November 2003 and March 2004 to coincide with the early dry, late dry and wet seasons, respectively. In light of the high flow rates and flooding that occurs in the Fitzroy River during the monsoonal wet season (which preclude access to a vast majority of the system) sampling for freshwater fish was primarily conducted ~300 km from the mouth in the main channel at Geikie Gorge (between 18.110°S, 125.699°E and 18.013°S, 125.764°E). Geikie Gorge is a large permanent pool with extensive sandy shallows and backwaters. Flow rates are low or non-existent except during the peak wet season. Due to only low numbers of freshwater sawfish *Pristis pristis* and the bull shark *Carcharhinus leucas* being encountered in Geikie Gorge during the study some additional samples were collected from freshwater pools ~150 km downstream below Camballin Barrage (18.187°S, 124.492°E). This site is the next location downstream of Geikie Gorge that has road access, holds a comparable suite of fishes (see Morgan *et al.* 2004b) and was considered to have comparable densities and types of detritus, aquatic vegetation and large woody debris.

Opportunistic sampling of 18 teleost and two elasmobranch species was conducted during daylight hours using a combination of gill, seine and throw nets, and baited lines. In each season, efforts were made to collect at least 30 individuals (containing food in their stomachs) of each species that were representative of the size distribution present.

Dietary samples of *P. pristis* were obtained from a number of individuals that had been found dead or from those donated by indigenous fishers prior to consumption. Muscle tissue was also collected from these individuals for stable isotope analysis. Fin clips were also obtained for stable isotope analysis from captured individuals (prior to their release) with a total of nine tissue samples per season being collected. Zero, six and two dietary samples were obtained in the wet, early dry and late dry seasons, respectively.

Muscle tissue from nine, 13 and nine *C. leucas* was collected for stable isotope analysis in the wet, early dry and late dry seasons, respectively. Zero, 14 and 5 dietary samples were subsequently also obtained from these individuals.

### Stomach contents – identification and quantification

The stomach was removed from each fish, its contents were examined and each food item identified to the lowest possible taxon. The percentage contribution of each item to the total stomach content was estimated and allocated to one of 41 prey categories (Tables 1–4) based on their similar size, position occupied in the water column and mobility (subsequently referred to as dietary categories) (Gill & Morgan 1998, 2003). Broad dietary categories were also determined from these for ease of interpretation (see Table 5).

Diets were analysed using the points method which gives the relative contribution of each prey type to the volume (percentage contribution (%V)) of stomach content of the fish (Hynes 1950; Ball 1961). The mean

**Table 1** Average wet season diet (adjusted %V) of each fish species captured in freshwaters of the Fitzroy River. N.B. Cle - *Carcharhinus leucas*; Pp - *Pristis pristis*; Ne - *Nematalosa erebi*; Ng - *Neoarius graeffei*; Ma - *Melanotaenia australis*; Cl - *Cratocephalus lentiginosus*; Am - *Ambassis* sp. 1; Lc - *Lates calcarifer*; Ap - *Amniataba percoides*; Hj - *Hephaestus jenkinsi*; Lu - *Leiopotherapon unicolor*; Ga - *Glossamia aprion*; Tk - *Toxotes kimberleyensis*; and Gg - *Glossogobius giuris*.

Species and size category	Ne<100	Ne>100	Ng<150	Ng >150	Ma	Cl	Am	Lc	Ap >40	Hj	Lu	Ga	Tk<50	Tk>50	Gg<70	Gg>70
Length range (mm) min	57	151	110	216	26	23	11	487	51	120	33	44	19	59	23	74
max	87	332	130	391	55	38	53	951	83	362	107	180	49	91	67	155
<i>n</i> used in analysis	11	22	7	29	28	29	25	34	36	30	30	23	14	14	26	8
<b>Dietary component</b>																
Sand	0.45															
Diatom																
Filamentous algae	1.64	9.23	34.42	3.52					53.44	30.98	23.44					7.50
Fig/fruit		0.36		18.90				2.94		29.29						
Aquatic macrophyte										3.33						
Terrestrial vegetation		3.41	4.96	11.56				4.12		20.52				0.55		
Biofilm/silt	97.73	86.05										3.11				
Gastropoda			2.30	0.34				0.29	0.56	0.08						
Bivalvia		0.09		0.13						0.08						
Nematoda		0.09														
Annelida				0.17												0.38
Terrestrial Arachnida				0.34	4.29									10.61		
Aquatic Arachnida																
Ostracoda	0.18		3.30		0.89	14.38	1.00		1.71		0.17				47.97	
Cladocera		0.09				6.87	13.13		0.35							
Copepoda						1.21			0.14		0.33				0.77	1.25
Isopoda											1.00					
Amphipoda							4.00		0.14			0.87				
Shrimp (<15mm)				0.14												
<i>Macrobrachium spinipes</i>				9.36				40.29								
Diptera larvae			7.97		5.09	10.28	23.03		6.25		6.06	0.87	7.92		3.88	
Diptera pupae					4.61	30.86	28.63		0.14		2.12	0.87	18.42		20.95	
Aquatic Hemiptera		0.68	12.14		13.27	27.09	15.47		8.51		20.83	70.40	27.41	18.06	13.54	43.75
Trichoptera larvae			1.43		0.18				0.92		0.64			3.83	0.77	
Odonata larvae					1.79		1.20		1.60		2.24			3.57	2.69	
Ephemeroptera larvae					3.99	3.10	9.33		1.67		0.20	1.74				
Coleoptera larvae			5.49				0.60		10.28		1.00	1.30	13.93		7.50	
Aquatic Coleoptera adult			14.64	0.25	21.65				7.92		15.54	5.37	13.77	4.37	1.92	12.50
Diptera adult				0.17	3.04						1.50		0.75	1.90		
Ephemeroptera adult									0.28							
Lepidoptera adult				0.34										6.88		
Orthoptera adult			8.57	29.83				5.88		11.71	9.00		10.56	16.25		11.25
Odonata adult				0.34												
Terrestrial Coleoptera adult				18.77	3.21				0.67			2.17		15.46		
Hymenoptera (flying) adult					3.57								4.40	7.22		
Hymenoptera (non-flying) adult				0.28	34.42						2.22	1.09	2.84	11.31		
Teleost				2.07		3.45		46.47	6.11	3.33	10.33	12.20				23.38
Teleost Scales			4.76	3.46							3.38					
Teleost Egg						2.76	3.60									
Mammal																
Reptile																

**Table 2** Average early dry season diet (adjusted %V) of each fish species captured in freshwaters of the Fitzroy River. See Table 1 for species codes.

Species and size category	<i>Cle</i>	<i>Pp</i>	<i>Ne&lt;100</i>	<i>Ne &gt;100</i>	<i>Ng&lt;150</i>	<i>Ng&gt;150</i>	<i>Ma</i>	<i>Cl</i>	<i>Am</i>	<i>Lc</i>	<i>Ap&lt;40</i>	<i>Ap&gt;70</i>	<i>Hj</i>	<i>Lu</i>	<i>Ga</i>	<i>Tk &gt;50</i>	<i>Gg</i>
Length range (mm) min	778	912	25	138	92	207	41	16	19	434	17	72	137	40	20	50	13
max	1160	2271	56	340	132	380	54	48	46	928	37	87	325	108	120	193	48
<i>n</i> used for analysis	14	6	19	36	18	30	31	31	24	30	26	4	25	28	28	19	29
<b>Dietary component</b>																	
Sand		3.62		2.52	4.21	4.29				0.17		1.96	1.23				
Diatom				0.64													
Filamentous algae		13.89		24.18	6.02	5.11	23.23	0.86	4.17		0.58	45.39	70.88	18.63	2.42		
Fig/fruit					1.11	0.39	1.02						5.24	2.86			
Aquatic macrophyte	0.36					0.95											
Terrestrial vegetation	0.79	2.69	12.15	4.45	2.76	5.56							2.09	2.20		0.35	
Biofilm/silt		2.59		67.56									0.21				
Gastropoda					5.68	0.42						24.51					
Bivalvia				0.03	3.41												
Nematoda		0.33							4.79								
Annelida				0.34	2.83								0.44	2.50			
Terrestrial Arachnida							1.52										
Aquatic Arachnida							0.65										
Ostracoda								1.29	0.42					1.07	0.54		
Cladocera			47.31	0.27			14.92	4.43				21.88	0.22				2.07
Copepoda			40.43								1.65						
Isopoda											1.54						4.14
Amphipoda																	
Shrimp (<15mm)																	
<i>Macrobrachium spinipes</i>	0.71	10.24				3.98	0.85			20.83			9.60		3.57	0.53	
Diptera larvae					4.83	2.76	1.16	75.00	9.58		14.32	1.58	0.22	6.82	6.93		8.28
Diptera pupae									31.88		0.77	1.56		0.18	0.26		
Aquatic Hemiptera			0.11		28.09	6.36	8.18	10.05	24.58		9.28	3.13	3.59	26.90	24.80	6.67	10.17
Trichoptera larvae					2.56	1.46		0.51	5.00		9.38		0.24	8.79	3.85		30.69
Odonata larvae						5.38					0.20			9.58	5.45		
Ephemeroptera larvae						1.23	7.63	7.85			61.14			3.73	4.82		41.38
Coleoptera larvae					3.51	0.26	2.22		7.08		1.15			9.12	18.75		
Aquatic Coleoptera adult	7.14				18.84	1.38	7.22		12.50				2.19	1.70	15.79	17.50	
Diptera adult						0.54	5.32									2.51	
Ephemeroptera adult							0.76										
Lepidoptera adult						1.00											
Orthoptera adult					2.22	35.47	0.32								1.65	13.92	
Odonata adult						1.04										0.53	
Terrestrial Coleoptera adult					6.03	15.81	1.43						3.62			27.58	
Hymenoptera (flying) adult						2.22	0.65									11.96	
Hymenoptera (non-flying) adult								20.83								1.79	18.19
Teleost	83.14	66.63			5.68	2.86				79.00					9.46		3.28
Teleost Scales					2.22	1.54							0.22				
Teleost Egg							2.11							6.10			
Mammal	7.86																
Reptile																	

**Table 3** Average late dry season diet (adjusted %V) of each fish species captured in freshwaters of the Fitzroy River. See Table 1 for species codes.

Species and size category	<i>Cle</i>	<i>Pp</i>	<i>Ne&gt;100</i>	<i>Ng&gt;150</i>	<i>Ma</i>	<i>Cl</i>	<i>Am</i>	<i>Lc</i>	<i>Ap40-70</i>	<i>Ap&gt;70</i>	<i>Hj</i>	<i>Lu</i>	<i>Ga</i>	<i>Tk&lt;50</i>	<i>Tk&gt;50</i>	<i>Gg&lt;70</i>
Length range (mm) min	878	1040	143	167	27	20	18	360	45	72	81	31	19	15	85	19
max	1328	1587	420	455	74	55	63	770	67	109	262	112	117	42	219	66
<i>n</i> used in analysis	5	2	44	33	30	30	21	30	19	10	22	17	31	18	12	29
<b>Dietary component</b>																
Sand		5.49	26.36	1.49												
Diatom																
Filamentous algae			21.42	8.20	56.69	18.92			18.85	16.66	51.85	1.38				0.69
Fig/fruit			0.34	8.48							25.77					
Aquatic macrophyte					0.42								2.30			
Terrestrial vegetation		2.75	2.09	2.26							11.20					
Biofilm/silt		66.37	48.67													
Gastropoda				4.98						2.43						0.86
Bivalvia		1.65	0.05	1.62							0.33		0.18			
Nematoda						0.17										1.38
Annelida			0.05													
Terrestrial Arachnida														3.89		
Aquatic Arachnida					0.21		32.43									
Ostracoda				0.15	0.04	44.05	18.41		3.12	28.17		1.27	6.45			27.07
Cladocera			0.11			2.39				0.20			3.39			
Copepoda			0.27													
Isopoda							0.73			0.10						
Amphipoda			0.05													
Shrimp (<15mm)																
<i>Macrobrachium spinipes</i>		2.75		0.84				19.33			0.27		3.23			
Diptera larvae			0.05	0.36	0.13	3.75	5.58		13.25	3.02	0.33	10.75	7.85	15.33	0.42	9.58
Diptera pupae					2.33	13.72						13.21	4.52	33.19		2.11
Aquatic Hemiptera				2.17	8.62	6.03	19.94		7.98		0.99	15.23	18.72	31.09	8.43	27.61
Trichoptera larvae			0.32	0.24	0.17	7.19	8.40		2.98	1.68		10.55		1.31		3.83
Odonata larvae				5.45					10.53	39.42	1.84	20.59	7.67	2.61		
Ephemeroptera larvae									15.79			0.29				1.15
Coleoptera larvae					0.67	3.79	10.06		24.47			8.09	3.23			14.79
Aquatic Coleoptera adult				4.55	2.24		1.12				1.15	6.86	6.45	2.53	18.95	2.93
Diptera adult					3.29		3.33				0.25	0.88	1.61			
Ephemeroptera adult				1.82												
Lepidoptera adult															7.50	
Orthoptera adult				23.43											19.57	
Odonata adult				2.70					2.37		0.25	5.00		0.69	3.33	
Terrestrial Coleoptera adult				10.05	0.07									3.40	19.40	
Hymenoptera (flying) adult				3.03						8.33					0.83	
Hymenoptera (non-flying) adult					0.40	25.15									5.96	21.57
Teleost	80.00	20.99		6.36				80.67			5.50	5.88	29.03			8.00
Teleost Scales			0.23	7.19					0.66		0.25					
Teleost Egg													2.15			
Mammal				1.21												
Reptile	20.00			3.00									3.23			



**Table 4** Percentage contribution (%V) of food items found in the stomachs of fishes captured in low abundance or in only one season from freshwaters of the Fitzroy River.

Species <i>n</i>	<i>Elops hawaiiensis</i> 3	<i>Megalops cyprinoides</i> 16	<i>Neosilurus hyrtlui</i> 13	<i>Strongylura krefftii</i> 9	<i>Hammia greenwayi</i> 3	<i>Liza alata</i> 21
<b>Dietary component</b>						
Sand			0.48			22.03
Diatom						15.30
Filamentous algae	11.43		3.71	3.10	65.00	17.89
Fig/fruit						
Aquatic macrophyte						
Terrestrial vegetation			0.55			0.48
Biofilm/silt	28.57		6.25			43.47
Gastropoda			16.71			
Bivalvia		1.42	1.92			
Nematoda						0.06
Annelida			0.41			
Terrestrial Arachnid						
Aquatic Arachnid						
Ostracoda			64.01			
Cladocera			0.40			
Copepoda						
Isopoda						
Amphipoda						
Other microcrustacea						
Shrimp (<15mm)						
<i>Macrobrachium spinipes</i>						
Diptera larvae			1.84			
Diptera pupae						
Aquatic Hemiptera	38.57	37.74	0.55	13.33	10.00	
Trichoptera larvae			0.10			
Odonatan larvae		2.26		1.67		
Ephemeroptera larvae						
Coleoptera larvae						
Aquatic Coleoptera adult		24.53		5.71		
Diptera adult		1.32				
Ephemeroptera adult						
Lepidoptera adult						
Orthoptera adult		1.89				
Odonata adult		1.70				
Terrestrial Coleoptera adult		2.36				
Hymenoptera (flying) adult						
Hymenoptera (non-flying)						
Other terrestrial insect						
Unidentified insect part	21.43	13.21	3.08	8.81		
<i>Neoarius graeffei</i>						
<i>Glossamia aprion</i>						
<i>Nematalosa erebi</i>				27.14		
<i>Amniataba percoides</i>						
<i>Craterocephalus lentiginosus</i>		3.40		11.90	25.00	
Other/unidentified teleost		10.19		23.33		
Teleost scales						
Teleost egg						
Mammal						
Reptile				5.00		

percentage volumetric contribution (%V) of each of the reassigned dietary categories to the stomach contents of each of the fish species was calculated for each season.

#### Stomach contents – differences between size categories and seasons within a species

To investigate both ontogenetic and temporal changes in diet, the total lengths (mm) recorded for individuals

within each species were examined and three respective size categories (groupings) were assigned based on length frequency analyses. Size categories (mm) identified for the 12 most abundant teleost species (i.e. those for which sufficient numbers for analysis were collected in all seasons) were as follows: *Nematalosa erebi* <100, 100–250, >250; *Neoarius graeffei* <150, 150–250, >250; *Melanotaenia australis* <40, 40–50, >50; *Craterocephalus*

**Table 5** Summary of stomach contents (%V) of fishes in the Fitzroy River during the wet, early dry and late dry seasons. (*Cle*, *C. leucas*; *Pp*, *P. pristis*; *Ne*, *N. erebi*, 1<100mm, 2>100mm; *Ng*, *N. graeffei*, 1<150mm, 2>150mm; *Ma*, *M. australis*; *Cl*, *C. lentiginosus*; *Am*, *Ambassis* sp 1; *Lc*, *L. calcarifer*; *Ap*, *A. percoides*, 1<40mm, 2>40mm<70mm, 3>70mm; *Hj*, *H. jenkinsi*; *Lu*, *L. unicolor*; *Ga*, *G. aprion*; *Tk*, *T. kimberleyensis*, 1<50mm, 2>50mm; *Gg*, *G. giuris*, 1<70mm, 2>70mm).

Species and size	<i>Cle</i>	<i>Pp</i>	<i>Ne1</i>	<i>Ne2</i>	<i>Ng1</i>	<i>Ng 2</i>	<i>Ma</i>	<i>Cl</i>	<i>Am</i>	<i>Lc</i>	<i>Ap1</i>	<i>Ap2</i>	<i>Ap3</i>	<i>Hj</i>	<i>Lu</i>	<i>Ga</i>	<i>Tk1</i>	<i>Tk2</i>	<i>Gg1</i>	<i>Gg2</i>
Wet season <i>n</i>	0	0	11	22	7	29	28	29	25	34	0	36	0	30	30	23	14	14	26	8
<b>Biofilm/silt/sand</b>			<b>98</b>	<b>86</b>												<b>3</b>				
<b>Vegetation</b>			<b>2</b>	<b>13</b>	<b>40</b>	<b>34</b>				<b>8</b>		<b>53</b>		<b>84</b>	<b>23</b>			<b>&lt;1</b>		<b>8</b>
Aquatic vegetation			2	9	35	4						53		34	23					8
Terrestrial vegetation				4	5	30				8				50				<1		
<b>Aquatic Invertebrata</b>			<b>&lt;1</b>	<b>1</b>	<b>47</b>	<b>10</b>	<b>51</b>	<b>94</b>	<b>96</b>	<b>40</b>		<b>40</b>			<b>40</b>	<b>81</b>	<b>81</b>	<b>30</b>	<b>100</b>	<b>58</b>
Aquatic worms				<1		<1								<1						<1
Aquatic Mollusca				<1	2	<1				<1		<1		<1						
Aquatic Arthropoda				<1	45	10	51	94	96	40		40			40	81	81	30	100	58
<b>Terr. Invertebrata</b>					<b>9</b>	<b>50</b>	<b>49</b>			<b>6</b>		<b>&lt;1</b>		<b>12</b>	<b>13</b>	<b>3</b>	<b>19</b>	<b>70</b>		<b>11</b>
<b>Teleostei</b>					<b>5</b>	<b>6</b>		<b>6</b>	<b>4</b>	<b>46</b>		<b>6</b>		<b>3</b>	<b>14</b>	<b>12</b>				<b>23</b>
<b>Mammalia/ Reptilia</b>																				
Early dry season <i>n</i>	14	6	19	36	18	30	31	31	24	30	26	0	4	25	28	28	0	19	29	0
<b>Biofilm/silt/sand</b>		<b>6</b>		<b>70</b>	<b>4</b>	<b>4</b>				<b>&lt;1</b>			<b>2</b>	<b>1</b>						
<b>Vegetation</b>	<b>1</b>	<b>17</b>	<b>12</b>	<b>29</b>	<b>10</b>	<b>12</b>	<b>24</b>	<b>1</b>	<b>4</b>		<b>&lt;1</b>		<b>45</b>	<b>78</b>	<b>24</b>	<b>2</b>		<b>&lt;1</b>		
Aquatic vegetation	<1	14		25	6	6	23	1	4		<1		45	71	19	2				
Terrestrial vegetation	1	3	12	4	4	6	1							7	5			<1		
<b>Aquatic Invertebrata</b>	<b>8</b>	<b>11</b>	<b>88</b>	<b>1</b>	<b>70</b>	<b>23</b>	<b>43</b>	<b>99</b>	<b>96</b>	<b>21</b>	<b>99</b>		<b>53</b>	<b>14</b>	<b>63</b>	<b>85</b>		<b>25</b>	<b>97</b>	
Aquatic worms		<1		<1	3				5					<1	2					
Aquatic Mollusca				<1	9	<1	1						25							
Aquatic Arthropoda	8	10	88	<1	58	23	42	99	91	21	99		28	14	61	85		25	97	
<b>Terr. Invertebrata</b>					<b>9</b>	<b>56</b>	<b>31</b>							<b>4</b>		<b>3</b>		<b>75</b>		
<b>Teleostei</b>	<b>83</b>	<b>67</b>			<b>8</b>	<b>4</b>	<b>2</b>			<b>79</b>				<b>&lt;1</b>	<b>6</b>	<b>9</b>			<b>3</b>	
<b>Mammalia/ Reptilia</b>	<b>8</b>																			
Late dry season <i>n</i>	5	2	0	44	0	33	30	30	21	30	0	19	10	22	17	31	18	12	29	
<b>Biofilm/silt/sand</b>		<b>72</b>		<b>75</b>		<b>1</b>														
<b>Vegetation</b>		<b>3</b>		<b>24</b>		<b>19</b>	<b>57</b>	<b>19</b>				<b>19</b>	<b>17</b>	<b>89</b>	<b>1</b>	<b>2</b>			<b>&lt;1</b>	
Aquatic vegetation				21		8	57	19				19	17	52	1	2			<1	
Terrestrial vegetation		3		2		11								37						
<b>Aquatic Invertebrata</b>		<b>4</b>		<b>1</b>		<b>20</b>	<b>14</b>	<b>82</b>	<b>97</b>	<b>19</b>		<b>78</b>	<b>75</b>	<b>5</b>	<b>87</b>	<b>62</b>	<b>86</b>	<b>28</b>	<b>92</b>	
Aquatic worms				<1				<1											1	
Aquatic Mollusca		2		<1		7							2	<1		<1			<1	
Aquatic Arthropoda		3		1		14	14	82	97	19		78	73	5	87	61	86	28	89	
<b>Terr. Invertebrata</b>						<b>41</b>	<b>28</b>		<b>3</b>			<b>2</b>	<b>8</b>	<b>&lt;1</b>	<b>6</b>	<b>2</b>	<b>14</b>	<b>72</b>		
<b>Teleostei</b>	<b>80</b>	<b>21</b>		<b>&lt;1</b>		<b>15</b>				<b>81</b>		<b>&lt;1</b>		<b>6</b>	<b>6</b>	<b>31</b>			<b>8</b>	
<b>Mammalia/Reptilia</b>	<b>20</b>					<b>4</b>										<b>3</b>				



*lentiginosus* <30, 30–40, >40; *Ambassis* sp. 1 <25, 25–40, >40 (*sensu* *Ambassis* sp. 1 in Morgan *et al.* (2004) and *Ambassis* sp. in Allen *et al.* 2002); *Lates calcarifer* <550, 550–750, >750; *Amniataba percoides* <40, 40–70, >70; *Hephaestus jenkinsi* <150, 150–225, >225; *Leiopotherapon unicolor* <55, 55–85, >85; *Glossamia aprion* <40, 40–80, >80; *Toxotes kimmerleyensis* <50, 50–110, >110; *Glossogobius giuris* <30, 30–70, >70. Dietary data for all individuals of the six respective species collected in only low numbers or in one season were combined.

To compare dietary differences between size classes within each species, the volumetric data of each individual was used. Dietary categories that were unidentifiable were excluded as their inclusion has the potential to bias multivariate analysis (Pusey *et al.* 2000). All other values were subsequently adjusted upwards to sum 100%. This adjustment is based on the assumption that the removed unidentified fractions consist of the same proportions as the identified food items present in the stomach (Pusey *et al.* 2000).

The adjusted dietary data for individuals within each size category of each species within a season were then used to construct a similarity matrix using the Bray-Curtis similarity coefficient with PRIMER 5.1.2 (Clarke and Gorley 2001). A one-way analysis of similarity (ANOSIM) was subsequently used to determine if dietary differences between size categories were significant, and the R-stat values produced used to indicate the magnitude of these differences. Examination of R-statistics revealed that in no cases did values of 0.3 or less have p-values approaching anywhere near 0.05. Thus R-statistics of less than 0.3 were not considered to be significant. Size categories were combined if there was no significant difference. As only low numbers of *C. leucas* and *P. pristis* were collected, diet data for all individuals were combined for each season.

#### Stomach contents – comparisons between species within a season

Dietary data for individuals of each species within each reassigned size category were compared using a similar approach, i.e. using the data from the individual stomach and ANOSIM, to test the hypothesis that dietary overlap will be higher in the wet and late dry seasons than in the early dry season. As no *C. leucas* or *P. pristis* dietary samples were collected in the wet season these species were not included when calculating the percentage of non-significant results in the early dry season and late dry season. The overall mean diet of each species (and size category within) was subsequently calculated and used to generate dendrograms to illustrate the feeding groups present.

In addition to the 20 species/size categories used in the above analyses giant herring *Elops hawaiiensis*, oxeye herring *Megalops cyprinoides*, Hyrtl's tandan *Neosilurus hyrtlii*, freshwater longtom *Strongylura krefftii*, Greenway's grunter *Hannia greenwayi* and giant gudgeon *Oxyeleotris selheimi* were also caught during this study. As these species were caught in low numbers, in only one or two seasons and often had little or nothing in their stomachs, they were not used in the above analyses. When available their diets are reported and their flesh was used in the stable isotope analyses.

#### Stable isotope analyses – sample collection

In general, individual fish used for stable isotope analysis were the same as those upon which stomach content analysis was conducted. Fifteen individuals from each teleost species (and size category within a species identified by dietary analysis) and other food web components were analysed in each season. Nine samples were used for analysis of *P. pristis* and *C. leucas* in each season. In the case of *P. pristis*, an endangered species, analysis was based on either fin clips taken prior to their live release or muscle tissue attained from the few individuals from which the stomach was removed. Fin tissue has been shown to be a close predictor of muscle tissue values (see for example Kelly *et al.* 2006; Jardine *et al.* 2011) and was considered appropriate for investigating the trophic position of this rare species.

Cherabin (*Macrobrachium spinipes*), two gastropod molluscs (a small snail (Pomatiopsidae) and large snail (Hydrobiidae)) and two bivalve molluscs (a freshwater mussel (Hyriidae) and pea clam (Sphaeriidae)) were collected. The deposition of a thick layer of silt precluded the collection of the last of these species in the wet season. Terrestrial Orthoptera (grasshoppers; Acrididae) and aquatic hemipterans (water strider; Gerridae) were also collected. These latter taxa were amongst the only terrestrial and aquatic insects that could be readily collected in sufficient numbers to provide enough tissue for analysis.

Leaves from the most conspicuous riparian plant species in Geikie Gorge (and common throughout the Fitzroy River catchment), i.e. grasses, pandanus *Pandanus aquaticus*, river gum *Eucalyptus camaldulensis*, silver cadjeput *Melaleuca argentea* and the freshwater mangrove *Barringtonia acutangula* were collected by hand from the living plant. Filamentous algae was also collected by hand but could not be gathered in the wet season due to silt deposition. A seasonally abundant aquatic reed was also collected by hand during the late dry season. Three, 5 cm sediment cores were also collected in each season. All samples were placed into individual bags and placed on ice until they could be frozen.

#### Stable isotope analyses – sample preparation

All animal and plant samples were rinsed in distilled water. White muscle, which is less variable in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  than other tissues (Tieszen *et al.* 1983; Pinnegar & Poulin 1999), was carefully removed from fishes, eliminating as much bone, skin and red muscle as possible. Skin and cartilage were excluded from fin clips of *P. pristis*. Equal quantities of muscle tissue from between nine and 15 randomly selected individual fishes of each species (and size) were evenly divided into three replicates for each season. Where fewer than nine individuals were collected per species, muscle samples were combined and divided into three pseudo-replicates (as per Beatty *et al.* 2005).

Abdominal tissue (carapace and intestine removed) was removed from 15 *M. spinipes* per season and randomly assigned to three replicates. Muscle tissue from between 10 and 20 individuals (depending on size) of each mollusc was removed and randomly assigned to one of the three replicates within each season collected. Muscle tissue was also obtained from the hind legs of

approximately 20 orthopterans in the wet season. This quantity, however, was only sufficient for a single sample. At least 30 aquatic hemipterans were included in each replicate and macerated. Muscle tissue from all invertebrates was placed in 1 M HCl for 24 hours (for 48 hours in the case of whole aquatic hemipterans) to remove inorganic carbonates and thoroughly rinsed with distilled water prior to drying.

Leaf samples of each terrestrial vegetation type collected in each season were divided into three replicates and the woody petiole removed from the leaf to aid in drying and grinding. Three replicates (of five individual samples each) of both benthic algae and an aquatic reed (for each season present) were also assembled. Each of the three sediment core samples collected in each season were rinsed several times through a 150 µm sieve in order to collect organic detrital samples. Large detrital material was collected from the sieve and rinsed several times to provide samples of coarse particulate organic matter (CPOM). The fine material that passed through the sieve was washed and decanted several times with distilled water and collected to provide samples of fine particulate organic matter (FPOM). All samples were dried at 60 °C for 48 hours, and subsequently ground to a fine powder with a mortar and pestle.

#### Stable isotope analyses – analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Between 2 and 2.5 mg of each animal tissue, 3 to 6 mg of each plant tissue and 20 to 50 mg of each particulate organic matter sample were placed in a capsule, combusted and analysed (one in 20 samples being analysed in duplicate) using a Tracermass Iron Ratio Mass Spectrometer (*Europa PDZ*, UK) fitted with a *Roboprep* combustion system to oxidize the samples. The ratios of  $^{13}\text{C}:^{12}\text{C}$  and  $^{15}\text{N}:^{14}\text{N}$  were subsequently presented as the relative part per thousand (‰) differences between the signatures of the sample and that of the international standards of Pee Dee Belemite for  $\delta^{13}\text{C}$  and atmospheric nitrogen for  $\delta^{15}\text{N}$ . The precision of the analytical equipment was  $\pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$  and  $\pm 0.3\text{‰}$  for  $\delta^{15}\text{N}$ . The means of each sample category are presented  $\pm 0.01$  s.e.

#### Stable isotope analyses – trophic position

To reflect trophic position, the mean  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (‰) ratio of each sample was plotted in each season. Based on dietary analysis and dietary literature (see for example Bishop *et al.* 2001; Allen *et al.* 2002) each fish species was categorised as being either a piscivore, aquatic or terrestrial insectivore or detritivore/algivore and assigned a corresponding code (see Figures 4, 5 and 6). As terrestrial and aquatic invertebrates were only able to be collected in a single season, their  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures were also used in food web analyses in other seasons. In the case of the pea clam, which was deeply buried in silt during the wet season, values were not included in analyses as it was considered to be unavailable to fish.

The relative trophic position of each fish species to base level primary producers and potential food types were also estimated using the following formula (Post 2002):

$$\text{TL}_{\text{sc}} = 1 + (\delta^{15}\text{N}_{\text{sc}} - \delta^{15}\text{N}_{\text{base}}) / \Delta_n$$

where  $\text{TL}_{\text{sc}}$  is the trophic level of the consumer,  $\delta^{15}\text{N}_{\text{sc}}$  is the mean stable nitrogen ratio (‰),  $\delta^{15}\text{N}_{\text{base}}$  is the mean stable nitrogen ratio (‰) of the base of the food web (i.e. the overall mean  $\delta^{15}\text{N}$  signature of the primary producers (aquatic and terrestrial) collected in each season, respectively), and  $\Delta_n$  is the mean enrichment (‰) between trophic levels. During this study, a mean enrichment of 2.54 ‰ was used, in accordance with the meta-analysis of 134 estimates by Vanderklift & Ponsard (2003).

#### Stable isotope analyses – IsoSource mixing model

The isotopic signature of a consumer is rarely dependent upon the consumption of a single food source, but rather is a mixture and dependent upon the proportionate contributions of each food type (Fry & Sherr 1984). *IsoSource* (Phillips & Gregg 2003) was subsequently employed to investigate all the possible combinations of contributing sources of the mixture, by examining its proportions in small increments summed to 100%. Potential food sources used during analysis by *IsoSource* were those identified during stomach content analysis. Species relevant dietary literature (e.g. Bishop *et al.* 2001 and Allen *et al.* 2002) was also considered and any additional major prey item (i.e. not identified during our analyses of stomach contents) that was present in the Fitzroy River was included in the analysis. Dietary literature was particularly important for identifying potential food sources for those fish species encountered in only low abundance and those where stomachs were empty. In light of the relatively large number of potential food sources for each of the fishes analysed incremental increases of 2.5% were used to avoid impractical levels of computation. Although this is a relatively large value, Phillips & Gregg (2003) consider that it will provide an acceptable level of precision in determining the ranges of source contribution. The mass balance tolerance was also adjusted upwards from 0.5 ‰ (in increments of 0.1 ‰) until a feasible solution was achieved. While this upward adjustment reduces the precision of the computation and increases the range of the distributions, it does not alter the medians in feasible distributions (Phillips & Gregg 2003).

Six aquatic and terrestrial invertebrate food sources were collected during the current study. Although a wide range of invertebrate taxa are present and were encountered in the stomachs of fishes, the six taxa included in analysis were amongst the only invertebrate taxa that could be readily collected in sufficient abundance to provide enough tissue for analysis. While the signature of these taxa may not typify those of all aquatic and terrestrial invertebrates, these six taxa were considered to be suitable proxies for aquatic and terrestrial invertebrate food sources as all were encountered during stomach content analysis and in some cases were the most abundant taxa of their respective broader food type categories. It should be noted that the inclusion of the limited number of invertebrates during *IsoSource* analysis may lead to the overestimation of the alternative food sources included in the analysis.

## RESULTS

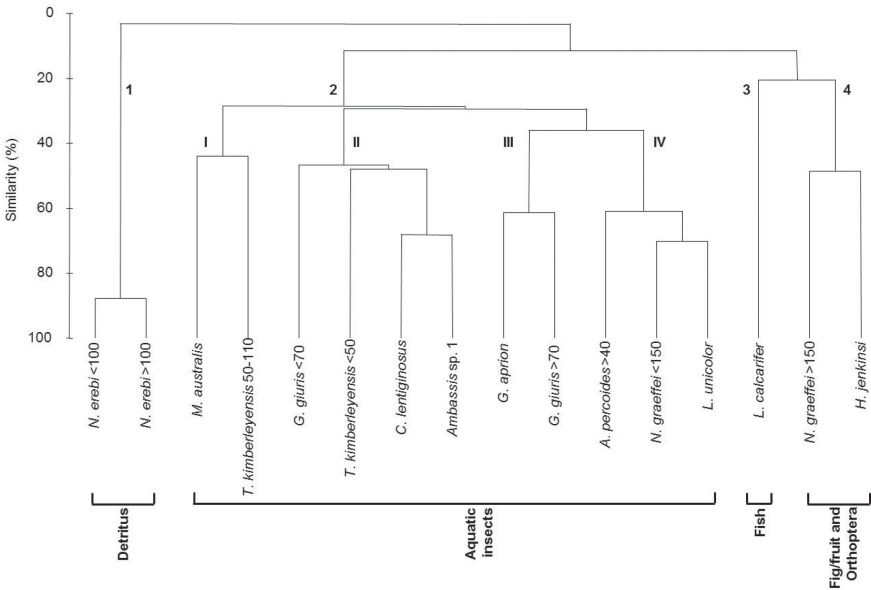
### Trophic relationships of the fishes of the Fitzroy River

Dietary and isotope analyses were generally in accordance with regard to demonstrating that the majority of species have broad diets and are reliant on aquatic and/or terrestrial invertebrates (Tables 1–7, Figures 1–3). For example, dietary analyses indicated that the majority of species are feeding on a wide range of aquatic and terrestrial invertebrates with many also ingesting plant material and/or fishes. Estimation of trophic level using stable isotopes (Table 6, Figures 4–6) indicated that in all seasons fishes were more enriched in  $\delta^{15}\text{N}$  than invertebrates, primary producers and detrital fractions. *IsoSource* modeling also confirmed the

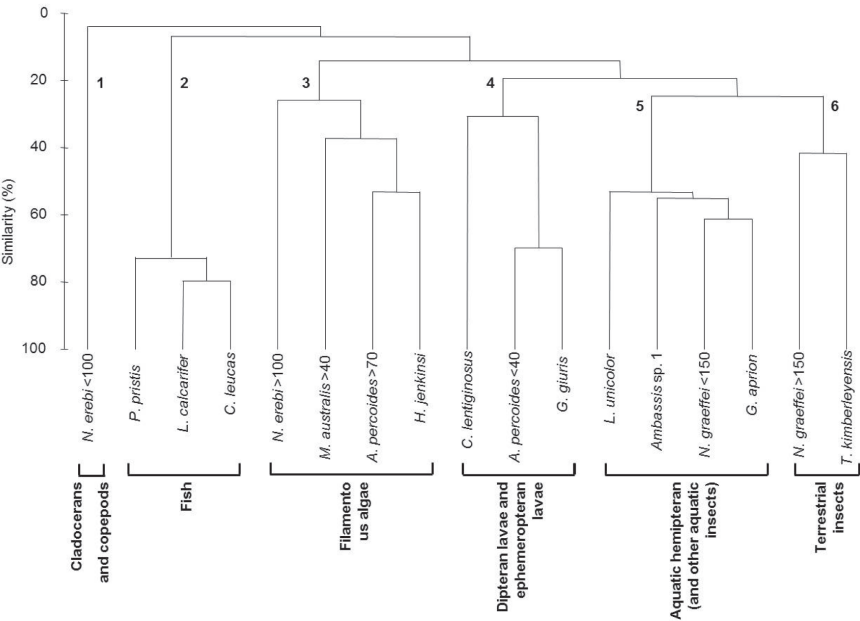
importance of invertebrates, plant material and fishes in those species in which they had been identified in the stomach contents (Table 7). Dietary data indicate that *C. leucas*, *P. pristis* and *L. calcarifer* are top order predators consuming fish, mammals and reptiles (*C. leucas*) or fish and large crustaceans (*P. pristis* and *L. calcarifer*) to the exclusion of almost all other dietary taxa. These species consistently occupied the highest trophic positions indicating their status as top order consumers and confirming their predominantly piscivorous diets. *IsoSource* modeling confirmed this scenario. The two methods were not concordant with regards to the diets of *N. erebi* where stomach contents suggested that this species fed predominantly on biofilm/silt/sand and plant material, or in the case of smaller fish during the early dry season on aquatic arthropods (see Table 2). While

**Table 6** Estimation of the trophic level ( $\text{TL}_{\text{SC}}$ ) of consumer species collected from the Fitzroy River during the wet, early dry and late dry seasons.

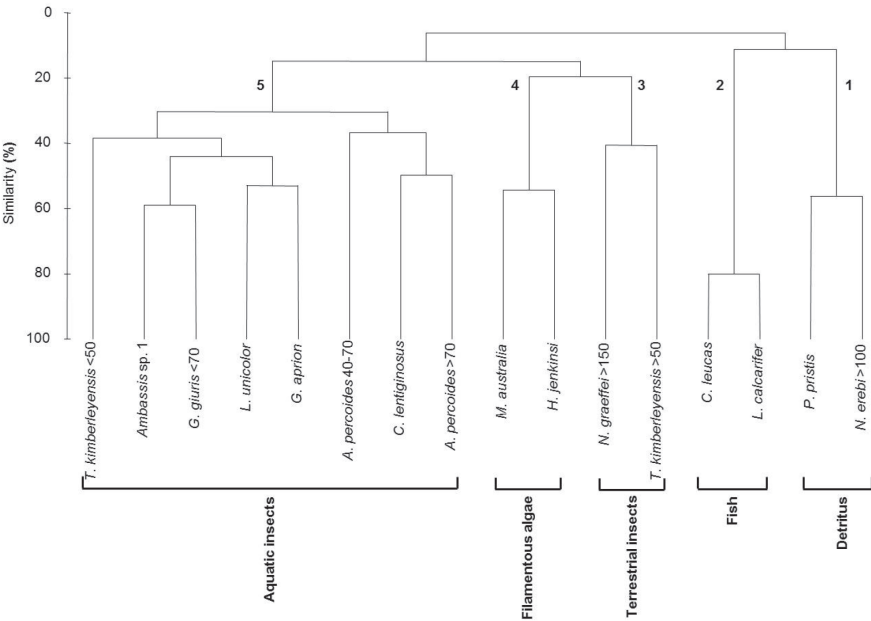
Consumer	Wet Season Mean $\delta^{15}\text{N}_{\text{base}} = 4.94$		Early Dry Season Mean $\delta^{15}\text{N}_{\text{base}} = 4.42$		Late Dry Season Mean $\delta^{15}\text{N}_{\text{base}} = 3.05$	
	$\delta^{15}\text{N}_{\text{SC}}$	$\text{TL}_{\text{SC}}$	$\delta^{15}\text{N}_{\text{SC}}$	$\text{TL}_{\text{SC}}$	$\delta^{15}\text{N}_{\text{SC}}$	$\text{TL}_{\text{SC}}$
<b>Elasmobranch</b>						
<i>C. leucas</i>	13.09	4.21	13.19	4.45	12.48	4.71
<i>P. pristis</i>	11.46	3.56	12.66	4.24	12.51	4.73
<b>Teleost</b>						
<i>N. erebi</i> <100	10.47	3.18	11.28	3.70	–	–
<i>N. erebi</i> >100	8.55	2.42	7.88	2.36	8.84	3.28
<i>E. hawaiiensis</i>	11.22	3.47	12.92	4.35	–	–
<i>M. cyprinoides</i>	11.46	3.56	–	–	12.69	4.79
<i>N. graeffei</i> <150	10.37	3.14	10.91	3.55	–	–
<i>N. graeffei</i> >150	–	–	11.28	3.70	11.23	4.22
<i>A. dahl</i>	9.82	2.92	–	–	–	–
<i>N. hyrtl</i>	8.35	2.34	–	–	–	–
<i>S. krefftii</i>	–	–	13.21	4.46	10.83	4.06
<i>M. australis</i>	10.16	3.05	10.93	3.56	9.13	3.39
<i>C. lentiginosus</i>	10.43	3.16	10.45	3.37	8.53	3.16
<i>Ambassis</i> sp.1	10.42	3.16	10.56	3.42	8.45	3.13
<i>L. calcarifer</i>	11.17	3.45	11.76	3.89	11.97	4.51
<i>A. percoides</i> <40	–	–	10.19	3.27	9.69	3.61
<i>A. percoides</i> >40	10.04	3.01	10.95	3.57	10.90	4.09
<i>H. greenwayi</i>	–	–	11.20	3.67	–	–
<i>H. jenkinsi</i>	9.82	2.92	11.72	3.87	10.19	3.81
<i>L. unicolor</i>	10.71	3.27	10.65	3.45	9.17	3.41
<i>G. aprion</i>	9.68	2.87	11.17	3.65	8.63	3.20
<i>T. kimberleyensis</i> <50	10.46	3.17	–	–	8.53	3.16
<i>T. kimberleyensis</i> >50	10.37	3.14	10.97	3.58	10.78	4.04
<i>O. selheimi</i>	9.50	2.79	–	–	–	–
<i>G. giuris</i> <70	10.46	3.17	9.12	2.85	8.07	2.98
<i>G. giuris</i> >70	10.04	3.01	–	–	–	–
<b>Crustacean</b>						
<i>M. spinipes</i> (cherabin)	9.39	2.75	10.23	3.28	9.47	3.53
<b>Mollusc</b>						
(F) Hyriidae (mussel)	7.52	2.01	9.07	2.83	6.58	2.39
(F) Pomatiopsidae (sm snail)	6.08	1.45	6.09	1.66	6.98	2.54
(F) Hydrobiidae (lg snail)	6.85	1.75	5.86	1.57	7.00	2.55
(F) Sphaeriidae (pea clam)	–	–	8.47	2.59	6.68	2.43
<b>Insect</b>						
(F) Gerridae (water strider)	–	–	–	–	6.05	2.18
(F) Acrididae (grass hopper)	7.99	2.20	–	–	–	–



**Figure 1** Classification of the mean volumetric dietary data of freshwater fishes of the Fitzroy River collected during the wet season, with major feeding groups indicated.



**Figure 2** Classification of the mean volumetric dietary data of freshwater fishes of the Fitzroy River collected during the early dry season, with major feeding groups indicated.



**Figure 3** Classification of the mean volumetric dietary data of freshwater fishes of the Fitzroy River collected during the late dry season, with major feeding groups indicated.

**Table 7** Feasible proportions (1st percentile, mean and 99th percentile) of food sources (determined by IsoSource) contributing to the diet of fish species (and sizes) captured in the Fitzroy River during the wet, early and late dry seasons. Potential food sources for each species were primarily determined from dietary analysis of fishes from the Fitzroy River.

Consumer	Food sources	Wet season			Early dry season			Late dry season		
		1st	mean	99th	1st	mean	99th	1st	mean	99th
<i>C. leucas</i>	<i>P. pristis</i>	0.60	0.78	0.95	0	0.96	1.00	0.25	0.72	0.98
	<i>N. erebi</i> <100	0	0.04	0.13	0	0	0	–	–	–
	<i>N. erebi</i> >100	0	0.02	0.08	0	0.01	0.03	0	0.01	0.03
	<i>N. graeffei</i> <150	0	0.12	0.30	0	0.01	0.03	–	–	–
	<i>N. graeffei</i> >150	–	–	–	0	0.03	0.10	0	0.26	0.73
	<i>L. calcarifer</i>	0	0.06	0.20	0	0.01	0.05	0	0.01	0.05
<i>P. pristis</i>	<i>N. erebi</i> <100	0	0.06	0.20	0	0	0	–	–	–
	<i>N. erebi</i> >100	0	0.03	0.13	0	0	0	0	0.02	0.08
	<i>N. graeffei</i> <150	0.43	0.68	0.88	0	0	0	–	–	–
	<i>N. graeffei</i> >150	–	–	–	0.93	0.94	0.95	0.90	0.95	1.00
	<i>M. spinipes</i>	0	0.10	0.40	0	0	0	0	0.03	0.10
	(F) Pomatiopsidae (sm snail)	0	0.3	0.13	0	0	0	0	0.01	0.05
	(F) Sphaeriidae (pea clam)	–	–	–	0	0	0	0	0.01	0.03
	Algae	–	–	–	0.05	0.06	0.08	0	0.00	0.03
	FPOM	0	0.01	0.08	0	0	0	0	0.00	0.03
	CPOM	0	0.02	0.08	0	0	0	0	0.00	0.03
<i>N. erebi</i> <100	(F) Pomatiopsidae (sm snail)	0	0.54	0.55	0	0.03	0.08	–	–	–
	(F) Sphaeriidae (pea clam)	–	–	–	0.93	0.93	0.95	–	–	–
	(F) Gerridae (water strider)	0	0.45	0.98	0	0.42	0.08	–	–	–
	Algae**	0	0.01	0.03	0	0	0	–	–	–
	<i>M. argentea</i> (silver cadjeput)	0	0.01	0.03	0	0	0	–	–	–
	FPOM	0	0.01	0.03	0	0	0	–	–	–
	CPOM	0	0.01	0.03	0	0	0	–	–	–
<i>N. erebi</i> >100	(F) Pomatiopsidae (sm snail)	0.80	0.89	0.96	0.03	0.64	0.98	0.88	0.95	1.00
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.18	0.50	0	0.00	0.03
	Algae**	0	0.02	0.03	0	0.15	0.45	0	0.01	0.03
	<i>M. argentea</i> (silver cadjeput)	0	0.06	0.03	0	0.01	0.05	0	0.00	0.03
	FPOM	0	0.02	0.08	0	0.01	0.08	0	0.01	0.03
	CPOM	0	0.04	0.04	0	0.02	0.08	0	0.014	0.05
<i>E. hawaiiensis</i>	<i>N. erebi</i> <100	0	0.01	0.05	0.03	0.46	0.70	–	–	–
	<i>N. erebi</i> >100	0	0.01	0.03	0	0.05	0.20	–	–	–
	<i>C. lentiginosus</i>	0	0.04	0.13	0	0.27	0.80	–	–	–
	(F) Gerridae (water strider)	0	0.02	0.08	0	0.02	0.10	–	–	–
	(F) Acrididae (grasshopper)	0.85	0.92	0.98	0.10	0.20	0.33	–	–	–
	Algae	–	–	–	0	0.01	0.08	–	–	–
	FPOM	0	0.02	0.05	0	0.01	0.05	–	–	–
<i>M. cyprinoides</i>	<i>N. erebi</i> <100	0	0.37	0.83	–	–	–	–	–	–
	<i>N. erebi</i> >100	0	0.06	0.20	–	–	–	0.55	0.78	0.95
	<i>C. lentiginosus</i>	0	0.27	0.78	–	–	–	0	0.10	0.10
	<i>Ambassis</i> sp.1	0	0.22	0.65	–	–	–	0	0.08	0.08
	(F) Hyriidae (mussel)	0	0.04	0.13	–	–	–	0	0.01	0.01
	(F) Sphaeriidae (pea clam)	–	–	–	–	–	–	0	0.01	0.01
	(F) Gerridae (water strider)	0	0.02	0.08	–	–	–	0	0.01	0.03
	(F) Acrididae (grasshopper)	0	0.03	0.15	–	–	–	0	0.03	0.04
<i>N. graeffei</i> <150	<i>N. erebi</i> <100	0	0.04	0.18	0.28	0.603	0.85	–	–	–
	<i>C. lentiginosus</i>	0	0.13	0.43	0	0.14	0.55	–	–	–
	<i>G. giuris</i> <70	0	0.17	0.53	0	0.10	0.43	–	–	–
	<i>M. spinipes</i>	0	0.13	0.48	0	0.03	0.15	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.03	0.13	0	0.05	0.02	–	–	–
	(F) Gerridae (water strider)	0	0.04	0.15	0	0.02	0.13	–	–	–
	(F) Acrididae (grasshopper)	0.25	0.45	0.70	0	0.02	0.08	–	–	–
	Algae	–	–	–	0	0.01	0.08	–	–	–
	CPOM	0	0.03	0.13	0	0.04	0.18	–	–	–



Consumer	Food sources	Wet season			Early dry season			Late dry season		
		1st	mean	99th	1st	mean	99th	1st	mean	99th
<i>N. graeffei</i> >150	<i>N. erebi</i> <100	–	–	–	0	0.04	0.15	–	–	–
	<i>C. lentiginosus</i>	–	–	–	0	0.04	0.15	0	0.07	0.30
	<i>G. giuris</i> <70	–	–	–	0	0.02	0.10	0	0.04	0.18
	<i>M. spinipes</i>	–	–	–	0.10	0.34	0.53	0.08	0.25	0.43
	(F) Pomatiopsidae (sm snail)	–	–	–	0	0.07	0.05	0	0.01	0.08
	(F) Gerridae (water strider)	–	–	–	0	0.01	0.08	0	0.02	0.08
	(F) Acrididae (grasshopper)	–	–	–	0	0.55	0.70	0.48	0.60	0.75
	Algae	–	–	–	0	0.01	0.05	0	0.01	0.05
	CPOM	–	–	–	0	0.00	0.03	0	0.08	0.05
<i>A. dahl</i>	(F) Hyriidae (mussel)	0.10	0.17	0.25	–	–	–	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.06	0.25	–	–	–	–	–	–
	(F) Gerridae (water strider)	0.55	0.71	0.85	–	–	–	–	–	–
	Algae**	0	0.04	0.15	–	–	–	–	–	–
	<i>M. argentea</i> (silver cadjeput)	0	0.01	0.05	–	–	–	–	–	–
	FPOM	0	0.01	0.05	–	–	–	–	–	–
<i>N. hyrtlii</i>	(F) Hyriidae (mussel)	0	0.09	0.07	–	–	–	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.29	0.22	–	–	–	–	–	–
	(F) Gerridae (water strider)	0.05	0.55	0.93	–	–	–	–	–	–
	Algae**	0	0.06	0.05	–	–	–	–	–	–
	FPOM	0	0.02	0.02	–	–	–	–	–	–
	CPOM	0	0.01	0.08	–	–	–	–	–	–
<i>S. krefftii</i>	<i>N. erebi</i> <100	–	–	–	0.43	0.78	0.95	–	–	–
	<i>N. erebi</i> >100	–	–	–	0	0.03	0.13	0.98	0.99	1.00
	<i>C. lentiginosus</i>	–	–	–	0	0.15	0.55	0	0.02	0.03
	(F) Gerridae (water strider)	–	–	–	0	0.02	0.08	0	0	0
	(F) Acrididae (grasshopper)	–	–	–	0	0.03	0.13	0	0	0
	Algae	–	–	–	0	0.01	0.05	0	0	0
<i>M. australis</i>	(F) Gerridae (water strider)	0	0.12	0.38	0.73	0.87	0.98	0.60	0.76	0.93
	(F) Acrididae (grasshopper)	0.6	0.81	0.98	0	0.06	0.13	0.05	0.18	0.04
	Algae	–	–	–	0	0	0	0	0.01	0.01
	FPOM	0	0.03	0.10	0	0	0	0	0.02	0.02
	CPOM	0	0.05	0.18	0.03	0.08	0.15	0	0.05	0.05
<i>C. lentiginosus</i>	(F) Pomatiopsidae (sm snail)	0	0.00	0.03	0	0.04	0.15	0	0.30	0.70
	(F) Sphaeriidae (pea clam)	–	–	–	0.48	0.66	0.78	0	0.23	0.55
	(F) Gerridae (water strider)	0	0.01	0.03	0	0.04	0.15	0	0.05	0.23
	(F) Acrididae (grasshopper)	0.98	0.99	1.00	0.10	0.26	0.48	0.20	0.39	0.53
	Algae	–	–	–	0	0.01	0.05	0	0.01	0.05
	FPOM	0	0	0	0	0.01	0.05	0	0.01	0.05
	CPOM	0	0	0	0	0.01	0.05	0	0.02	0.10
<i>Ambassis</i> sp.1	<i>C. lentiginosus</i>	0.73	0.78	0.83	0.78	0.89	0.98	0.03	0.06	0.10
	<i>M. spinipes</i>	0	0.06	0.13	0	0.07	0.20	0.90	0.94	0.98
	(F) Gerridae (water strider)	0	0	0	0	0.02	0.08	0	0	0
	(F) Acrididae (grasshopper)	0.15	0.17	0.20	0	0.02	0.08	0	0	0
	Algae	–	–	–	0	0.01	0.05	0	0	0
	CPOM	0	0	0	0	0.01	0.05	0	0	0
<i>L. calcarifer</i>	<i>N. erebi</i> <100	0.35	0.58	0.80	0	0.07	0.20	–	–	–
	<i>N. erebi</i> >100	0	0.04	0.13	0	0.04	0.13	0	0.21	0.14
	<i>N. graeffei</i> <150	0.05	0.29	0.53	0	0.15	0.48	–	–	–
	<i>N. graeffei</i> >150	–	–	–	0.43	0.63	0.83	0.30	0.48	0.07
	<i>M. spinipes</i>	0	0.09	0.25	0	0.12	0.40	0	0.32	0.68
<i>A. percoides</i> <40	<i>C. lentiginosus</i>	–	–	–	0.28	0.60	0.88	0.38	0.72	0.93
	<i>G. giuris</i> <70	–	–	–	0	0.16	0.60	0	0.15	0.55
	(F) Pomatiopsidae (sm snail)	–	–	–	0	0.04	0.18	0	0.04	0.15
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.12	0.33	0	0.04	0.13
	(F) Gerridae (water strider)	–	–	–	0	0.03	0.15	0	0.02	0.08
	(F) Acrididae (grasshopper)	–	–	–	0	0.04	0.15	0	0.04	0.13
	Algae	–	–	–	0	0.01	0.08	0	0.00	0.03
	FPOM	–	–	–	0	0.01	0.08	0	0.00	0.03

Table 7 (cont.)

Consumer	Food sources	Wet season			Early dry season			Late dry season		
		1st	mean	99th	1st	mean	99th	1st	mean	99th
<i>A. percoides</i> >40	<i>C. lentiginosus</i>	0	0.18	0.50	0.73	0.83	0.90	0.73	0.87	0.98
	<i>G. giuris</i> <70	0	0.34	0.63	0	0.05	0.18	0	0.06	0.25
	(F) Pomatiopsidae (sm snail)	0	0.01	0.05	0	0.01	0.05	0	0.01	0.05
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.01	0.05	0	0.01	0.05
	(F) Gerridae (water strider)	0	0.01	0.08	0	0.01	0.08	0	0.01	0.03
	(F) Acrididae (grasshopper)	0.35	0.45	0.55	0.03	0.10	0.18	0	0.05	0.20
	Algae**	0	0.01	0.03	0	0.01	0.05	0	0	0
	FPOM	0	0.01	0.05	0	0.00	0.03	0	0	0
<i>H. greenwayi</i>	<i>N. erebi</i> <100	–	–	–	0.80	0.80	0.80	–	–	–
	<i>C. lentiginosus</i>	–	–	–	0	0	0	–	–	–
	(F) Gerridae (water strider)	–	–	–	0	0	0	–	–	–
	Algae	–	–	–	0	0	0	–	–	–
	<i>E. camaldulensis</i> (river gum)	–	–	–	.03	.04	.05	–	–	–
	<i>M. argentea</i> (silver cadjeput)	–	–	–	0.15	0.16	0.18	–	–	–
	<i>P. aquaticus</i> (pandanus)	–	–	–	0	0	0	–	–	–
	FPOM	–	–	–	0	0	0	–	–	–
<i>H. jenkinsi</i>	<i>N. erebi</i> <100	0	0.31	0.73	0.03	0.41	0.75	–	–	–
	<i>N. erebi</i> >100	0	0.28	0.68	0	0.04	0.18	0.55	0.83	0.98
	<i>N. graeffei</i> <150	0	0.07	0.28	0	0.27	0.63	–	–	–
	<i>C. lentiginosus</i>	0	0.13	0.45	0	0.18	0.68	0	0.12	0.43
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.04	0.18	0	0.01	0.05
	(F) Gerridae (water strider)	0	0.06	0.25	0	0.02	0.10	0	0.01	0.03
	(F) Acrididae (grasshopper)	0	0.05	0.23	0	0.04	0.18	0	0.04	0.15
	Algae**	0	0.02	0.10	0	0.01	0.08	0	0	0
<i>L. unicolor</i>	<i>M. argentea</i> (silver cadjeput)	0	0.06	0.20	0	0.01	0.08	0	0	0
	CPOM	0	0.04	0.18	0	0.01	0.08	0	0.00	0.03
	<i>N. erebi</i> <100	0	0.00	0.03	0	0.12	0.38	–	–	–
	<i>C. lentiginosus</i>	0	0.06	0.23	0	0.12	0.43	0	0.08	0.33
	<i>G. giuris</i> <70	0.05	0.26	0.40	0	0.07	0.28	0	0.04	0.18
	<i>M. spinipes</i>	0	0.03	0.10	0	0.41	0.78	0.43	0.62	0.78
	(F) Pomatiopsidae (sm snail)	0	0	0	0	0.03	0.15	0	0.02	0.08
	(F) Gerridae (water strider)	0	0	0	0	0.05	0.20	0	0.02	0.08
<i>G. aprion</i>	(F) Acrididae (grasshopper)	0.48	0.65	0.70	0	0.19	0.48	0.10	0.23	0.33
	Algae**	0	0.01	0.05	0	0.03	0.13	0	0.01	0.08
	<i>N. erebi</i> <100	0	0.17	0.48	0	0.32	0.70	–	–	–
	<i>C. lentiginosus</i>	0.05	0.54	0.88	0	0.25	0.78	0	0.22	0.73
	<i>A. percoides</i> <40	–	–	–	0	0.22	0.75	0	0.28	0.78
	(F) Sphaeriidae (pea clam)	–	–	–	0	0.05	0.20	0	0.26	0.58
	(F) Gerridae (water strider)	0	0.08	0.23	0	0.05	0.20	0	0.11	0.40
	(F) Acrididae (grasshopper)	0	0.22	0.48	0	0.10	0.30	0	0.09	0.35
<i>T. kimberleyensis</i> <50	Algae	–	–	–	0	0.03	0.13	0	0.04	0.15
	<i>Ambassis</i> sp.1	0	0.43	0.75	–	–	–	0	0.20	0.60
	<i>M. spinipes</i>	0	0.34	0.90	–	–	–	0	0.35	0.68
	(F) Pomatiopsidae (sm snail)	0	0.12	0.28	–	–	–	0	0.09	0.28
	(F) Gerridae (water strider)	0	0.08	0.28	–	–	–	0	0.10	0.33
	(F) Acrididae (grasshopper)	0	0.03	0.13	–	–	–	0.10	0.27	0.40
	<i>Ambassis</i> sp.1	0.63	0.82	0.98	0	0.03	0.10	0	0.08	0.30
	<i>M. spinipes</i>	0	0.08	0.28	0.55	0.66	0.73	0.48	0.64	0.80
<i>T. kimberleyensis</i> >50	(F) Pomatiopsidae (sm snail)	0	0.01	0.05	0	0.00	0.03	0	0.03	0.13
	(F) Gerridae (water strider)	0	0.01	0.05	0	0.01	0.03	0	0.03	0.13
	(F) Acrididae (grasshopper)	0	0.10	0.20	0.28	0.31	0.35	0.10	0.23	0.40



Consumer	Food sources	Wet season			Early dry season			Late dry season		
		1st	mean	99th	1st	mean	99th	1st	mean	99th
<i>O. selheimi</i>	<i>N. erebi</i> <100	0	0.01	0.08	–	–	–	–	–	–
	<i>N. erebi</i> >100	0	0.01	0.05	–	–	–	–	–	–
	<i>C. lentiginosus</i>	0	0.09	0.35	–	–	–	–	–	–
	<i>Ambassis</i> sp.1	0.10	0.55	0.88	–	–	–	–	–	–
	<i>G. giuris</i> <70	0	0.18	0.73	–	–	–	–	–	–
	<i>M. spinipes</i>	0	0.13	0.53	–	–	–	–	–	–
	(F) Pomatiopsidae (sm snail)	0	0.02	0.08	–	–	–	–	–	–
<i>G. giuris</i> <70	(F) Gerridae (water strider)	0	0.03	0.13	–	–	–	–	–	–
	<i>N. erebi</i> <100	0	0.04	0.13	0.03	0.43	0.73	–	–	–
	<i>C. lentiginosus</i>	0.40	0.72	0.95	0	0.09	0.35	0	0.19	0.70
	<i>A. percoides</i> <40	–	–	–	0	0.24	0.78	0	0.15	0.50
	<i>G. aprion</i>	0	0.16	0.55	0	0.01	0.08	0.05	0.53	0.88
	(F) Gerridae (water strider)	0	0.01	0.08	0	0.19	0.33	0	0.11	0.28
	(F) Acrididae (grasshopper)	0	0.07	0.18	0	0.02	0.03	0	0.02	0.10
<i>G. giuris</i> >70	Algae	–	–	–	0	0.05	0.18	0	0.02	0.05
	<i>N. erebi</i> <100	0	0.08	0.28	–	–	–	–	–	–
	<i>C. lentiginosus</i>	0.03	0.48	0.88	–	–	–	–	–	–
	<i>G. aprion</i>	0	0.28	0.88	–	–	–	–	–	–
	(F) Gerridae (water strider)	0	0.04	0.15	–	–	–	–	–	–
	(F) Acrididae (grasshopper)	0	0.13	0.33	–	–	–	–	–	–

\*\* Despite no filamentous algae being collected during the wet season, the isotopic signature of filamentous algae collected in the early dry season was substituted for use in IsoSource analysis, for those species where algae was recognised as a significant dietary prey item.

IsoSource agreed with dietary data that aquatic arthropods were important prey for smaller *N. erebi* in some seasons, the major energy source of both large and small *N. erebi* may be of molluscan origin.

Six species were caught in very low numbers and often had stomachs that were either almost or entirely empty. Of these species, the major content of *Elops hawaiiensis* was ~40% biofilm/silt/sand and algae, and ~60% insects, those of *Megalops cyprinoides* were ~85% insects and ~15% fish, and those of *Hannia greenwayi* were 65% algae, 10% hemipterans and 25% fish (Table 4). In contrast to dietary analyses, IsoSource modeling indicated that fish were the most important component of the diets of these species (Table 7), with insects only being the most important item for *E. hawaiiensis* during the wet season. In the cases of *Strongylura krefftii* and *Neosilurus hyrtlilii*, the stomach contents and IsoSource modeling were in accord in that both indicated that *S. krefftii* is a piscivore that includes a small proportion of aquatic insects in its diet, whereas *N. hyrtlilii* feeds almost exclusively on aquatic snails and arthropods. The remaining species, *Oxeleotris selheimi*, never contained anything in its stomach but IsoSource indicated that fish made up the vast majority of its diet.

#### Differences in diets between size categories

The stomach contents of five species, i.e. *N. erebi*, *N. graeffei*, *A. percoides*, *T. kimberleyensis* and *G. giuris* differed between size classes in at least one season (Tables 1–3, 5). For example, during the wet season although *N. erebi* <100 mm and >100 mm both consumed large quantities of biofilm/silt, individuals >100 mm also consumed a large amount of vegetation (~13%). During the early dry season the stomach contents of the smaller fish were

dominated by aquatic invertebrates (~88%), whereas larger fish continued to consume soil/silt (~70%) and vegetation (~29%). In the cases of *N. graeffei* and *T. kimberleyensis*, smaller fish consumed far larger quantities of aquatic invertebrates than terrestrial invertebrates (47–86% cf. 9–19%), whilst the opposite was the case for larger individuals (10–30% cf. 41–75%). Large and small individuals of *G. giuris* consumed large quantities of aquatic invertebrates (58–100%), however, larger individuals also ingested terrestrial invertebrates and aquatic vegetation as well as more fish. The stomach contents of *A. percoides* <40 mm consisted almost entirely of aquatic invertebrates whereas those of larger fish also contained large amounts of aquatic vegetation (17–53%).

#### Differences and overlap in diets within a season

Within the wet season (Figure 1, Tables 1, 5, 8), classification of mean dietary data identified four major feeding groups. Group 1 was comprised of *N. erebi* <100 mm and *N. erebi* >100 mm on the basis that they consumed biofilm/silt. Group 2 contained the greatest number of species, all of which consumed large quantities of aquatic insects, in particular aquatic hemipterans. Four subgroups (I–IV) were identified within Group 2. Subgroup I (*M. australis* and *T. kimberleyensis* 50–110 mm) also consumed a substantial volume of terrestrial hymenopterans and arachnids. Members of Subgroup II included *G. giuris* <70 mm, *T. kimberleyensis* <50 mm, *C. lentiginosus* and *Ambassis* sp. 1 whose diets were dominated by dipteran pupae. Species in Subgroup III (*G. aprion* and *G. giuris* >70 mm) were the only species that consumed a large proportion of teleost prey in Group 2, whilst fishes in Subgroup IV (*A. percoides* >40 mm, *N. graeffei* <150 mm and *L. unicolor*) commonly consumed large amounts of filamentous algae.

*Lates calcarifer* was the only species constituting Group 3, had a diet largely of teleost prey and *Macrobrachium spinipes* and had a diet significantly different to all other species. Group 4 included *N. graeffei* >150 mm and *H. jenkinsi* and were separated on the basis that the diet contained terrestrial vegetation and fig/fruit, with ANOSIM indicating that the diet of *N. graeffei* was significantly different to all other species except *H. jenkinsi*. There was also some overlap between *H. jenkinsi* and *L. unicolor*. ANOSIM suggested that the diets of both large and small *N. erebi* were significantly different to all other species, but were not significantly different to each other. Within Group 2, ANOSIM suggested that there were no significant differences in the prey consumed by the species within each subgroup. There were, however, differences between species in one subgroup when compared to those in another.

Classification of mean dietary data collected in the early dry season (Figure 2, Tables 2, 5, 9) revealed seven major feeding groups. The diet of Group 1 (*N. erebi* <100 mm) was made up almost entirely of cladocerans and copepods and this group had a diet significantly different to all other species. Group 2 (*P. pristis*, *L. calcarifer* and *C. leucas*) consumed a high proportion of fish, with significant differences found between *L. calcarifer* and both *P. pristis* and *C. leucas* only. Filamentous algae and biofilm/silt were major components of the diet in *N. erebi* (>100 mm), the single member of Group 3 and this was significantly different to all others. Group 4 (*M. australis*, *A. percoides* >70 and *H. jenkinsi*) consumed a large proportion of filamentous algae. Group 5 included species that consumed a high proportion of dipteran and ephemeropteran larvae, with *C. lentiginosus* different to all other species across all groups, while *A. percoides* (<40 mm) was different to all other species, except *G. giuris*. The species in Group 6 (i.e. *L. unicolor*, *Ambassis* sp. 1, *N. graeffei* <150 and *G. aprion*) consumed a broad range of aquatic invertebrates and exhibited considerable dietary overlap. Those in Group 7 (*N. graeffei* >150 and *T. kimberleyensis*) were separated on the basis that they consumed mainly terrestrial insects.

Classification of mean dietary data collected in the late dry season (Figure 3, Tables 3, 5, 10) recognised five major feeding groups. Group 1 (*N. erebi* >100 mm and *P. pristis*) diets were dominated by detritus but as *P. pristis* also consumed teleosts each species diets were significantly different. Group 2 (*C. leucas* and *L. calcarifer*) diets contained a large proportion of fish and were not significantly different to each other. *Lates calcarifer* diets were significantly different to all other species. The fish in Group 3 (*N. graeffei* >150 mm and *T. kimberleyensis* >50 mm) were separated from other groups on the basis that they consumed higher quantities of terrestrial insects. While their diets were not significantly different to each other, they were generally significantly different to most other species. The fish in Group 4 (i.e. *M. australis* and *H. jenkinsi*) consumed a large portion of filamentous algae, in addition to a number of aquatic insects. The stomach contents of these species were significantly different to all other species, but were not significantly different to each other. Group 5 contained the remaining eight species, all of which had ingested a range of smaller aquatic invertebrates and on many occasions there were significant differences between the prey consumed between these species and those in other groups.

Overall, the highest dietary overlap was observed in the wet season when 30% (i.e. 36 of 120) of the dietary pairwise comparisons between species (and size classes) were not significantly different (Table 8). Overlap then decreased to 20% in the early dry season (i.e. 21 of the 105 pairwise comparisons were similar) (Table 9) before rising to ~26% (24 of the 91) the late dry season (Table 10).

#### Stable isotope analyses – seasonal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures and trophic position

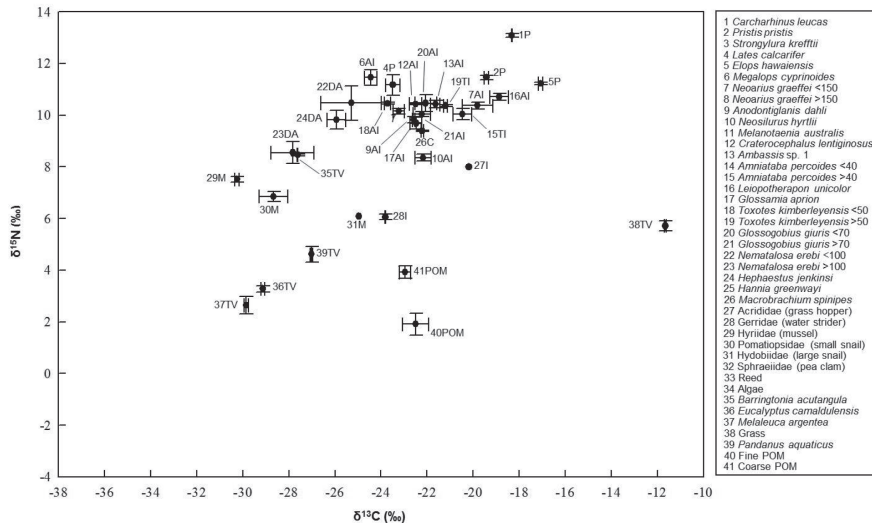
The variation in  $\delta^{15}\text{N}$  (Table 6) and  $\delta^{13}\text{C}$  values of insectivorous fishes in each season provides further indication of the seasonal variability in food sources and dependency by fishes upon them. For example,  $\delta^{15}\text{N}$  signatures of a number of insectivores were lower in the late dry season than in the wet or early dry season. Furthermore, this feeding guild experienced greater variability in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  signatures than piscivores, terrestrial insectivores and detritivores.

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  analysis provided some clarification of the feeding habits of several species, including several of those poorly represented by dietary analysis. For example, analysis of *E. hawaiiensis* and *M. cyprinoides* indicated  $\delta^{15}\text{N}$  values of a piscivorous diet. Similarly, *H. jenkinsi* and *H. greenwayi*, which were considered to be detritivores/algivores from stomach content analysis, had  $\delta^{15}\text{N}$  values closer to, and indeed above, that of insectivorous fishes, indicating a greater importance in higher order food types such as invertebrates and/or fishes, than the algae consumed. Stomach content analysis revealed the consumption of cladocerans by small *N. erebi* (<100 mm TL) in the early dry season rather than detritus. The assimilation of a higher order prey source in the tissues determined by isotopic analyses indicated the importance of cladocerans in the diet and growth of small *N. erebi*.

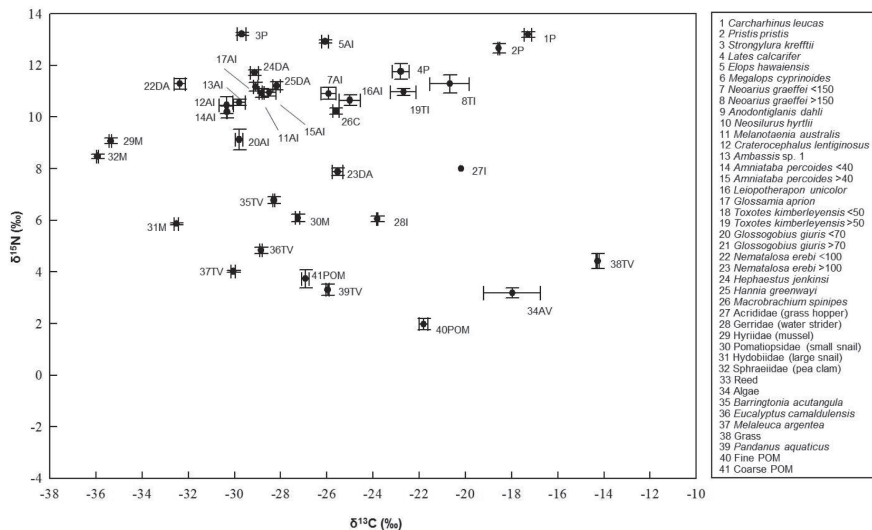
#### Stable isotope analyses – assimilation of food sources in fishes of the Fitzroy River

Stomach content analysis indicates that a large number of the fish species collected from the Fitzroy River would be considered insectivores. This was indeed the case for *Ambassis* sp. 1, *A. percoides*, *L. unicolor*, *G. aprion*, *T. kimberleyensis*, *O. selheimi* and *G. giuris*. While *IsoSource* supports the prevalence of insects in the diets of these fishes, isotope analysis also suggested that fishes and *M. spinipes*, although less frequently ingested (or rarely observed in the analysis of stomach content) may be equally, if not more, important than insects in terms of the energy that they provided to these species (Table 7). For example, while terrestrial Orthoptera appeared to be the main food source of *E. hawaiiensis* in the wet season, the fishes *C. lentiginosus* and small *N. erebi* (<100 mm TL) appeared to be the most important prey in the early dry season. These latter prey species plus *Ambassis* sp. 1, were apparently also the main source of energy to *M. cyprinoides* in the wet season, while larger *N. erebi* appeared to provide this energy in the late dry. Indeed, they provide between 55 and 95% of the energy to the species in that season.

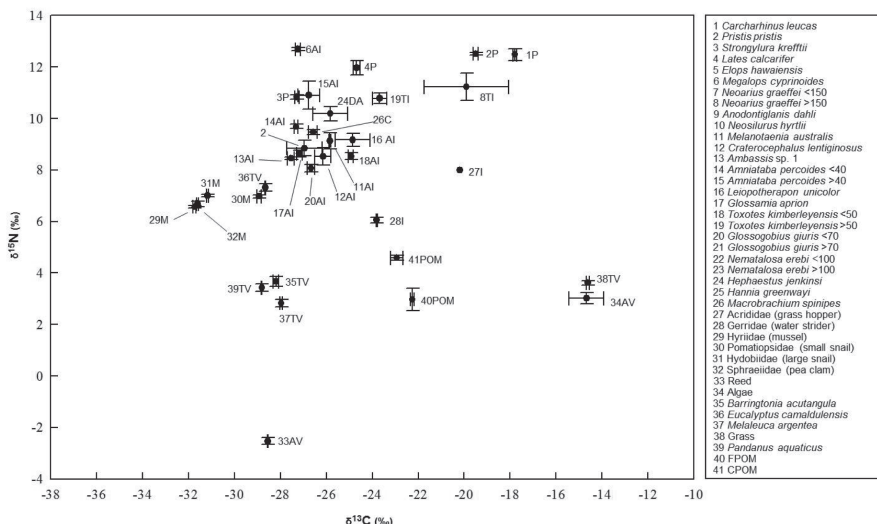
Despite vast quantities of filamentous algae being recorded from the diets of *N. erebi* >100 mm TL, *IsoSource*



**Figure 4** The isotopic composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) (‰) of the different fish, insects, molluscs, vegetation and organic matter samples collected from the Fitzroy River during the wet season. Species categorisations for comparative purposes are based on dietary analyses undertaken during the current study, Bishop *et al.* (2001) and Allen *et al.* (2002) (POM: Particulate organic matter, TV: Terrestrial vegetation, AV: Aquatic vegetation, M: Mollusc, I: Insect, C: Crustacean, DA: Detritivore/Algivore, AI: Aquatic Insectivore, TI: Terrestrial Insectivore, P: Piscivore).



**Figure 5** The isotopic composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) (‰) of the different fish, insects, molluscs, vegetation and organic matter samples collected from the Fitzroy River during the early dry season. Species categorisations for comparative purposes are based on dietary analyses undertaken during the current study, Bishop *et al.* (2001) and Allen *et al.* (2002) (POM: Particulate organic matter, TV: Terrestrial vegetation, AV: Aquatic vegetation, M: Mollusc, I: Insect, C: Crustacean, DA: Detritivore/Algivore, AI: Aquatic Insectivore, TI: Terrestrial Insectivore, P: Piscivore).



**Figure 6** The isotopic composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) (‰) of the different fish, insects, molluscs, vegetation and organic matter samples collected from the Fitzroy River during the late dry season. Species categorisations for comparative purposes are based on dietary literature by analyses undertaken during the current study, Bishop *et al.* (2001) and Allen *et al.* (2002) (POM: Particulate organic matter, TV: Terrestrial vegetation, AV: Aquatic vegetation, M: Mollusc, I: Insect, C: Crustacean, DA: Detritivore/Algivore, AI: Aquatic Insectivore, TI: Terrestrial Insectivore, P: Piscivore).

**Table 8** R-statistic values for pairwise ANOSIM comparisons of the diets of fish species examined from freshwaters of the Fitzroy River in the wet season. Significant dietary differences are represented by \* where  $p < 0.05$  and \*\* $p < 0.01$  and R-stat  $> 0.300$ . Global R = 0.430. See Table 1 for species codes.

Species	Ne <100	Ne >100	Ng <150	Ng >150	Ma	Cl	Am	Lc	Ap >40	Hj	Lu	Ga	Tk <50	Tk 50–110	Gg <70
Ne >100	0.001	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ag <150	0.866**	0.937**	–	–	–	–	–	–	–	–	–	–	–	–	–
Ag >150	0.860**	0.853**	0.606**	–	–	–	–	–	–	–	–	–	–	–	–
Ma	0.493**	0.636**	0.246	0.593**	–	–	–	–	–	–	–	–	–	–	–
Cl	0.528**	0.660**	0.340**	0.669**	0.267	–	–	–	–	–	–	–	–	–	–
Am	0.460**	0.632**	0.217	0.647**	0.241	0.049	–	–	–	–	–	–	–	–	–
Lc	0.458**	0.568**	0.390**	0.435**	0.412**	0.419**	0.390**	–	–	–	–	–	–	–	–
Ap >40	0.502**	0.475**	0.049	0.592**	0.396**	0.380**	0.348**	0.464**	–	–	–	–	–	–	–
Hj	0.584**	0.582**	0.201	0.276	0.529**	0.555**	0.518**	0.430**	0.206	–	–	–	–	–	–
Lu	0.371**	0.460**	0.046	0.456**	0.153	0.186	0.169	0.321**	0.100	0.240	–	–	–	–	–
Ga	0.785**	0.849**	0.619**	0.799**	0.288	0.209	0.306**	0.451**	0.438**	0.670**	0.120	–	–	–	–
Tk <50	0.822**	0.913**	0.313**	0.716**	0.121	0.069	0.039	0.441**	0.331**	0.608**	0.002	0.245	–	–	–
Tk 50–110	0.891**	0.938**	0.579**	0.363**	0.096	0.334**	0.344**	0.458**	0.489**	0.569**	0.121	0.389**	0.271	–	–
Gg <70	0.785**	0.859**	0.581**	0.816**	0.429**	0.071	0.273	0.537**	0.484**	0.686**	0.364**	0.544**	0.398**	0.649**	–
Gg >70	0.786*	0.925**	0.236	0.704**	0.200	0.198	0.199	0.306**	0.343**	0.486**	0.010	0.177	0.129	0.324**	0.574**

**Table 9** R-statistic values for pairwise ANOSIM comparisons of the diets of fish species examined from freshwaters of the Fitzroy River in the early dry season. Significant dietary differences are represented by \* where  $p < 0.05$  and \*\* $p < 0.01$  and R-stat  $> 0.300$ . Global R = 0.547. See Table 1 for species codes.

Species	Cle	Pp	Ne <100	Ne >100	Ng <150	Ng >150	Ma >40	Cl	Am	Lc	Ap <40	Ap >70	Hj	Lu	Ga	Tk >50
Pp	0.370*	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ne <100	0.629**	0.575**	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Ne >100	0.963**	0.976**	0.886**	–	–	–	–	–	–	–	–	–	–	–	–	–
Ag <150	0.712**	0.700**	0.707**	0.937**	–	–	–	–	–	–	–	–	–	–	–	–
Ag >150	0.718**	0.603**	0.692**	0.811**	0.368**	–	–	–	–	–	–	–	–	–	–	–
Ma >40	0.534**	0.384**	0.305**	0.616**	0.230	0.415**	–	–	–	–	–	–	–	–	–	–
Cl	0.851**	0.874**	0.743**	0.937**	0.705**	0.702**	0.557**	–	–	–	–	–	–	–	–	–
Am	0.403**	0.322**	0.406**	0.775**	0.127	0.458**	0.285	0.495**	–	–	–	–	–	–	–	–
Lc	0.093	0.298	0.657**	0.868**	0.678**	0.690**	0.589**	0.781**	0.537**	–	–	–	–	–	–	–
Ap <40	0.813**	0.837**	0.720**	0.937**	0.678**	0.662**	0.475**	0.545**	0.466**	0.747**	–	–	–	–	–	–
Ap >70	0.753**	0.883**	0.480**	0.926**	0.575**	0.529**	0.015	0.782**	0.140	0.682**	0.760**	–	–	–	–	–
Hj	0.933**	0.794**	0.834**	0.814**	0.749**	0.632**	0.232	0.898**	0.557**	0.788**	0.888**	0.370**	–	–	–	–
Lu	0.560**	0.423**	0.527**	0.682**	0.041	0.335**	0.170	0.474**	0.147	0.610**	0.376**	0.056	0.315**	–	–	–
Ga	0.339**	0.250	0.451**	0.746**	0.022	0.344**	0.216	0.440**	0.079	0.462**	0.344**	0.180	0.514**	0.034	–	–
Tk >50	0.688**	0.703**	0.638**	0.933**	0.480**	0.259	0.263	0.811**	0.339**	0.684**	0.770**	0.689**	0.831**	0.480**	0.317**	–
Gg	0.486**	0.456**	0.448**	0.785**	0.385**	0.503**	0.329**	0.479**	0.291	0.558**	0.044	0.389**	0.659**	0.242	0.239	0.512**

**Table 10** R-statistic values for pairwise ANOSIM comparisons of the diets of fish species examined from freshwaters of the Fitzroy River in the late dry season. Significant dietary differences are represented by \* where  $p < 0.05$  and \*\* $p < 0.01$  and R-stat  $> 0.300$ . Global R = 0.558. See Table 1 for species codes.

Species	<i>Cle</i>	<i>Pp</i>	<i>Ne &gt;100</i>	<i>Ng &gt;150</i>	<i>Ma</i>	<i>Cl</i>	<i>Am</i>	<i>Lc</i>	<i>Ap 40–70</i>	<i>Ap &gt;70</i>	<i>Hj</i>	<i>Lu</i>	<i>Ga</i>	<i>Tk &lt;50</i>	<i>Tk &gt;50</i>
<i>Pp</i>	0.345	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ne &gt;100</i>	0.996*	0.433**	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ag &gt;150</i>	0.196	0.097	0.639**	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ma</i>	0.966**	0.975**	0.907**	0.396**	–	–	–	–	–	–	–	–	–	–	–
<i>Cl</i>	0.903**	0.911**	0.912**	0.435**	0.672**	–	–	–	–	–	–	–	–	–	–
<i>Am</i>	0.609**	0.611**	0.928**	0.322**	0.800**	0.452**	–	–	–	–	–	–	–	–	–
<i>Lc</i>	0.019	0.480*	0.917**	0.409**	0.855**	0.823**	0.695**	–	–	–	–	–	–	–	–
<i>Ap 40–70</i>	0.635**	0.640**	0.887**	0.211	0.566**	0.533**	0.293	0.708**	–	–	–	–	–	–	–
<i>Ap &gt;70</i>	0.764**	0.804*	0.962**	0.098	0.774**	0.331**	0.382**	0.742**	0.193	–	–	–	–	–	–
<i>Hj</i>	0.787**	0.815**	0.872**	0.185**	0.270	0.636**	0.732**	0.728**	0.458**	0.582**	–	–	–	–	–
<i>Lu</i>	0.542**	0.564**	0.943**	0.219**	0.794**	0.564**	0.286	0.649**	0.125	0.222	0.702**	–	–	–	–
<i>Ga</i>	0.011	0.031	0.785**	0.158	0.558**	0.406**	0.160	0.310**	0.095	0.061	0.399**	0.010	–	–	–
<i>Tk &lt;50</i>	0.926**	0.948**	0.993**	0.307**	0.818**	0.657**	0.457**	0.791**	0.444**	0.854**	0.887**	0.202	0.058	–	–
<i>Tk &gt;50</i>	0.737**	0.761*	0.984**	0.022	0.796**	0.866**	0.552	0.739**	0.573**	0.760**	0.835**	0.494**	0.150	0.571**	–
<i>Gg &lt;70</i>	0.412**	0.444*	0.848**	0.307**	0.648**	0.201	0.139	0.556**	0.150	0.202	0.591**	0.146	0.089	0.197	0.431**



indicated that a higher calorific taxa (in this case molluscs) may be of much greater importance in the diet of this species than indicated by stomach contents analysis. A similar situation is also apparent for small *N. erebi*, *H. jenkinsi* and *H. greenwayi*. The energy assimilated by the first of these species may be derived from aquatic invertebrates (a result supported by stomach content analysis), whereas in the other two species much of their energy appears to be derived from fishes.

*IsoSource* also indicated seasonal shifts between energetically favourable food types. For example, while terrestrial insects were the most important food source of small *N. graeffei* (<150 mm TL) in the wet season, fishes (*C. lentiginosus* and *G. giuris* <70 mm TL) and *M. spinipes* were also assimilated. In contrast, insects appeared less important in the diet of small *N. graeffei* in the early dry season, when a greater proportion of fishes, in particular small *N. erebi*, *C. lentiginosus* and *G. giuris* (<70 mm TL), were consumed.

Stomach content analysis indicated that *N. erebi* and *N. graeffei* were important prey for the piscivorous *C. leucas*, *P. pristis* and *L. calcarifer*. Although the current study supported this finding for the latter species, *IsoSource* suggested that *P. pristis* is the most energetically important prey source of *C. leucas* in all seasons.

## DISCUSSION

Stomach content analyses of fishes of the Fitzroy River were generally consistent with the few data available from other systems in tropical Australia (e.g. Pusey *et al.* 2000; Morgan *et al.* 2004a; Davis *et al.* 2010, 2013). However, stable isotope analysis indicated that the food resource most frequently encountered during stomach content analysis may not be the most energetically important prey resource of that species and indeed may not accurately depict the 'dietary' guild to which it has historically been assigned. Stable isotope analysis indicated that the freshwater fish fauna of northern Australia may not differ as markedly as previously believed to those of Asia, Africa and South America. In the latter systems, terrestrial plant material, insects (aquatic and terrestrial) and detritus are major direct food sources for many fishes and these communities generally also support a diverse and abundant range of piscivores (Lowe-McConnell 1987). While insects were observed to be of particular importance to the freshwater fishes of the Fitzroy River, stable isotope analysis revealed that fish may also be an energetically important food source for a majority of the species present.

Diets of the fishes collected from the Fitzroy River showed some consistency with published accounts of the diets of these species from other river systems in northern Australia and confirmed the importance of aquatic insects as a food source in tropical freshwater systems (Angermeier & Karr 1983; Bishop *et al.* 1986, 2001; Pusey *et al.* 2000, 2004; Morgan *et al.* 2004a; Davis *et al.* 2010, 2013). Nevertheless, differences to published accounts were observed for a number of species. For example, although *A. percoides* and *M. australis* are commonly regarded as carnivorous elsewhere in Australia, filamentous algae was the single largest food type consumed by *A. percoides* in all seasons in the

Fitzroy River and by *M. australis* in the early and late dry seasons. While filamentous algae was reported to be the major food consumed by *L. unicolor* in Lake Kununurra (Morgan *et al.* 2004a), in the Fitzroy River, this species ingested very little filamentous algae and fed almost exclusively on aquatic insects (see also Davis *et al.* 2010). Terrestrial insects, in particular orthopterans and coleopterans, were a major prey item of *N. graeffei* in the Fitzroy River, whereas they were only minor contributors to the diet of this species captured elsewhere (Morgan *et al.* 2004a). The diet of *G. aprion* in the Fitzroy River (and in Lake Kununurra (Morgan *et al.* 2004a)) was dominated by aquatic insects (especially aquatic hemipterans), whereas this species has been reported to consume high proportions of fish and macro-crustaceans elsewhere in Australia (Bishop *et al.* 2001).

## Ontogenetic changes in the diets of Fitzroy River fishes

Approximately half of the freshwater fishes collected from the Fitzroy River during this study demonstrated some degree of ontogenetic change in their diet, i.e. *N. erebi*, *N. graeffei*, *A. percoides*, *T. kimberleyensis* and *G. giuris*. The current study indicated that a number of factors, other than a physical ability to swallow a prey, are responsible for these changes in diet. As noted by Schmitt & Holbrook (1984) variation in the diets of different sized fishes may be influenced by habitat utilisation, foraging behaviours and feeding rates, in addition to size-related morphological constraints. Changes in food utilisation may be observed as a 'shift' in the food items consumed at a particular stage in ontogeny or as a gradual increase in the size (and type) of food items ingested as the fish grows. Changes in the diet associated with major morphological developments and/or changes in habitat utilisation often result in abrupt and major changes in diet, whereas changes with growth may be less abrupt and often include an overall broadening of the diet (see for example Hyndes *et al.* 1997; Gill & Morgan 1998, 2003; Huskey & Turingan 2001; Cocheret de la Morinière *et al.* 2003; Nunn *et al.* 2007a, 2007b; Davis *et al.* 2010).

During this study, smaller *N. graeffei* <150 mm were shown to consume relatively large proportions of small aquatic invertebrates, while the diet of *N. graeffei* >150 mm was dominated by larger food items including terrestrial coleopterans and orthopterans, and during the wet season also figs. Frugivory of northern Australian terapontids was previously reported by Davis *et al.* (2010) at times of the year when this food type was available. An increase in the number of food types with growth (11 cf. 18 and 16 cf. 22 in the wet and early dry seasons, respectively) was also observed. Pusey *et al.* (1995) suggested that an increase in mouth gape was closely correlated to an increased reliance on terrestrial prey in fishes of tropical Australia. However, in the case of *N. graeffei* in the Fitzroy River, the ingestion of large food items with a terrestrial origin is also likely to be attributable to changes in foraging behaviours and the habitat utilised. An increase in size not only results in a food item 'fitting' the larger mouth, but also improves mobility and reduces the likelihood of predation thereby allowing utilisation of previously unavailable and/or dangerous habitats by larger individuals.

At the time of early dry season sampling, Geikie

Gorge was experiencing an apparent 'bloom' of cladocerans and copepods. During this period, the diet of small *N. erebi* was dominated by these microcrustaceans (~90%), whereas in larger *N. erebi* a similar proportion of the diet was made up of filamentous algae and biofilm/silt. During the wet season, the diets of both small and large *N. erebi* were comprised almost exclusively of filamentous algae and biofilm/silt.

In the case of *A. percoides*, *T. kimberleyensis* and *G. giuris*, the number of food types ingested by each of these individual species is roughly comparable between the small and large individuals. However, whilst the number of food types may be similar the categories that make up that number can vary considerably between the respective size groups. For example, in the early dry season small *A. percoides* consumed large quantities of small aquatic invertebrates, whereas the diets of large *A. percoides* consisted of algae, gastropods and ostracods. In the late dry season, when the smaller size group of *A. percoides* had increased from <40 mm to between 40 and 70 mm, their diet now not only included smaller aquatic invertebrates, but also a significant proportion of larger aquatic invertebrates such as odonatan and coleopteran larvae. In this season large *A. percoides* continued to ingest ostracods and also consumed a high proportion of odonatan larvae, but were no longer feeding on gastropods or filamentous algae to the same extent, which contrasts the study of Davis *et al.* (2010). This suggests that there is a progression of diet from small aquatic invertebrates to filamentous algae and larger and more robust aquatic invertebrates. This gradual change is indicative of an opportunistic omnivore that can optimise its diet dependent on its ability to ingest available food resources. The change to larger prey, such as odonatan larvae and more robust prey, including ostracods and gastropods, is likely to be attributable to an increase in gape size and the development and ossification of pharyngeal plates which aid in processing prey with a hard exoskeleton or shell.

*Toxotes kimberleyensis* also exhibited a 'shift' in diet from predominantly aquatic invertebrates to between 50 and 70% (dependent upon season) terrestrial and flying insects. Despite possessing the ability to spurt water from a very small size, the power generated by the muscles of the buccal floor can only force a low volume of water at a low pressure over a short distance (Vailati *et al.* 2012). Thus, transition to terrestrial prey in larger *T. kimberleyensis* is more likely attributed to the power, volume and accuracy of the jet that can be generated by larger fishes, than a physical ability for an individual to pass a prey beyond its jaws.

*Glossogobius giuris*, like *A. percoides* and *T. kimberleyensis*, exhibited a 'shift' in the diet between small and larger fish. Small *G. giuris* consumed a high proportion of ostracods, dipteran pupae and aquatic hemipterans. In contrast, larger *G. giuris* did not consume any ostracods or dipteran pupae, but consumed more aquatic hemipterans and also a significant proportion of large aquatic coleopterans, orthopterans and fish. None of these latter taxa were ingested by small *G. giuris*. As all sizes of *G. giuris* were captured within the same microhabitats (i.e. shallow bank waters over sandy substrates), differences in diet are presumably attributable to the ability of larger individuals to ingest

larger prey items, rather than changes in foraging behaviour or habitat utilisation.

### Energetically important food sources of the fishes of the Fitzroy River: Comparison of stomach contents analysis and stable isotope analysis

The Fitzroy River is considered comparatively 'rich' in terms of its fish diversity (Morgan *et al.* 2004b, 2011). The permanence of deep water throughout the year, extensive shallow littoral zones and dense riparian vegetation present in Geikie Gorge undoubtedly contribute to the abundant and diverse range of food types present. Despite the widespread consumption of filamentous algae, *IsoSource* suggested that energetically this food source may be of less importance than would be assumed from the large quantities ingested by many of the fishes. This finding supports those of Bunn *et al.* (1998, 1999, 2001) where filamentous algae and macrophytes were found to be an insignificant component of consumer food webs. Results of stomach content analysis during the current study, and findings by others (see Bishop *et al.* 2001; Allen *et al.* 2002), suggest that *N. erebi* is a detritivore/algivore. However, *IsoSource* indicated that pea clams were a very important source of assimilated energy as were aquatic invertebrates for small individuals in some seasons, a finding also reflected by dietary analysis. As small molluscs were rarely found in the diets of *N. erebi*, this result may be an overestimation of *IsoSource* analysis due to the exclusion of a wide range of invertebrate taxa (see Methods section). However, energy is undoubtedly derived from taxa higher than biofilm/silt or algae. It is therefore possible that epiphytic micro-invertebrates present on filamentous algae have a signature closer to that of pea clams and it is these epiphytic invertebrates that provide energy to *N. erebi* and other apparent algal feeders. Support for this notion that algae is less energetically important in the diets of these species, is provided by isotopic studies on the Ord River, Western Australia (Trayler *et al.* 2003). For example, Trayler *et al.* (2003) revealed that filamentous algae and macrophytes were not significant contributors to consumer biomass or the food web but rather that non-filamentous benthic algae and an additional unknown algal source were.

Dietary analysis also indicated that small *N. erebi* (<100 mm TL) opportunistically fed on small invertebrates. The importance of this food source was confirmed by isotopic analysis which indicated that small *N. erebi* were far more enriched in  $\delta^{15}\text{N}$  than larger individuals of this species. Numerous authors have suggested the ability of small individuals to utilise higher calorific prey items which result in high growth rates earlier in the life cycle and thereby lead to the rapid attainment of a size that provides both a competitive feeding advantage and the reduced risk of predation (Grossman 1980; Brown 1985; Wainright & Richard 1995; Huskey & Turingan 2001; Lima-Junior & Goitein 2003).

*IsoSource* indicated the widespread assimilation of fish in species occurring in the Fitzroy River. While complimentary results of dietary and stable isotope analysis confirmed the presence of three large piscivores (*C. leucas*, *P. pristis* and *L. calcarifer*), fish was identified as an important prey source to an additional 11 species, including *H. greenwayi* and *H. jenkinsi* which are



generally considered to be algivores and *T. kimberleyensis* which is considered to be a strict insectivore.

Of particular note during the current study was that *IsoSource* suggested *P. pristis* is the most energetically important prey source of *C. leucas* in all seasons. *Pristis pristis* is protected in Australia under the EPBC Act 1999 and listed as critically endangered by the International Union for Conservation of Nature (IUCN). Predation of *P. pristis* by *C. leucas* was reported from northern Australian rivers by Thorburn & Rowland (2008). Although these authors suggested that overall *P. pristis* represented only a small dietary contributor (~2.5% by volume), the comparatively high numbers of *P. pristis* occurring in the Fitzroy River as opposed to other rivers surveyed in northern Australia (see for example Thorburn *et al.* 2003, 2007) may suggest that *P. pristis* is a far greater prey source of *C. leucas* in this system than in the other rivers surveyed.

### Dietary shifts, resource partitioning and overlap in the Fitzroy River

Despite some seasonal variation in prey abundances being reflected in the diets of individual species, few data supported the notion that the diets of each species were 'narrower' in times of low productivity. Dietary analysis indicated that 'shifts' or 'replacements' in the types of prey consumed were often made to 'functionally' similar prey types, for example, between different types of aquatic larvae, or between aquatic hemipterans and aquatic coleopterans. The lack of contrast may be attributed to the permanence of water in Geikie Gorge, relative stability of the available habitat and an apparent 'richness' in prey types and abundances. Much of the variation in fish diets is undoubtedly attributable to the hatching of aquatic and terrestrial insect larvae, coinciding with the wet season and early dry season (Zaret & Rand 1971; Angermeier & Karr 1983; Sumpton & Greenwood 1990; Bunn & Arthington 2002). Thus, the majority of species investigated during the current study had broad diets, were opportunistic in their feeding habits and showed little 'real' change in their diets between seasons. Such a conclusion is consistent with the results of Kennard (1995), who found little temporal variation in fish diets over an eight month monitoring period in the Normanby River, Queensland.

A main aim of this study was to investigate how dietary overlap varies between seasons and in response to changes in the availability of prey. Increase in dietary overlap can occur when food becomes very limited, when fish will have to consume any type of food that is available to them in order to survive (see Matthews 1988). However, overlap can also occur as a result of an abundance of prey sources, such as during the wet season, when fish can opportunistically consume any of the wide variety of foods present.

Although the magnitude of change in dietary overlap between seasons was relatively small during the current study, dietary overlap was higher in the wet season (no dietary difference existed in ~30% of pairwise comparisons) and became reduced in the early dry season (no dietary difference existed in ~20% of pairwise comparisons) possibly reflecting the contraction of food resources and the return of fishes to more specialised feeding behaviours, as hypothesised. Overlap was again

shown to increase in the late dry season (no dietary difference existed in ~26% of pairwise comparisons). The reasons behind this small magnitude of change may be attributed to two possible factors. Firstly, Geikie Gorge is a relatively stable environment that contains large quantities of water throughout the year. Thus, seasonal differences in its productivity (as noted in the preceding section) will be less than in tributaries and small pools of the catchment. Secondly, three species are apparently obligate piscivores (*C. leucas*, *L. calcarifer* and *P. pristis*) and one species is a specialised detrital feeder (*N. erebi*). If these species are not considered during pairwise comparisons of dietary overlap, the proportions of fishes with similar diets changes considerably. During the wet season, for example, there was no discernable difference in ~42% of the pairwise comparisons, which reduced to ~25% in the early dry and increased back to ~40% in the late dry. Thus, if species that are highly specialised for a particular diet, i.e. those that are less likely to be able to readily change their diets in response to changes in food availability, are removed from analysis, comparisons of those species that can respond strongly support this hypothesis.

Contention remains as to whether dietary (and resource) overlap of freshwater fish communities is highest or lowest in periods of low production, such as the tropical late dry season (Schoener 1974). Some argue, for example, that dietary overlap decreases in periods of low production in support of the 'competitive exclusion principle' (Zaret & Rand 1971; Angermeier & Karr 1983; Pusey & Bradshaw 1996). Alternatively, other studies indicate that dietary overlap increases when habitat and food resources become limited (Arthington 1992), and thus predators become less selective (Blaber 1986). The current study in some ways supports both theories, as the types and amount of foods present and the inclusion or exclusion of specialist feeders in analyses has a significant bearing upon the interpretation of data. The apparent contradiction of these two views can be resolved by considering the magnitude of the reduction in food availability. Thus when food is abundant, the probability of encountering many foods types is high, the return for capture/handling of many of these food types, even if they are of low calorific value, is likely to provide a net positive gain in energy. If a food type's density becomes reduced below a certain point, organisms will maximise energy returns by selecting foods to which they are particularly well adapted to capturing/processing. If food becomes even less abundant, organisms may have no choice other than the consumption of whatever food they can find/catch/process, in order to survive. When considering resource overlap and/or resource partitioning, it is therefore vitally important to consider how limiting the resource may be.

$\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values also suggest that dietary overlap was highest in the wet season, lowest in the early dry and increased again in the late dry season. For example, the distribution of  $\delta^{13}\text{C}$  vs  $\delta^{15}\text{N}$  values of the fishes in the wet season is contracted, indicating similarities in the food items assimilated. In the early dry season data points are expanded, whereas in the late dry season these points are again compressed. A 'compression' of food web structure was also observed during the Ord River isotope study by Trayler *et al.* (2003). In that study, the food web structure present in September (comparable to

the late dry season in this study) was compressed in comparison to that observed in June (comparable to the early dry season in this study).

## CONCLUSIONS

The use of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  isotope and stomach content analysis indicated that differences often exist between the food types consumed and those that are energetically important to a species. For example, while this study supported the finding that omnivory is prevalent in the Fitzroy River, it strongly suggests that filamentous algae and other plant sources may not be as important in the diet as first suspected. Stable isotope analysis also indicated that prey types that persist throughout the year, including fish, molluscs and *M. spinipes*, may in fact be more important sources of the energy than dietary data revealed. This study also supports the view that juvenile fishes target high energy food items. Finally this study supports the notion that many species will maximise their energy intake in response to changes in resource availability.

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