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Generalist niche, specialist strategy: the diet of an Australian percichthyid

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Dietary analysis revealed that an impoundment population of Australian bass *Macquaria novemaculeata* holds a generalist niche, but one arising from persistent individual specialization and interindividual variation. This 'individual specialist' strategy appeared adaptive, but the strength of individual specialization was largely independent of variation in diet composition, except during blooms of *Daphnia* sp. Diet composition and dietary overlap showed only moderate ontogenetic variation, and niche breadth showed no relationship with ontogeny. *Macquaria novemaculeata* showed an asymmetric predator and prey size distribution, consistent with many aquatic predators, with positive relationships between fish size and average, maximum and minimum prey size. There was no asymmetry in the relative size-based niche breadths of individuals, however, which indicates that the niche is a fixed 'window' of relative prey sizes. The difference in the dietary niche and prey-size relationships of *M. novemaculeata* at the population and individual levels highlights the necessity of assessing the niche at both these levels.

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Key words: interindividual variation; *Macquaria novemaculeata;* ontogeny; predation.

INTRODUCTION

Identifying the dietary niche of aquatic predators is essential to understanding the structure of aquatic ecosystems. A dietary analysis is key to the assessment of feeding strategy (Amundsen *et al*., 1996) and the breadth of a predator's diet (*i.e.* niche width; Schoener, 1971), which ultimately identify the functional role of a predator in an ecosystem. The main division of feeding strategies is that of generalist or specialist, where predators with a diverse diet or broad dietary niche are described as generalists, and specialists are predators that have low prey diversity or narrow niche width (Bridcut & Giller, 1995; Amundsen *et al*., 1996). Feeding strategies, however, have traditionally been described for populations of predators under the assumption that

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the individuals within the population share identical strategies (Bolnick *et al*., 2003). There are recent examples of individual feeding strategies differing from that defined by a population's niche, with individual predators within a generalist population actually holding more specialized niches (Fry *et al*., 1999; Bolnick *et al*., 2003).

Identifying interindividual variation in feeding strategies within a population has increasingly been recognized as an important part of population ecology, because it allows the creation of individual-based models (Bolnick *et al*., 2003) and provides a mechanistic understanding of population dynamics (Svanbäck & Bolnick, 2007). So while the population's niche can largely describe the impact on a particular prey assemblage, *i.e.* a generalist can influence a diverse prey assemblage and a specialist influences only a sub-set (Jiang & Morin, 2005), the information obtained from interindividual variation gives information on the actual feeding strategy adopted by a predator. It is becoming increasingly evident that a population's niche is truly the product of individual feeding strategies (Bolnick *et al*., 2010). Much research is now focusing on interindividual variation (Fry *et al*., 1999; Bolnick *et al*., 2003, 2007; Quevedo *et al*., 2009), but empirical studies examining the strength of individual variation within a broad dietary context are needed.

Niche width and feeding strategies can be evaluated using several approaches, that includes calculating diversity indices and dietary overlap (Krebs, 1989; Marshall & Elliott, 1997), constructing diet plots (Costello, 1990; Amundsen *et al*., 1996) and examining the variation in prey size (Pearre, 1986). Niche theory, in particular, is useful for identifying interindividual variation in feeding strategies. Roughgarden (1974), for example, helped shift the focus of niche theory to the role of the individual, by proposing that the total niche width (W_{TN}) of a population be expressed as both a within-individual component (C_{WI}) and a between-individual component (C_{BI}). When the C_{WI} comprises a large proportion of the W_{TN}, there is little dietary variation between individuals; but when the proportion is small, individual specialization is large (Bolnick *et al*., 2003). Thus, niche theory can be used to estimate the degree of individual specialization with the ratio $C_{WI}{:}W_{TN}$ (Bolnick *et al*., 2002). Despite individual specialization being examined in fishes, $C_{WI}{:}W_{TN}$ values are not often published for fish species (Bolnick *et al*., 2003), and not at all for Australian species. The aim of this study was to combine qualitative and quantitative diet analyses to address the broader question of the individual contribution to the niche of a population using a widely distributed Australian aquatic predator, Australian bass *Macquaria novemaculeata* (Steindachner 1866).

Australia's major group of native freshwater predators, the Percichthyidae, are predominately classed as generalist carnivores (Allen *et al*., 2002), which have a key structuring role in lotic and lentic food webs. *Macquaria novemaculeata* is a top-level percichthyid common in the fresh waters of eastern Australia. Despite studies of diet in this species (Harris, 1985) and in other Australian percichthyids (Howell *et al*., 2004; Ebner, 2006; Baumgartner, 2007; Ingram & De Silva, 2007; Sternberg *et al*., 2008), an analysis of the feeding niche of a percichthyid is lacking. Quantitative analysis of fine-scale dietary traits, such as size-specific prey selection, ontogenetic shifts and intraspecific niche overlap are also uncertain for the Percichthyidae. Furthermore, *M. novemaculeata* is commonly stocked in reservoirs of eastern Australian states where substantial fisheries have been established (Wilde & Sawynok, 2005). The influence of releases of this predatory species on aquatic communities is uncertain, and an analysis of feeding strategy is essential if such impacts are to be measured (Taylor & Suthers, 2008). So using an impoundment population of *M. novemaculeata*, this study aimed to examine (1) differences in the niche and feeding strategy at the population and individual level, (2) ontogenetic and temporal variation of the niche and (3) size-specific prey selection and how this relates to the observed dietary niche.

MATERIALS AND METHODS

STUDY AREA AND POPULATION

Macquaria novemaculeata were collected at Brogo Dam, NSW, Australia (36·491° S; 149·740° E) over 3 days within each month of May (late autumn), August (winter) and December (summer) in 2008 and March 2009 (early autumn). Surface water temperatures for these sampling periods were 17·0, 9·8, 21·3 and 21·0° C, respectively. Brogo Dam (capacity of 9000 Ml) is 28 m at its deepest point and has a largely undeveloped 400 km^2 catchment. It thermally stratifies at 5–10 m from November to June and has a conductivity of between 50 and 100 µS cm^{-1}. The reservoir provides downstream irrigation and can have large fluctuations in storage level as a result of rainfall variation and water extraction. Brogo Dam contains a substantial recreational fishery and is stocked most years with *M. novemaculeata*, including releases of *c*. 200 000 fingerlings over the last 10 years (NSW Department of Industry and Investment, pers. comm.). Other than short-finned eels *Anguilla australis* Richardson 1841, there are no other large predatory fishes found in Brogo Dam.

SAMPLING AND DIETARY ANALYSIS

Fish were collected during the day and night by electrofishing or gillnetting, immediately euthanized in 100 mg l^{-1} benzocaine (Barker *et al*., 2002), and then frozen until dissected. An effort was made to ensure sampling encompassed as many habitats and depths as possible within each sampling period. Up to 10 fish in each of six size classes (<100, 101–150, 151–200, 201–250, 251–300 and >300 mm total length, L_T) were collected for dietary analysis during each sampling period. Size classes were arbitrarily chosen, but an interval of 50 mm was considered small enough to observe any ontogenetic diet shifts. No fish <100 mm were collected in the August 2008 sampling period. In May and August, a 200 µm plankton net of 40 cm diameter was towed along the surface for 3 min at 3·704 km h^{-1} (2 knots), near both the edge and the middle of the reservoir to quantify the abundance of pelagic crustaceans.

The L_T and mass of each *M. novemaculeata* were measured, and the gut from oesophagus to intestine was removed and preserved in 5% formalin. The height of the mouth gape at full extension was measured using vernier callipers for a sub-set of fish, to determine if oral morphology influenced stomach contents. Only the contents of the stomachs were used in the analysis, as the contents of the intestine could not be identified. Each stomach was weighed and then re-weighed with the contents removed, and the difference was considered the total prey wet mass. Prey items were identified, enumerated and sorted into taxonomic groups before being dried separately in a drying oven for 72 h at 60° C, to determine a taxa-specific dry mass. Prey types were identified to varying taxonomic levels, which were based on a desired parity with functional prey groups, the proficiency of the sorter and the level of digestion of the prey.

The lengths (longest axis, not including antennae) of ≤10 individual prey items per taxonomic group were measured to the nearest µm using a dissecting microscope with an eyepiece graticule and used to estimate an average prey length per taxon. The largest and smallest prey items were also measured to determine the range of prey sizes for each fish. A total average prey length was calculated by weighting the average lengths of individual prey taxa by their abundance. This total average length was used in the size-specific predator and prey relationships, which are essential to defining a species' complete dietary

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niche. The lengths of partially digested items, particularly fishes, were estimated by comparing dimensions of intact body parts, such as vertebrae, with whole specimens (Madenjian *et al.*, 1998).

STATISTICAL ANALYSIS

Relative importance of prey items, for interpretation of the feeding strategy, was constructed graphically using a variation of the Costello method (Costello, 1990) proposed by Amundsen *et al.* (1996). This variation incorporates prey-specific measurements to improve the resolution of a feeding strategy and the variation in the feeding of individual fish (Amundsen *et al.*, 1996) and plots the prey-specific percentage abundance (*i.e.* each prey item's percentage contribution by number in only those stomachs that contained that prey) against the percentage occurrence (*i.e.* in how many fish the prey occurred). Feeding strategies are defined as follows (Amundsen *et al.*, 1996): prey items with high prey-specific % abundance and high % occurrence indicate specialization by the population, and prey items with high prey-specific % abundance and low % occurrence indicate specialization by individuals; a generalist diet would be indicated by all prey types having low prey-specific % abundance and moderate-to-high % occurrence, *i.e.* most individuals utilize many prey types simultaneously. Prey types with low % abundance and low % occurrence are classed as 'rare' and can reasonably occur to some degree within any feeding strategy, although many points here suggest a generalist diet (Amundsen *et al.*, 1996).

Niche breadth, which increases as feeding becomes more generalized, was quantified for individual fish and for groups, by calculating the diversity of prey types by mass using the adjusted Levins index (B_{A}) (Hurlbert, 1978): $B_{\mathrm{A}} = (B - 1)(n - 1)^{-1}$ and $B = \left(\sum p_j^2\right)^{-1}$, where p_j is the proportion of prey type j in the diet, n is the total number of prey types found in all seasons, and B is the Levins index. Niche breadth, based on the diversity of prey sizes, was calculated as the S.D. of the $\log_{10}$ transformed prey sizes (S_{LH}), weighted to the abundance of prey types and with the exclusion of individuals with fewer than three prey items (Pearre, 1986). To measure the degree of individual specialization, the ratio ($C_{\mathrm{WI}}{:}W_{\mathrm{TN}}$) of the within-individual niche component (C_{WI}) and total niche width (W_{TN}) was calculated using the Shannon index of niche width (Bolnick *et al.*, 2002): $W_{\mathrm{TNS}} = -\sum q_j \ln q_j$ and $C_{\mathrm{WIS}} = \sum p_i \left(-\sum p_{ij} \ln p_{ij}\right)$, where W_{TNS} is the discrete index of total niche width, C_{WIS} is the discrete index of within-individual component, q_j is the proportion of the jth prey type in the population's total niche, p_i is the proportion of all prey used by the population that is used by individual i and p_{ij} is the proportion of the jth prey type in individual i's diet. Prey masses were used for these calculations, and this method was repeated using the adjusted Levins index of niche breadth.

Temporal and ontogenetic differences in diet composition (as proportions by mass) were examined with a two-factor permutational MANOVA (PERMANOVA). The two factors were 'time' (May, August and December 2008 and March 2009) and 'size' (the six size classes). The analysis was run on a Bray–Curtis similarity resemblance matrix of arcsine transformed data, with 1999 permutations. A 'dummy species' with negligible mass was added to control for empty stomachs, with the acknowledgement that a negligible mass is less likely to dampen the similarities between non-sparse samples (Clarke *et al.*, 2006). Pair-wise comparisons were made to examine the differences between size classes within each season.

Diet overlap was measured to examine any ontogenetic niche shifts and was measured between size classes using the % similarity index (Krebs, 1989). It calculates a sum of the minimum prey proportions between two groups according to the following: $P_{jk} = \sum \text{minimum}\ (p_{ij}, p_{ik})$, where P_{jk} is the proportion of overlap between groups j and k, and p_{ij} and p_{ik} represent the proportion of prey i in the diet of group j and group k. A value $>0{\cdot}6$ is often used to indicate significance in overlap indices (Krebs, 1989). The index was used to calculate the mean overlap between the six size classes within each sampling period and to create a frequency histogram of overlap values between individuals within each sampling period by bootstrapping 500 comparisons with replacement.

Prey size can also be used to calculate the degree of individual specialization (Bolnick *et al.*, 2002), but this was not used here as, given the nature of the diversity index (Bolnick *et al.*, 2002), the results may be confounded by an increasing prey-size range. This could be a problem if a large range of predator sizes was examined simultaneously and positive size-specific prey selection existed (which was the case here). Instead, size-specific prey selection was examined in the context of the niche width to explore how these size relationships might contribute to the overall dietary niche. Thus, linear relationships between prey size and predator size were created after transforming ($\log_{10}$) all size data, after the exclusion of *M. novemaculeata* with fewer than three prey items in their stomachs.

All parametric tests were performed in JMP (SAS 7.0; www.sas.com). Normality was assessed using a normal probability plot, and residuals were examined for homogeneity of variance. Multivariate analyses were undertaken using Primer (version 6.0, Plymouth Marine Laboratory; www.primer-e.com), with the PERMANOVA+ add-on.

RESULTS

FEEDING STRATEGY

Feeding strategy plots (Fig. 1) showed that *M. novemaculeata* hold a generalist niche, but one with periods of comparative specialization. Populations of *M. novemaculeata* showed considerable specialization in August, when almost 80% of stomachs contained an average of 80% *Daphnia* sp., and moderate population specialization in May, when over half of the *M. novemaculeata* caught had diets consisting of 75% Chaoboridae larvae. The feeding strategy plots revealed prey types, which strongly indicated a generalist diet in every sampling period, *e.g.* unidentified insects and fishes in May; Chaoboridae in August; fishes, unidentified insects and Ecnomidae in December; Chironomidae and Culicidae in March. These plots also position prey types which indicate some individual specialization in some periods, *e.g.* adult Diptera and *Daphnia* sp. in December and copepods in March.

Individual diet specialization, as quantified using niche theory and indicated by a low $C_{\mathrm{WI}}{:}W_{\mathrm{TN}}$ value, appeared strong in *M. novemaculeata* (Table I). The individual contributed between 31 and 45% (Shannon index) or 17 and 24% (adjusted Levins index) of the population's niche, with values <50% indicating relatively strong individual specialization (Bolnick *et al.*, 2003). This level of individual specialization was also persistent, though varying slightly in August.

ONTOGENETIC VARIATION

Piscivory was observed in *M. novemaculeata* as small as 67 mm, but was not common until fish exceeded 100 mm, and fish prey consisted of Australian smelt *Retropinna semoni* (Weber 1895) and flathead gudgeons (*Philypnodon* spp.). Piscivory increased in autumn (March and May), particularly in *M. novemaculeata* 101–250 mm in L_{T}. No prey types were unique to any size class, with the exception of copepods and ostracods, which were only taken by *M. novemaculeata* <100 mm. *Daphnia* sp. dominated the diets of fish <200 mm in August, which matched their increased abundance: zooplankton tows in May found 1·8 ± 1·8 *Daphnia* sp. 100 m^{-3} (mean ± S.E.) in the middle of the reservoir and none near the edges, which increased to 2350 ± 276 *Daphnia* sp. 100 m^{-3} near the edge and 5730 ± 2350 *Daphnia* sp. 100 m^{-3} in the middle of the reservoir in August. *Daphnia* sp. was observed in the diet of all size classes, but was consumed less often for *M. novemaculeata* of >200 mm.

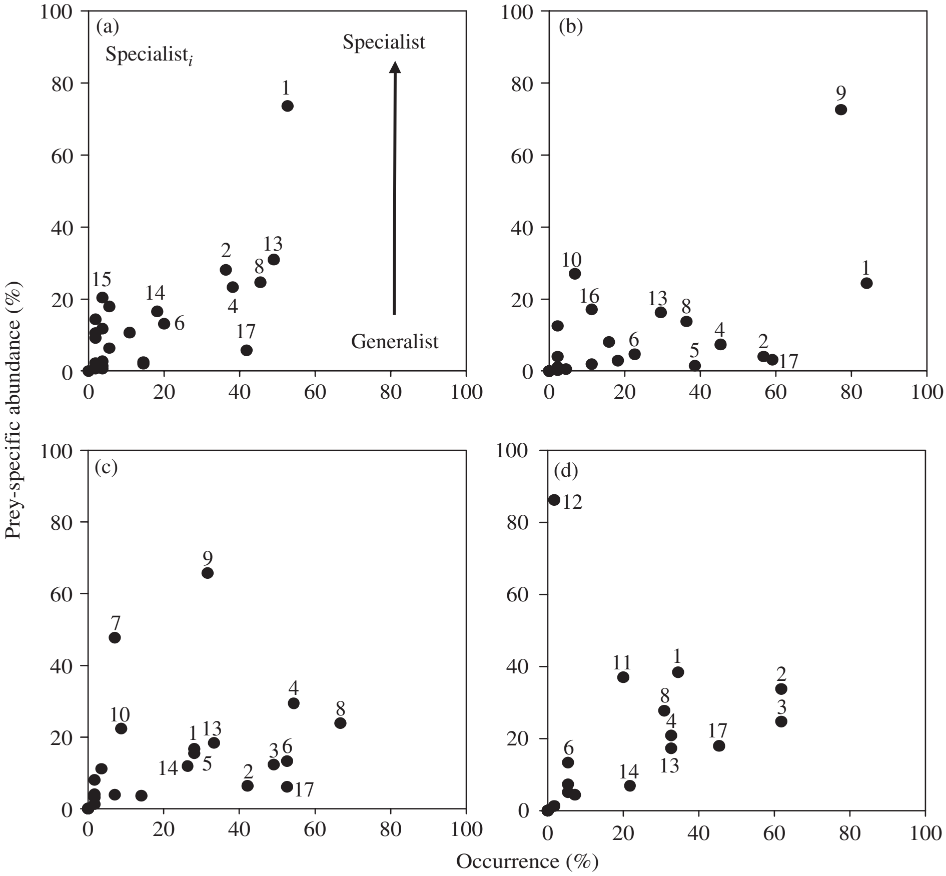

FIG. 1. Feeding strategy plots for *Macquaria novemaculeata* in (a) May 2008, (b) August 2008, (c) December 2008 and (d) March 2009. Prey types are numbered as follows (insect groups are larvae unless otherwise noted): 1, Chaoboridae; 2, Culicidae; 3, Chironomidae; 4, Ecnomidae; 5, Dytiscidae; 6, Odonata; 7, Diptera adults; 8, unidentified insects; 9, *Daphnia* sp.; 10, Atyidae (shrimp); 11, Ostracoda; 12, Copepoda; 13, fishes; 14, Nematoda; 15, Acarina; 16, plant material; 17, unidentified material. To simplify the plot, not all points are numbered. (a) has been labelled to indicate the feeding strategies associated with different areas of the plot, including individual specialization (Specialist$_i$); adapted from Amundsen *et al*. (1996).

A two-factor PERMANOVA [Table II(a)] indicated there were significant differences between sampling periods and between size classes, but with a significant interaction term. Pair-wise comparisons designed to examine the significant interaction term [Table II(b)] showed *M. novemaculeata* of <100 mm had different diets from all other size classes, except in May 2008 (and unknown in August 2008). In August 2008, seven of the 10 sampled size classes showed significant differences in diet composition.

Niche breadth of individual fish, as measured by the diversity of prey types or relative prey sizes, did not show ontogenetic variation (Fig. 2). The overlap of the dietary niches of different size classes was variable and ranged from 9 to 89% (Table III), but only one significant niche overlap (>60%) occurred between size classes >100 mm

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TABLE I. Values for the total niche width (W_{TN}), within-individual component (C_{WI}) and the ratio of the two (C_{WI}:W_{TN}) for *Macquaria novemaculeata*, calculated using the Shannon and adjusted Levins indices. The ratio indicates the proportional contribution of the average individual to the population's niche

	W_{TN}	C_{WI}	C_{WI}:W_{TN}
Shannon			
May 08	1·987	0·884	0·445
Aug 08	1·738	0·537	0·309
Dec 08	2·292	0·936	0·409
Mar 09	2·159	0·795	0·368
Levins			
May 08	0·230	0·040	0·174
Aug 08	0·162	0·038	0·235
Dec 08	0·350	0·062	0·177
Mar 09	0·322	0·056	0·174

TABLE II. (a) Two-factor permutational MANOVA (PERMANOVA) results, comparing arcsine transformed proportions of prey types in the diet of *Macquaria novemaculeata*. Size classes are numbered 1–6 and represent fish 100, 101–150, 151–200, 201–250, 251–300 and >300 mm total length, respectively. (b) The *P*-values of pair-wise comparisons of size classes are shown

(a) Two-factor PERMANOVA

	d.f.	MS	pseudo-*F*	*P*-value
Time	3	29 282·0	10·6	<0·001
Size	5	6691·4	2·4	<0·001
Time × size	14	5234·5	1·9	<0·001
Residual	188	2749·7		

(b) Pair-wise comparisons

Size classes	May 08	Aug 08	Dec 08	Mar 09
1 *v*. 2	0·485	NA	<0·01	<0·05
1 *v*. 3	0·181	NA	<0·001	<0·01
1 *v*. 4	0·436	NA	<0·01	<0·01
1 *v*. 5	0·151	NA	<0·01	<0·001
1 *v*. 6	0·364	NA	<0·05	<0·001
2 *v*. 3	0·841	0·075	0·146	0·598
2 *v*. 4	0·961	<0·01	<0·05	0·391
2 *v*. 5	0·456	<0·01	0·155	0·108
2 *v*. 6	0·918	<0·001	0·286	0·179
3 *v*. 4	0·305	<0·05	0·094	0·384
3 *v*. 5	0·051	0·059	0·713	0·117
3 *v*. 6	0·345	<0·01	0·638	0·361
4 *v*. 5	0·844	0·189	0·790	<0·05
4 *v*. 6	0·965	<0·05	0·425	0·202
5 *v*. 6	0·937	<0·01	0·951	0·659

NA, a comparison which was not possible due to missing data.

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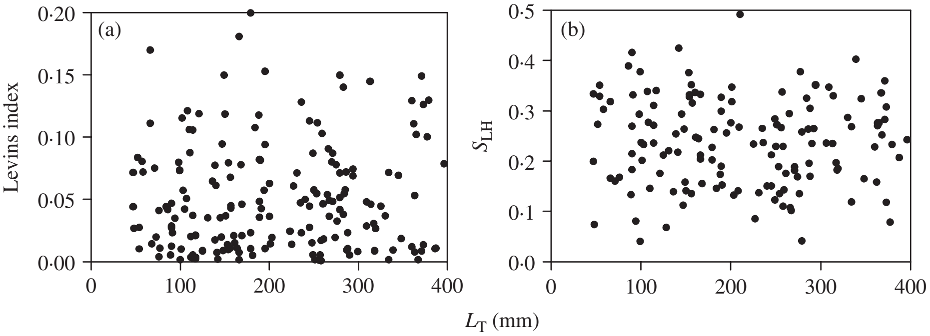

FIG. 2. Relationships between total fish length (L_T) and two indices of niche breadth (a) adjusted Levins and (b) in transformed prey sizes (S_{LH}) for *Macquaria novemaculeata*. The linear regressions for the Levins index ($r^2 = 0·003$, $P = 0·471$) and S_{LH} ($r^2 \leq 0·001$, $P = 0·944$) were non-significant.

TABLE III. Dietary overlap of proportional diet composition (by prey mass) between each total length class (bold, in mm) of *Macquaria novemaculeata* for each sampling period. Values >60% (highlighted in grey) are generally considered significant (Krebs, 1989)

May 08					1·00	**>300**
				1·00	0·51	**251–300**
			1·00	0·57	0·56	**201–250**
		1·00	0·72	0·40	0·57	**151–200**
	1·00	0·77	0·59	0·29	0·47	**101–150**
1·00	0·49	0·65	0·61	0·42	0·58	**<100**
<100	**101–150**	**151–200**	**201–250**	**251–300**	**>300**	
Aug 08					1·00	**>300**
				1·00	0·29	**251–300**
			1·00	0·44	0·26	**201–250**
		1·00	0·12	0·50	0·19	**151–200**
	1·00	0·89	0·09	0·50	0·15	**101–150**
NA	NA	NA	NA	NA	NA	**<100**
<100	**101–150**	**151–200**	**201–250**	**251–300**	**>300**	
Dec 08					1·00	**>300**
				1·00	0·48	**251–300**
			1·00	0·81	0·58	**201–250**
		1·00	0·52	0·64	0·57	**151–200**
	1·00	0·29	0·34	0·28	0·46	**101–150**
1·00	0·35	0·34	0·35	0·32	0·57	**<100**
<100	**101–150**	**151–200**	**201–250**	**251–300**	**>300**	
Mar 09					1·00	**>300**
				1·00	0·60	**251–300**
			1·00	0·57	0·39	**201–250**
		1·00	0·63	0·57	0·53	**151–200**
	1·00	0·65	0·86	0·54	0·45	**101–150**
1·00	0·28	0·54	0·25	0·27	0·28	**<100**
<100	**101–150**	**151–200**	**201–250**	**251–300**	**>300**	

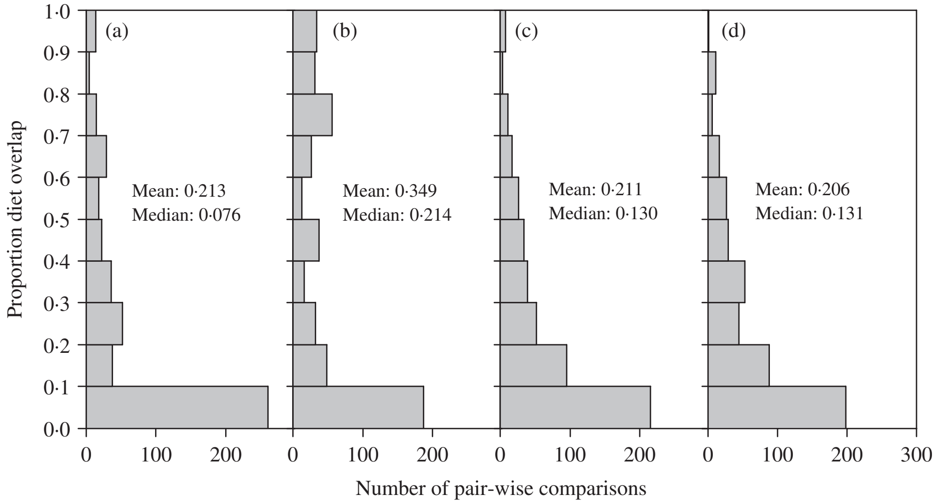

FIG. 3. Frequency histogram of the overlap of the dietary niches of individual *Macquaria novemaculeata* in each sampling period (a) May 2008, (b) August 2008, (c) December 2008 and (d) March 2009, calculated using the per cent similarity index (Krebs, 1989). The median and mean of the resulting distributions are also given.

apart. The mean overlap between the niches of two individuals was *c*. 21%, which increased to 35% in August 2008, although a skewed distribution revealed that the majority of overlap values were much lower in all sampling periods (Fig. 3).

SIZE-SPECIFIC PREY SELECTION

Mouth gape (y) in *M. novemaculeata* (Fig. 4) was found to increase linearly with L_T ($y = 0{\cdot}1L_T + 0{\cdot}726$; $r^2 = 0{\cdot}97$, $P < 0{\cdot}001$), which is the same general relationship found in other members of the Percichthyidae (Ingram & De Silva, 2007). Significant linear regressions (Table IV) between the L_T of *M. novemaculeata* and average, maximum and minimum prey lengths (all $\log_{10}$-transformed) indicated size-specific prey selection in all sampling periods for this population of fish (Fig. 4). The maximum and minimum relationships, after interpretation of the $\log_{10}$ scale, revealed an asymmetric predator and prey size distribution. The prey-sized niche breadth analysis (S_{LH}; Fig. 2) revealed that the range of relative prey sizes did not vary with L_T.

DISCUSSION

FEEDING STRATEGY

The *M. novemaculeata* population studied here exploits prey items from a diversity of environments (pelagic plankton, terrestrial insects and benthic invertebrates). When the variability in relative abundances of prey types is considered, it is clear *M. novemaculeata* holds a generalist niche. A population of a species which hold a

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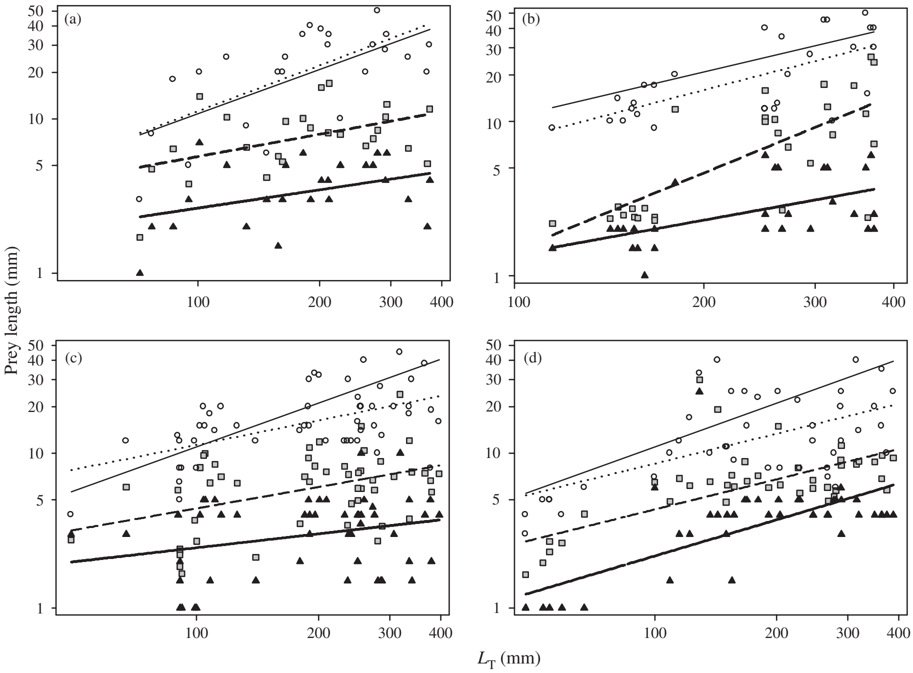

FIG. 4. Relationships between fish total length (L_T) and mean prey sizes (···□···), maximum prey sizes (···○···) and minimum prey sizes (—▲—) of *Macquaria novemaculeata* in each sampling period (a) May 2008, (b) August 2008, (c) December 2008 and (d) March 2009, on a $\log_{10}$-$\log_{10}$ plot (see Table IV). The relationship between mouth gape (y) and L_T (x) ($y = 0{\cdot}1x + 0{\cdot}726$; $r^2 = 0{\cdot}97$, $P \leq 0{\cdot}001$) is indicated (——).

generalist niche will be made up of individuals with either many narrow but different dietary niches or a few shared broader niches (Pianka, 1994). This population of *M. novemaculeata* displayed a high level of individual specialization in all sampling periods, which means that although the population holds a broad niche, individuals have much narrower niches. *Macquaria novemaculeata* therefore, as an example of a 'population generalist, individual specialist', supports the paradigm shift that individuals are not all alike, and high levels of individual specialization can occur within predator populations (Fry *et al.*, 1999; Bolnick *et al.*, 2003). The diversity in this population's diet, plus the high level of individual specialization, also supports the idea that the more generalized the population, the higher the level of individual specialization (Bolnick *et al.*, 2007).

Holding a generalist niche has been proposed as an adaptive strategy in fishes and most common when food availability is unpredictable (Dill, 1983). Adaptive flexibility has also been proposed as a necessary precaution for variable Australian environments (Sternberg *et al.*, 2008). Adaptive flexibility, most commonly observed as opportunistic feeding, has been recorded in other Australian freshwater generalists (Warburton *et al.*, 1998), including two species of percichthyid (Howell *et al.*, 2004; Sternberg *et al.*, 2008). In the current study, since *Daphnia* sp. was the only prey to be quantified in the environment, the influence of prey abundance on the foraging behaviour of *M. novemaculeata* is uncertain, but given that *M. novemaculeata*

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TABLE IV. Results of the least-squares regressions between $\log_{10}$-transformed fish total length (L_T) and average, maximum and minimum prey sizes (L_{prey}) of *Macquaria novemaculeata*. The t-ratio and P-value evaluate the null hypothesis that the slope between $\log_{10} L_T$ and $\log_{10} L_{prey} = 0$

	May 2008			August 2008			December 2008			March 2009		
	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum	Mean	Maximum	Minimum
Intercept	−0·169	−0·857	−0·423	−3·185	−1·243	−1·342	−0·278	0·004	−0·210	−0·662	−0·355	−1·221
b	0·463	0·950	0·424	1·674	1·063	0·740	0·461	0·525	0·299	0·649	0·645	0·779
r^2	0·200	0·415	0·178	0·534	0·465	0·307	0·185	0·304	0·077	0·416	0·362	0·474
n	25	25	25	28	28	28	51	51	51	42	42	42
t-ratio	2·39	4·04	2·23	5·46	3·40	11·97	3·33	4·63	2·01	5·34	4·76	6·00
P-value	<0·05	<0·001	<0·05	<0·001	<0·01	<0·01	<0·01	<0·001	<0·05	<0·001	<0·001	<0·001

exploited a proliferation of *Daphnia* sp., diet composition showed large temporal variation, and adaptive flexibility has been observed in other Australian freshwater generalists, it seems likely the generalist niche of *M. novemaculeata* is also adaptive.

Given the potential adaptive significance of the generalist strategy for Australia freshwater predators, how then does the 'population generalist, individual specialist' pattern arise? Two potential forces thought to be involved in shaping such a pattern are stochastic variability (*i.e.* foraging in a patchy environment) and underlying biological mechanisms (*i.e.* phenotypic or behavioural variation) (Bolnick *et al.*, 2003). As no morphological differentiation (such as in jaw size; Roughgarden, 1974) was evident between *M. novemaculeata*, behavioural or stochastic variability probably underpin the patterns here. The literature suggests that a change in W_{TN} is ultimately the result of environmental fluctuations (Schoener, 1971; Roughgarden, 1974), while individual specialization is far more stable (Bolnick *et al.*, 2010) and the result of persistent biological mechanisms, such as the development of unique foraging behaviours (Schindler *et al.*, 1997; Bolnick *et al.*, 2007). Thus, the mechanistic view of the dietary niche of Australia's freshwater predators is that they hold a generalist niche because they are adaptive 'specialists' in a variable environment. A similar feeding strategy to that of the *M. novemaculeata* has been observed in young pond-reared silver perch *Bidyanus bidyanus* (Mitchell 1838), which is another Australian generalist (Warburton *et al.*, 1998). The authors found perch frequently specialized on the dominant prey item and with little between-individual variation, but would target different prey when the prey community became more diverse. This latter case, when there was no single dominant prey type, suggests specialist strategies, but an overall generalist niche.

Conclusively discovering the underlying cause of the feeding strategy of *M. novemaculeata* is beyond the scope of this study. Distinguishing between 'variable specialization' (*i.e.* narrow niches, which can move in respect to prey composition) and 'consistent specialization' (*i.e.* narrow niches, which always contain the same prey) requires following individuals through time (Schindler *et al.*, 1997), or measuring the carbon and nitrogen isotopic composition of body tissue (Fry *et al.*, 1999). Nevertheless, this study provides evidence that, in *M. novemaculeata*, stochastic factors influence the total possible niche of the population (*i.e.* temporal variability in diet composition), and biological mechanisms drive the 'individual specialist' strategy (*i.e.* a high level of individual specialization amidst this temporal variability). Thus, *M. novemaculeata* show an interesting combination of adaptive generalization at the population level and strong specialization at the individual level. The mechanism through which this reasonably stable level of individual specialization is maintained alongside large variations in diet composition is an intriguing unknown, yet this pattern does add support to the idea that a population's niche is driven by interindividual variation, not the extent of individual specialization (Bolnick *et al.*, 2010).

Whether the feeding strategy of this impoundment population of *M. novemaculeata* reflects the strategy of riverine populations is uncertain. The diet composition (and therefore the generalist niche) of this population generally agrees, however, with that observed for riverine *M. novemaculeata* by Harris (1985), except for the importance of *Daphnia* sp. as prey in August. Given that a population's niche is driven by mechanisms at the level of the individual (Bolnick *et al.*, 2007, 2010), it is suggested that the similar population niche indicates a similar feeding strategy between impoundment and riverine *M. novemaculeata*. This could be tested by applying the analyses used in this study to riverine populations.

The high degree of individual specialization calculated using the Shannon and Levins indices is underestimated by the feeding strategy plots, which show only some specialization in December 2008 and March 2009. This discrepancy is due to a limitation of feeding strategy plots. Two-dimensional diet plots use mean values for % prey-specific abundance, which underestimates the strength of individual specialization if the feeding strategy for a particular prey type is mixed (Amundsen *et al.*, 1996). While this limitation is unlikely to affect the identification of a population's niche, it could result in an underestimation of individual specialization. This highlights the advantage of a quantitative niche analysis.

ONTOGENETIC VARIATION

The significant interaction term in the PERMANOVA analysis and the results of the pair-wise comparisons showed that ontogenetic differences were not consistent across sampling periods, which is supported by the dietary overlap calculations. Factors that vary temporally thus have a stronger influence on dietary composition than factors that vary with ontogeny, which adds further support to the idea that stochastic factors largely influence the total available niche of the population. This is particularly obvious in the lack of a relationship between niche breadth and fish size. Observed differences in diet composition in *M. novemaculeata* <100 mm (except in May 2008) are due to reduced piscivory, and two unique prey types in this size class: ostracods and copepods. These two taxa were more common in the March period, which probably contributed to the significant differences in the PERMANOVA for this size class. Small taxa are known to be more important for smaller *M. novemaculeata* and very important for percichthyid fry and larvae (Ingram & De Silva, 2007).

Intraspecific diet partitioning, indicated by consistently small dietary overlap values, means a species can belong to different feeding groups within its life (Rezsu & Specziár, 2006). Dietary overlap values for *M. novemaculeata* are frequently >50% and show substantial temporal variation between the same size classes. That only one of the 11 significant overlap values (*i.e.* >60%) occurred between size classes >100 mm apart means that, while consistent size-based feeding groups are unlikely to be distinguishable, broad ontogenetic variation in prey types does occasionally exist. This relatively weak and inconsistent intraspecific diet partitioning indicates the potential for strong food competition between *M. novemaculeata* of all sizes. This could explain the consistently strong level of individual specialization in *M. novemaculeata*, as this is known to increase as the strength of intraspecific competition increases (Svanbäck & Bolnick, 2007); however, this cannot be tested without information on resource availability.

The difference between the overlap of size classes and the mean overlap of individuals is due to the 'individual specialist' strategy: any two individuals, with their narrow niches, have a median dietary overlap of just 13·8%, while size classes, with their different niches pooled, have greater levels of overlap averaging around 50%. This difference clearly shows the strength of individual specialization in *M. novemaculeata* and the relevance of the generalist feeding strategy only at the population level. The highly skewed distribution of bootstrapped niche overlap measures, an unexpected

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distribution in a population of 'generalists', may be indicative of individual specialization and deserves investigation in other species.

SIZE-SPECIFIC PREY SELECTION

A dietary niche is not only defined by the types of prey consumed but also the sizes of prey, which is particularly relevant when exploring the ontogeny of a niche. The significant positive relationship between maximum prey size and fish size, and to some extent average prey size and fish size, is facilitated by the linear increase in mouth gape throughout ontogeny. Gape-related limitation of prey size is especially common in fishes that swallow their prey whole, as is the resulting positive relationship between fish length and size range of prey (Pearre, 1986; St John, 1999; Scharf *et al*., 2000). While mouth gape imposes a physical limitation on prey size, however, other factors such as foraging ability, prey availability and prey preference may dictate a predator and prey size relationship (Ney, 1990; Byström & García-Berthou, 1999; Ward *et al*., 2006). In the current study, the increase in maximum prey size closely resembles the increase in mouth gape. There are some prey items larger than mouth gape, but this is probably because the longest prey dimension was not the one at which the prey was swallowed. For example, the body depth of fish prey (Scharf *et al*., 2000), as opposed to fish length (Pearre, 1986; Madenjian *et al*., 1998), has been used in similar relationships. Nonetheless, the close relationship between mouth gape and the upper limit of maximum prey length suggests mouth gape does limit maximum prey size for *M. novemaculeata* of all sizes. The observed average prey size for *M. novemaculeata* was always much smaller than the maximum prey size, suggesting larger prey types, such as shrimp or fishes, were either less available (Balcombe *et al*., 2005) or harder to catch than the smaller prey, such as insects or *Daphnia* sp.

Although there were significant positive relationships between minimum prey length and L_T of *M. novemaculeata*, it is clear that all but the smallest prey items continue to be taken throughout a fish's lifetime. This supports the belief of the widespread occurrence of asymmetric predator and prey size distributions in aquatic ecosystems (Scharf *et al*., 2000) and is the same general pattern as that observed in juvenile pond-reared Percichthyidae (Ingram & De Silva, 2007). Does this mean, however, based on prey size, that the dietary niche increases with ontogeny? Not if the size-specific niche breadth of individuals is considered, as calculated using the S_{LH} method of Pearre (1986). The lack of relationship in S_{LH} means that, although *M. novemaculeata* consume a wider range of prey sizes as they grow, the relative size range of prey consumed remains the same. Thus, *M. novemaculeata* of any size generally select prey between 1 and 10% of their own length. This pattern agrees with existing research that suggests a constant size-based niche breadth may be common (Pearre, 1986; Scharf *et al*., 2000), and this examination helps fill the gap in research examining ratio-based predator and prey relationships over a large size range (Scharf *et al*., 2000).

In conclusion, the Percichthyidae have been widely described as generalists; however, this study shows that this is the result of a population of individuals having different narrow niches. This study also suggests that a reasonably consistent level of individual specialization can be maintained alongside an adaptive dietary response to a variable environment and an asymmetric predator and prey size distribution.

Species which show individual specialization (including *M. novemaculeata*) highlight the point that 'generalist' cannot be considered a sufficient description of a predator's feeding strategy and only describes the relative width of a population's niche. Considering the contextual nature of the specialist–generalist division and the increasingly individual-based mechanistic view of the niche, a robust study of either niche or feeding strategy should include a range of analyses at the population and individual level, and report W_{TN} and C_{WI} components as context.

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