

Ontogenetic variation in the diurnal food and habitat associations of an endemic and an exotic fish in floodplain ponds: consequences for niche partitioning

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Synopsis

In floodplain ponds with low piscivore abundance, both endemic Midgley's gudgeons, *Hypseleotris* sp. 5, and exotic mosquitofish, *Gambusia holbrooki*, showed significant ontogenetic variation in the use of food and space. Small gudgeons were generally associated with surface and benthic habitats, then restricted their distribution to benthic habitats at a size of approximately 24 mm (standard length). The ontogenetic variation in mosquitofish habitat use was less discrete, and could be described as a tendency for larger individuals to be associated with the bottom of the littoral macrophyte beds than with the surface of the macrophyte beds or surface of the limnetic zone. Small gudgeons exhibited high spatial overlap with mosquitofish within the surface habitats of the ponds. All size-class/species comparisons showed significant partitioning of food resources, however, the diets of small gudgeons and mosquitofish were very similar. Therefore, juvenile gudgeons may have to pass through a similar spatial and trophic niche to introduced mosquitofish before recruiting to the adult stage. Possible mechanisms driving the ontogenetic variation in gudgeon and mosquitofish habitat use are discussed. This paper demonstrates that ontogenetic niche shifts at fine spatial scales can affect our interpretation of interactions between native and introduced fishes.

Introduction

Exotic species are second only to habitat loss as a cause for decline of endemic species (Everett 2000). It is somewhat surprising therefore that we know very little about the ecological effects of exotic species worldwide. Not all exotics are harmful to endemics, however it is generally agreed that they use some resources within the system they invade, some of which may be usurped from endemics (Mills et al. 1994). We now know that introduced species can cause major changes in community structure and ecosystem function (Vitousek 1986, Lodge 1993). Freshwater

lakes are among the ecosystems most vulnerable to species invasion (Ricciardi & MacIsaac 2000). Species invasions in freshwater lakes have been shown to cause major changes in the distribution and abundance of endemic organisms, thereby changing the flow of energy and nutrients (Lodge 1993, Mills et al. 1994, Ricciardi & MacIsaac 2000). In particular, exotic fishes can displace endemic fishes in lakes, and can cause changes in food web structure, hence possibly ecosystem functioning (Mills et al. 1994, Vander Zanden et al. 1999, Ricciardi & MacIsaac 2000).

Australia has many floodplain ponds due to its flat topography, and prevalent lowland meandering rivers.

Like most Australian lowland freshwaters, floodplain ponds have been plagued with exotic fish species, yet we know very little about the ecology of fishes, endemic or exotic, in these systems.

The mosquitofish, *Gambusia holbrooki*, native to Central America (McDowall 1996), has invaded Australian floodplain ponds and can now reach extremely high densities in these systems. Its ability to reach these high densities, coupled with its pugnacity and trophic flexibility has raised concerns regarding its interactions with endemic species (Fletcher 1986). Where they have been introduced outside their natural range, mosquitofish have been confirmed as a cause of declines and losses of some North American endemic fishes (Meffe et al. 1983, Meffe 1984). In Australian systems, we know they may compete with endemic fishes for space and food in lowland rivers (e.g. Lloyd 1990, Pen & Potter 1991). It has however been hypothesised that their ability to affect endemic fishes will be greater in Australian lakes than in rivers, as they are more suited to such habitats (Pen & Potter 1991). However, any suggested competition between mosquitofish and endemic floodplain pond species is speculative because we have no empirical data on the spatial and/or trophic dimensions of the niche of endemic species or mosquitofish in floodplain ponds.

The structure of floodplain pond communities is highly variable (e.g. Rodríguez & Lewis 1997). As part of a larger project, we found a strong negative relationship between the abundance of European perch, *Perca fluviatilis*, and the abundance of mosquitofish and Midgley's gudgeons (henceforth gudgeon; *Hypseleotris* sp. 5) among individual ponds (Figure 1; adapted from Stoffels 1998). In the absence of perch piscivory, mosquitofish can reach extremely high densities, hence the potential for competition with endemic fishes is high. The present study deals with the spatial and trophic dimensions of the gudgeon and mosquitofish niche in floodplain ponds without, or containing low densities of, piscivorous perch (Study ponds circled in Figure 1). Therefore, the primary aim of this study was to determine patterns of food and habitat association of gudgeons and mosquitofish in ponds with low piscivory. A secondary aim was to determine whether mosquitofish and gudgeons partition the spatial and trophic dimensions of their niche in floodplain ponds with low piscivore abundance. We paid particular attention to how habitat and food associations may scale with body size.

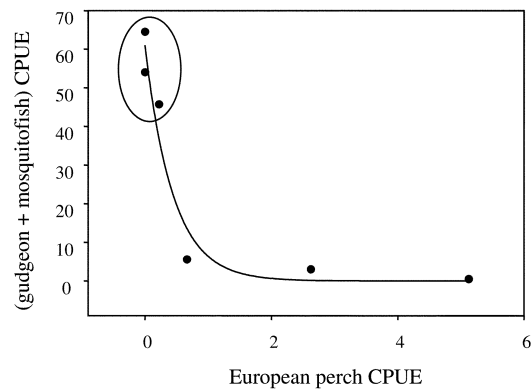


Figure 1. The combined abundance of gudgeons and mosquitofish as a function of European perch abundance within six individual floodplain ponds. Ponds selected for the present study are circled (Smoother described by exponential loss function: $y = 61 \times e^{-2.25x}$ ($R^2 = 0.95$; non-linear regression; Adapted from Stoffels 1998)).

Methods

Study site and field methods

The study was conducted on the Oven's River floodplain, in the Killawarra State Forest (approximately 146°15'E, 36°15'S), Victoria. The three ponds studied had very similar macrophyte communities, dissolved oxygen levels, conductivity, pH and temperature. The surface area of Dohnut, Hole and Big Ponds was 572 m, 452 m, 4901 m, respectively, the maximum depths were 2.5 m, 1 m, 1 m, respectively, and secchi depth 53 cm, 49 cm, 23 cm, respectively.

The floodplain ponds were divided into either four or five major habitats, depending on habitat availability:

- (1) Macrophyte edge (ME): any section of the littoral zone less than 30 cm deep containing macrophyte beds with a surface area greater than or equal to 2 m².
- (2) Macrophyte benthic (MB): the bottom of any section of the littoral zone greater than 40 cm deep containing macrophyte beds with a surface area greater than or equal to 2 m².
- (3) Bare edge (BE): any section of the littoral zone less than 30 cm deep that did not contain macrophyte beds, and more than 2 m from any macrophyte bed.
- (4) Limnetic surface (LS): the top 30 cm of the water profile within the limnetic zone.

- (5) Limnetic benthic (LB): the bottom of the limnetic zone.

Because the abundance of small fishes in the limnetic zone may vary with distance from the nearest macrophyte bed, limnetic samples were consistently taken from between 2–4 m out from the edge of the littoral macrophyte beds. Dohnut and Hole Ponds contained the ME, MB, LS and LB habitats, while Big Pond had all five habitats.

All habitats were sampled using randomly positioned unbaited minnow traps. These minnow traps are constructed from a collapsible frame ($45 \times 25 \times 25$ cm, with an opening 7 cm in diameter each end) covered in 3 mm nylon square mesh. Habitat use data was collected over 2 months, April and May, in 1998. Sampling took place between 0900 and 1600 on each sampling date. Each trap was set for 2 h. Four replicate samples per habitat were collected from Hole Pond, whereas eight samples were taken per habitat in Dohnut, and 10 per habitat in Big Pond.

Fish were killed with an overdose of anaesthetic (benzocaine [ethyl *p*-amino-benzoate]) then fixed in 10% formalin and returned to the lab for analysis. Non-target species caught in traps were released. Fish were kept in 10% formalin for 4 days before being rinsed and transferred to 70% ethanol.

Laboratory methods

Mosquitofish and gudgeons were enumerated in each sample. Standard length (SL) was measured to the nearest millimetre using vernier calipers. All gudgeons in each sample were measured, whereas up to 50 randomly selected mosquitofish were measured per sample.

Gut contents of mosquitofish and gudgeons from Dohnut and Hole Ponds were analysed to determine if food resources were being partitioned between species and size class (samples from Big Pond were unavailable for gut contents analyses). Because we have very little information on the life history of mosquitofish and gudgeons in Australia, we had to arbitrarily divide the populations into 'small' and 'large' individuals to examine ontogenetic variation in diet. Mosquitofish ≤ 18 mm and ≥ 20 mm SL and gudgeons ≤ 20 mm and ≥ 28 mm SL were examined. Approximately equal numbers of individuals from each species/size-class were randomly selected from each pond. However, as individual fish diet is often habitat-specific, the number

of fish taken from each habitat for gut contents analysis was approximately proportional to their natural occurrence in that respective habitat.

Only the contents of the stomach were used to determine the diet of each size-class, in order to minimise biasing effects of differential digestion among prey types (Bowen 1996). A dissecting microscope (80 \times magnification) was used to remove and open stomachs, and for sorting and counting all prey items.

We used measures of frequency of occurrence, mean contribution (volume %) to total stomach contents, and prey-specific volume to describe diet. Frequency of occurrence indicates the percentage of individuals in the sampled population that contained a given prey taxon. The mean contribution to total stomach contents expresses the mean volumetric contribution of each prey taxon to the total available volume (based on points estimates, see below) in the sample. Prey-specific volume is defined as the percentage volume a prey taxon comprises of all prey taxa in only those predators in which the actual prey occurs (Amundsen et al. 1996). Volume was subjectively estimated using a points method (e.g. Donald & Alger 1993, Wilhelm et al. 1999): The stomach contents of individual fish were assigned a total value of 10 points. Then, each of the prey taxa was recorded as comprising from 1 to 10 points, depending on its contribution to the total volume of food, regardless of stomach size or absolute volume of food.

We plotted prey-specific volume against frequency of occurrence in order to use the graphical method of Amundsen et al. (1996) to display and compare the feeding strategy of each species/size-class. This method allows prey importance and feeding strategies in terms of specialisation and generalisation, both at the individual and population level, to be easily interpreted. Figure 2 shows how plotting prey taxa as a function of prey-specific volume and frequency of occurrence can explain the feeding habits of predators. Interpreting diet data presented this way is easy when accompanied by an explanatory diagram (Figure 2). See Amundsen et al. (1996) for a detailed description of how the method was derived and how it applies.

Analyses

Differences in gudgeon and mosquitofish abundance among habitats were analysed separately using single-factor ANOVAs, where habitat was the single factor. Individual ponds were considered replicates

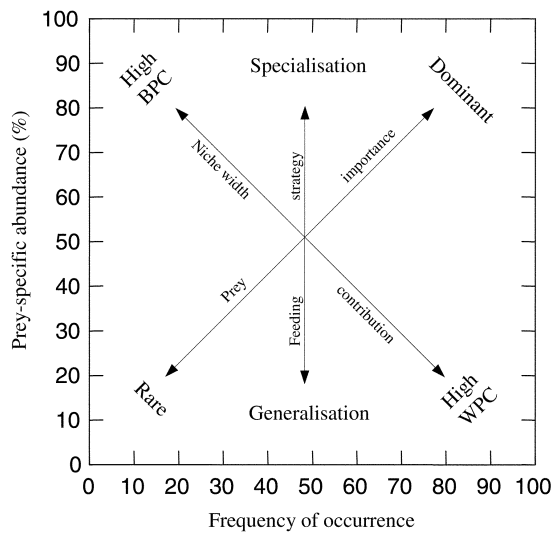


Figure 2. Explanatory diagram for feeding strategy plots (modified from Amundsen et al. 1996). BPC & WPC = between-phenotype contribution and within-phenotype contribution to population niche width, respectively.

($n = 3$), therefore, all samples taken from within each pond were pooled by habitat, and the percentages of total numbers of fish occupying each habitat type was calculated for each pond and used as the dependent variable in the ANOVAs. Using percentages enabled us to standardise for variation in overall fish densities among ponds. We excluded the habitat BE from this analysis as it was unreplicated; BE was only present in Big Pond. Assumptions of normality and homoscedasticity were examined through the use of normal probability plots and scatterplots of stored residuals against fitted values. Untransformed gudgeon percentages met ANOVA assumptions, however, mosquitofish percentages were square-root-transformed to overcome kurtosis (Sokal & Rohlf 1995: pp. 415–417).

One millimetre size frequency distributions were generated for all gudgeons and mosquitofish collected from each habitat in each pond. Habitats that yielded less than 20 individuals were not included in analyses, as the smaller the sample size the higher the probability that the distribution will be shaped by chance. Because the size-frequency distributions did not consistently assume a normal distribution, we used non-parametric Kolmogorov–Smirnov two-sample tests to test for differences in the location, dispersion and skewness of two distributions (Sokal & Rohlf 1995: pp. 434–439). Therefore, our null hypothesis (H_0) was that there was no difference in the location, dispersion

and skewness of the size distributions of either gudgeons or mosquitofish collected from any two given habitats. Because we made multiple significance tests of distributions from the same pond, we lowered our experimentwise error rate by adjusting significance levels using the Bonferroni method. Thus, each comparison was made using a significance level of $\alpha'' = \alpha/k$ (where k = number of tests. Sokal & Rohlf 1995, pp. 236–240) to maintain the overall α -level of 0.05.

Dietary overlap among species/size-classes was calculated using Schoener's (1970) similarity index:

$$C_{xy} = 1 - 0.5 \left(\sum |p_{xi} - p_{yi}| \right)$$

where C_{xy} is the index value, p_{xi} is the proportion, by points, of food type i used by species x , p_{yi} is the proportion, by points, of food type i used by species y , and the vertical bars mean absolute (positive) values of the difference. Values of C_{xy} range from 0, for no overlap, to 1 for complete dietary overlap. C_{xy} values greater than 0.6 generally indicate significant overlap in the diet of species/size-classes.

Results

The relative abundances of gudgeons differed significantly among habitats (Figure 3a (Power ($\alpha = 0.05$) = 0.992)). Post-hoc Tukey's Tests indicated that the mean percentage of gudgeons collected from benthic habitats is significantly greater than the mean percentage of gudgeons collected from surface habitats, in floodplain ponds with low piscivory ($P < 0.05$; Figure 3a). The mean percentages of gudgeons collected from benthic habitats, LB and MB were 38% and 43%, respectively, compared with 6% and 12% collected from surface habitats, LS and ME, respectively.

The relative abundance of mosquitofish did not differ significantly among habitats (Figure 3b). However, the results of this ANOVA must be treated with caution as the power of the test with an α value of 0.05 was only 0.424. This low power is primarily caused by low replication ($n = 3$), and by moderate inter-pond variability in the abundance and distribution of mosquitofish. Although we tried to control for this by selecting three ponds that were as ecologically similar as was possible, the treatment of individual ponds as replicates is extremely difficult, due to the profound inter-pond variation of their communities. There is a trend for mosquitofish association with surface habitats, LS and

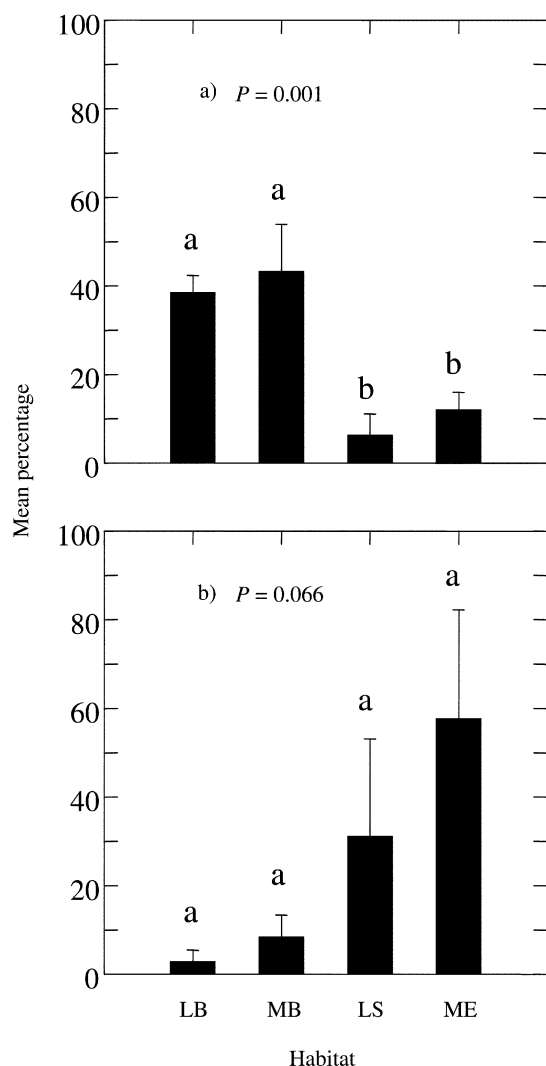


Figure 3. Mean percentage (+1 SE) of gudgeons (a) and mosquitofish (b) collected from LB, MB, LS and ME habitats among three floodplain ponds (habitats annotated with the same letter do not contain significantly different fish abundances, as determined from post-hoc Tukey's Tests).

ME (Figure 3b); the mean percentages of mosquitofish collected from habitats LS and ME were 31% and 58%, respectively, compared with 3% and 8% from LB and MB, respectively.

For gudgeons, H_0 was rejected for all comparisons of distributions among surface (LS, ME and BE) and benthic habitats (LB and MB) across all three ponds (Table 1, Figure 4). Large gudgeons (>24 mm) were predominantly associated with benthic habitats, and small gudgeons (<24 mm) were generally associated

Table 1. Matrices of paired, maximum unsigned differences among habitat-specific length-frequency distributions of gudgeons, obtained from two-sample Kolmogorov–Smirnov tests.

(a) Dohnut Pond					
	LB	MB	ME		
LB	—				
MB	0.112	—			
ME	0.663*	0.698*	—		
(b) Hole Pond					
	LB	MB	LS	ME	
LB	—				
MB	0.028	—			
LS	0.374*	0.369*	—		
ME	0.339*	0.338*	0.087	—	
(c) Big Pond					
	LB	MB	LS	ME	BE
LB	—				
MB	0.122*	—			
LS	0.515*	0.516*	—		
ME	0.518*	0.486*	0.250*	—	
BE	0.434*	0.436*	0.262*	0.150	—

* $p \leq 0.05$ (Bonferroni adjusted).

with surface habitats (Figure 4a), or with all habitats (Figure 4b,c). Within Big Pond however, in addition to the significantly different comparisons among all benthic and surface distributions, H_0 was rejected for comparisons MB \times LB within the benthic habitats, and for comparisons LS \times ME and LS \times BE within the surface habitats. The mean size of gudgeons was significantly greater in MB than in LB (Table 1, Figure 4c). Gudgeons were significantly smaller in LS when compared with ME and BE (Table 1, Figure 4c).

For mosquitofish, H_0 was rejected for 2 comparisons in Dohnut Pond, and for 3 comparisons in Hole Pond (not enough mosquitofish were obtained from more than one habitat (ME) in Big Pond to make comparisons). In Dohnut Pond, the mosquitofish size distribution from MB was significantly different from habitats LS and ME (Table 2a, Figure 5a). In Hole Pond, the mosquitofish size distribution from MB was significantly different from LS, ME and LB (Table 2b, Figure 5b). Mean mosquitofish size in MB habitat is significantly greater than in all other habitats. These differences in mean length were only subtle, however, if 95% confidence intervals are constructed around these means, they still do not overlap in any case (Figure 5).

In Dohnut and Hole Ponds, both large and small gudgeons and mosquitofish display a very broad feeding niche (Table 3), however, mosquitofish generally consumed a greater number of taxa than gudgeons

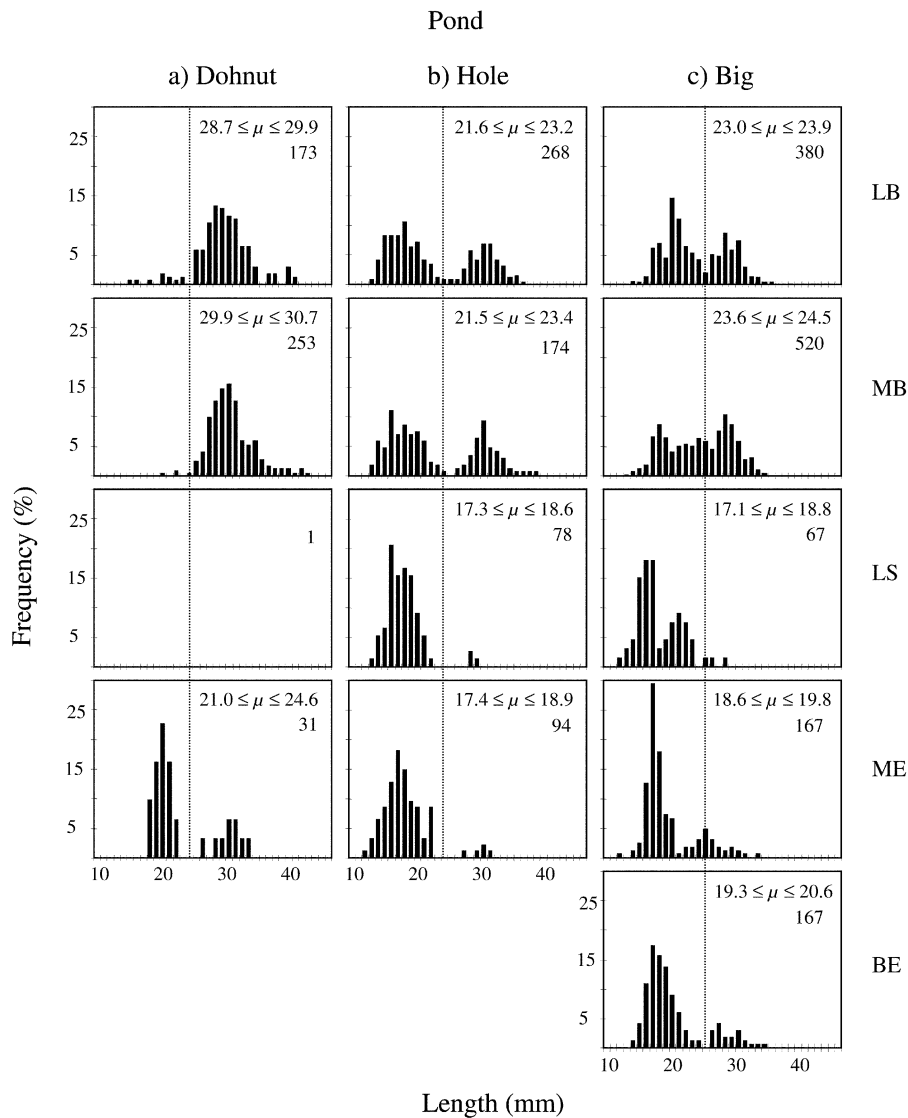


Figure 4. Size distributions of gudgeons collected from different habitats (rows) in three floodplain ponds (columns). LB = limnetic benthic, MB = macrophyte benthic, LS = limnetic surface, ME = macrophyte edge, BE = bare (no macrophytes) edge (rows 1–5, respectively). Dohnut and Hole Ponds did not contain habitat BE. Confidence intervals and sample sizes given in top right of each box; sample sizes $n < 20$ were not graphed. Dashed line drawn at 24 mm size class (mean gudgeon size pooled from all ponds).

(Table 3, Figure 6). Chironomids, microcrustacea, planktonic algae, blue-green algae (*Oscillatoria* spp.) and detritus made the greatest average volumetric contribution to the diets of mosquitofish and gudgeons in the ponds studied (Table 3). Consumption of algae and detritus was probably not incidental. Among the types of planktonic algal cells consumed were commonly *Euglena*, *Pinnularia* and *Closterium*, which

collectively had a size range from 200 to 450 μm . Up to 500 individual alga could be counted in a single fish gut. Filaments of *Oscillatoria* spp. were commonly approximately 50 μm in width and up to 15 mm long. Detritus included fungal hyphae, sediment and filamentous algae. The contents of numerous full fish guts were found to be homogeneously composed of these food types.

Table 2. Matrices of paired, maximum unsigned differences among habitat-specific length-frequency distributions of mosquitofish, obtained from two-sample Kolmogorov–Smirnov tests.

(a) Dohnut Pond				
	MB	LS	ME	
MB	—			
LS	0.247*	—		
ME	0.284*	0.072	—	
(b) Hole Pond				
	LB	MB	LS	ME
LB	—			
MB	0.398*	—		
LS	0.200	0.494*	—	
ME	0.183	0.363*	0.150	—

* $p \leq 0.05$ (Bonferroni adjusted).

At the population level, gudgeons showed moderate specialisation on a limited number of taxa. Small gudgeons exhibited some specialisation on chydorids; the chydorid taxon is approaching the top right corner of the plot (Figure 6a, Figure 2). Rotifers were also an important taxon to juvenile gudgeons (Figure 6a). Large gudgeons were specialising, albeit to a lesser degree than juveniles, on chironominae and *Oscillatoria* (Figure 6b).

With respect to general mosquitofish feeding strategies, most prey types were rare in the diet of small and large individuals (prey importance axis; Figure 2, Figure 6c,d); no individual prey type appears to be particularly important to mosquitofish. That is, mosquitofish generally showed high generalisation at the population level. However, small mosquitofish did show some specialisation on chydorids (Figure 6c, Ch).

All C_{xy} values were below 0.6 for all species/size-class comparisons (Table 4), suggesting that gudgeons and mosquitofish may be partitioning food resources within these floodplain ponds. The highest overlap indices (>0.5) were recorded between the diets of small gudgeons and small mosquitofish, and between small mosquitofish and large mosquitofish (Table 4).

Discussion

Aspects of the gudgeon and mosquitofish spatial niche

The ontogenetic variation in gudgeon habitat use is extremely pronounced. Large gudgeons appear to have

quite a restricted distribution, and were only found in the benthic habitats, whereas small gudgeons were far more general in their distributions, and were most consistently associated with surface habitats, yet may be common in the benthic habitats of certain ponds. There were also subtle, yet statistically significant differences in gudgeon size-structure within the benthic and surface habitats. On average, larger gudgeons are found in the MB habitat, than in the LB habitat, and smaller gudgeons occupy the limnetic surface habitat when compared with surface habitats around the edge of the ponds (ME and BE). Unlike gudgeons, the differences in mosquitofish size composition among habitats was not great, however the differences were consistent among the two ponds that contained enough mosquitofish for comparisons, Dohnut and Hole. Within these ponds, the MB habitat supported larger mosquitofish on average than the LS or ME habitats.

The possible mechanisms causing the ontogenetic variation in habitat association are particularly difficult to define in these systems. The size at which gudgeons appear to shift to the benthic habitat is between 22–24 mm, and is consistent among ponds. Three hypotheses can be tentatively presented to explain this shift. Firstly, the distribution of large gudgeons may be restricted by size-specific predation at the surface. Size-specific predation is known to be a major cause of ontogenetic niche shifts in bluegill (Mittelbach 1981, Werner & Hall 1988) and European perch (Persson 1986, Persson & Greenberg 1990a,b), whereby predation restricts smaller size-classes to vegetated littoral habitats. With respect to the present study, avian predators (kingfishers, herons etc.) and European perch may impose such a restriction on specific size-classes of prey. Avian predators have been postulated to be size-specific, preying on larger individuals (Britton & Moser 1982, Power 1984), and may affect the vertical distribution of susceptible size-classes of fish in lakes (e.g. Rowe & Chisnall 1996). Perch are largely visual predators, and increased light levels at the surface of floodplain ponds may sufficiently aid the foraging efficiency, hence increase the intensity of perch piscivory at the surface (Piet & Guruge 1997). However, this does not explain the persistence of the ontogenetic variation in gudgeon distribution within the ponds studied, which either have very few or no perch in them. Moreover, if large gudgeons are being sufficiently affected by avian and/or aquatic predators at the surface, then one could suggest that mosquitofish, which can be of a similar size and occur at high densities at the surface,

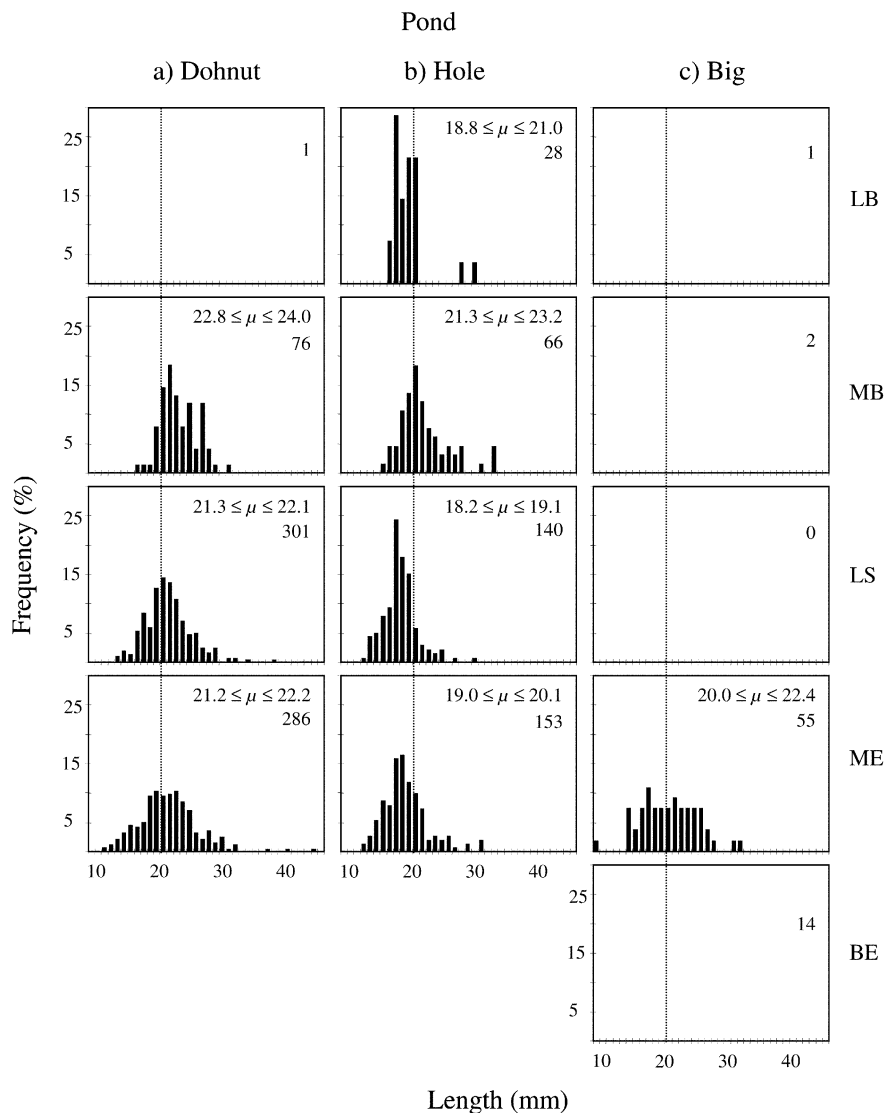


Figure 5. Size distributions of mosquitofish collected from different habitats (rows) in three floodplain ponds (columns). LB = limnetic benthic, MB = macrophyte benthic, LS = limnetic surface, ME = macrophyte edge, BE = bare (no macrophytes) edge (rows 1–5, respectively). Ponds Dohnut and Hole did not contain habitat BE. Confidence intervals and sample sizes given in top right of each box; sample sizes $n < 20$ were not graphed. Dashed line drawn at 21 mm size class (mean size of mosquitofish pooled from all ponds).

would be similarly affected. However, mosquitofish were very abundant at the surface of the limnetic (where there is little or no refuge) and littoral zones in these ponds. Therefore, unless predators actively select large gudgeons over similar sized mosquitofish, predation does not seem the likely factor limiting the vertical distribution of large gudgeons in floodplain ponds.

Similar to that for large gudgeons, the distribution of small gudgeons may be restricted by size-specific predation in the benthic habitats. However, the idea that juvenile gudgeons are restricted in any way from benthic habitats is unlikely, as small gudgeons were abundant in the benthic habitats of Hole and Big Ponds. Therefore, size-specific predation on either juveniles or adults does not seem to be the

Table 3. Mean volumetric contribution (percentage points) of each prey taxon found in non-empty stomachs of small and large gudgeons and mosquitofish in Dohnut and Hole Ponds.

	Small gudgeons	Large gudgeons	Small mosquitofish	Large mosquitofish
Chironomidae				
Chironominae	12.6	26.7	8.8	5
Tanypodinae	1.7	4.1	4.3	1.9
<i>Chaoborus</i> sp.	0	9.4	2.7	0
Adult Chironomid	0	0.5	13.1	22
Ceratopogonidae	4	3.8	2	1.7
Cladocera				
<i>Daphnia</i> spp.	0	0	0.3	0.9
Chydoridae	37.2	3.3	26.1	14.3
Rotifera	13.2	0	3	2.2
Copepoda				
Cyclopoid	14.7	7.7	2.4	2.4
Calanoid	0.8	2.3	0	0
Nauplii	0.4	0	1.4	0
Algae				
<i>Oscillatoria</i> spp.	0.5	23.6	4.6	4.4
Planktonic algae	4.4	1	17.6	0
Detritus	2.6	14.8	2.7	12.4
<i>Paratya</i> spp.	0	1.6	0	13.9
Terrestrial	0	0	5.4	5.7
Oribatidae	0	0	0.3	0
Hydracarina	0	0.2	1.9	0.4
Baetidae	0	0	2.4	0
Nematoda	7	0.7	0	0.9
Ostracoda	0.9	0.1	0	0
<i>Physa</i> sp.	0	0	0	1.9
Notonectidae	0	0	0	1.9
Dytiscidae	0	0	0	1.9
Fish	0	0.2	0	2.2
Zygoptera	0	0	0	4.1
Unknown	0	0	1.1	0
Total no. of taxa	13	16	18	19

likely mechanism causing the ontogenetic variation in gudgeon habitat use.

The spatial distribution of fish may be affected by interspecific competitors (Persson & Greenberg 1990b, Osenberg et al. 1992). Thus, the second hypothesis is that mosquitofish, which occurred at very high densities at the surface of these ponds, could be asymmetrically affecting gudgeon stages, imposing their greatest impact on large gudgeons, thereby restricting them to the benthos. In Big Pond however, mosquitofish abundance was comparatively very low in surface habitats, and no mosquitofish were detected in the surface of the limnetic zone. Yet, in the absence of mosquitofish, large gudgeons were still associated with the benthic habitats, making this hypothesis unlikely.

Thirdly, large gudgeons may shift from the surface habitats to the benthic habitats in response to changing foraging demands. For a given fish size, certain habitats provide greater foraging returns per unit effort than others, and the relative foraging profitabilities of habitats vary as fish grow (Mittelbach 1981, Werner et al. 1981). For large gudgeons, the foraging returns associated with feeding on chironomids and other large prey in the benthos may be greater than that of feeding on planktonic taxa in the water column. Few studies have attempted to quantitatively demonstrate that animals select habitats that provide maximum energetic gain. However, Mittelbach (1981) showed that large bluegill sunfish maximise foraging return, switching habitats as their relative foraging profitabilities change through

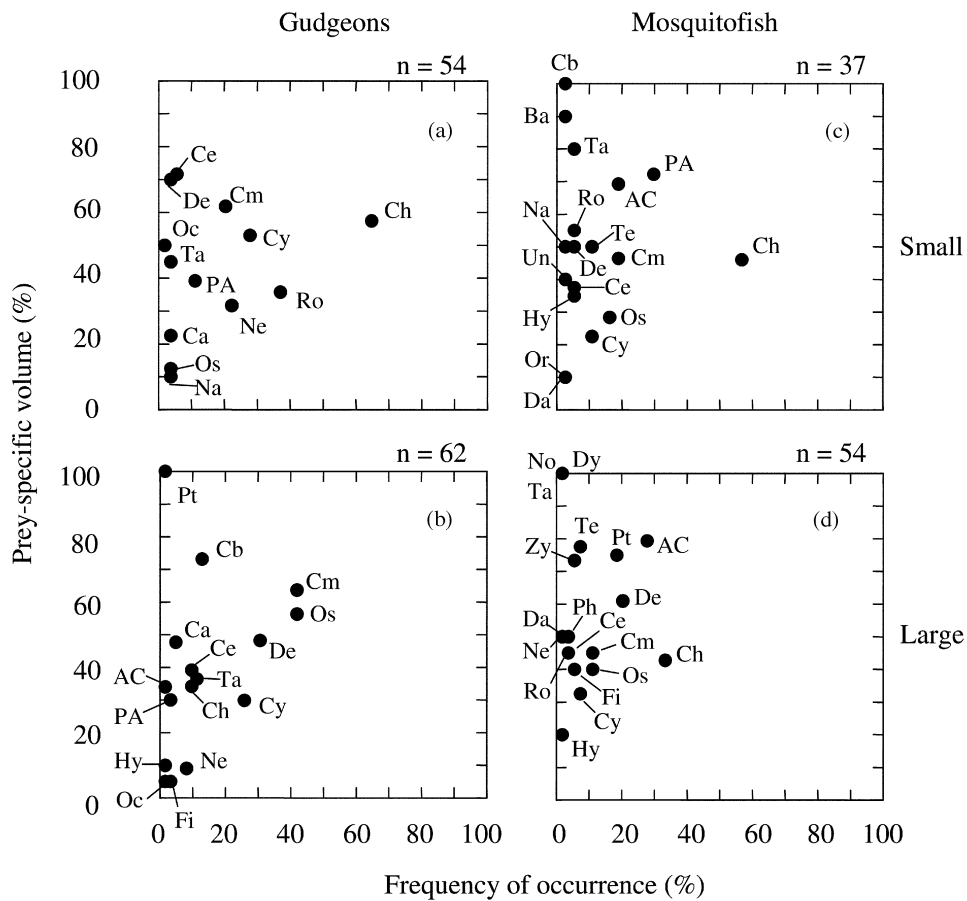


Figure 6. Feeding strategy plots for small gudgeons (a) and mosquitofish (b), and large gudgeons (c) and mosquitofish (d), collected from Ponds Dohnut and Hole; n = no. of fish examined with food in the stomach. Prey items identified as: Cm = Chironominae, Ta = Tanypodinae, Cb = *Chaoborus* sp., AC = adult chironomid, Ce = Ceratopogonidae, Ch = Chydoridae, Ro = Rotifera, Cy = cyclopoid copepods, Ca = calanoid copepods, Na = nauplii, Da = *Daphnia* spp., Os = *Oscillatoria* spp., PA = planktonic algae, De = detritus, Pt = *Paratya* spp., Te = terrestrial, Un = unknown invertebrate, Or = Oribatidae, Hy = Hydracarinae, Ba = Baetidae nymphs, Ne = Nematoda, Oc = Ostracoda, Ph = *Physa* sp., No = Notonectidae, Dy = Dytiscidae, Fi = unidentified fish parts, Zy = Zygoptera.

Table 4. Paired Schoener's dietary overlap indices among species/size-classes. S = small, L = large, G = gudgeon, M = mosquitofish.

	SG	LG	SM	LM
SG	—			
LG	0.35	—		
SM	0.52	0.32	—	
LM	0.31	0.34	0.54	—

time (see also Werner et al. 1981). Hence, it may be possible that the ontogenetic variation in gudgeon habitat association is a response to foraging demands that scale with body size.

The above hypotheses are based on the premise that the ontogenetic variation in habitat association of gudgeons is a flexible response to variable environmental conditions (predation risk, competition and/or food supply). However, this behaviour may be a fixed trait in gudgeons. The consistent size at which gudgeons shift to benthic habitats among ponds may be evidence that the shift is genetically determined, as has been suggested for a similar shift in the bluegill sunfish (Werner & Hall 1988).

The ontogenetic variation in habitat association of mosquitofish was certainly not as distinct as that for gudgeons. Rather than finding a particular size range of individuals being predominantly exclusive

to a particular habitat, the habitat use of various mosquitofish sizes appears to be far more flexible, and could be described as a tendency to find more large individuals in the MB habitat, than in other habitats. Similar causal mechanisms to those discussed for gudgeons may apply to the ontogenetic variation in mosquitofish habitat association.

The spatial overlap among size classes is being limited at a very fine scale. Microhabitats such as MB and ME were often separated by little more than 50 cm–1 m, yet, differences in size composition among them were profound, particularly for gudgeons. Most previous research of stage-structured fish populations in lakes has occurred in larger systems, hence these studies have demonstrated that ontogenetic habitat separation occurs at a much larger scale, usually between the major lake compartments. For example, European perch and bluegill sunfish, *Lepomis macrochirus*, shift between the pelagic zone and the littoral zone (Person 1986, Werner & Hall 1988, Persson & Greenberg 1990a, Byström & Garcia-Berthou 1999). However, not all ontogenetic habitat shifts are between major lake compartments. Rowe (1994) and Rowe & Chisnall (1996) have respectively demonstrated that different developmental stages of smelt, *Retropinna retropinna*, and dune lakes galaxias, *Galaxias gracilis*, exhibit spatial separation within the limnetic zone of some New Zealand lakes, however, the degree of separation is still at a relatively coarse spatial scale (5–15 m). This study demonstrates that fishes inhabiting very small floodplain ponds exhibit ontogenetic variation in habitat use, even though those habitats may only be separated by tens of centimetres.

The spatial niche of an animal greatly expands when we take into account the age-structure component of that niche (Polis 1984), and various habitats may no longer be classified as sub-optimal habitats that support lower abundances of the species, rather as important habitats for earlier stages recruiting into the adult phase (reviewed by Werner & Gilliam 1984). In the present study, when age-structure is disregarded, the general patterns of habitat association are that mosquitofish are associated with surface habitats both in the limnetic and littoral zones, and that gudgeons were associated with benthic habitats, both in the limnetic and littoral zones. Thus, when we disregard the age-structure component of the fish's niche, it would appear that mosquitofish and gudgeons are spatially separated (Figure 3). However, doing so obscures the reality of the spatial relationship between

these two species. When we take into account ontogenetic variation in habitat association, it is obvious that small gudgeons are generally occupying the same habitats as mosquitofish, particularly small mosquitofish.

Aspects of the gudgeon and mosquitofish trophic niche

The dietary overlap indices presented herein suggest that there was no significant overlap between any of the species/size-classes. Coupled with the observation that small gudgeons overlap spatially with mosquitofish, this may provide support for the observation of Ross (1986), who noted that fish partition their niche primarily on the trophic axis, rather than on the spatial axis. However, the overlap index values must be treated with caution as they do not necessarily tell us that mosquitofish are having no impact on the resource use of juvenile gudgeons.

Comparisons of diet among species are not definitive measures of the impact of an introduced fish on the trophic ecology of endemic fishes. The primary reason for this is that introduced fishes may actually displace the trophic niche of endemic fishes. Vander Zanden et al. (1999) studied the trophic ecology (through the use of C and N isotopes) of endemic lake trout (*Salvelinus namaycush*) in Canadian lakes that were either invaded with non-endemic bass (*Micropterus dolomieu* and *Ambloplites rupestris*) or free of non-endemic bass. Where bass have been introduced, they deplete the abundance of littoral prey fish, the preferred prey of lake trout, causing lake trout to shift towards a more pelagic trophic niche. Therefore, although the diets of small gudgeons and mosquitofish are slightly different in the present study, we cannot say that mosquitofish have no impact on the trophic ecology of small gudgeons.

The two most similar diets were that of small and large mosquitofish. This is not a great surprise given that their spatial niche is relatively similar, and that they are largely generalist, opportunistic feeders. The next two most similar diets were those of small gudgeons and mosquitofish ($C_{xy} > 0.50$). Small individuals of both species shared chydorids as the single most important item in their diet. Therefore, although small mosquitofish in general had a slightly different diet than small gudgeons, small mosquitofish may still be depleting a favoured prey resource of small gudgeons.

Conclusion

This study has a limited temporal context, but the patterns presented prompt many questions, and may have important consequences for our understanding of endemic-introduced fish interactions. The hypotheses presented regarding mechanisms driving the ontogenetic variation in gudgeon and mosquitofish habitat use are tentatively presented, and are intended to serve a heuristic purpose. This study indicates that the spatial and trophic relationships between a single endemic species (gudgeons) and a single introduced species (mosquitofish) can be complex. It also demonstrates that ontogenetic niche shifts can occur at a very fine spatial scale, and that they must be taken into account if we are to elucidate the nature of interactions between endemic and exotic fishes. Gudgeons and mosquitofish exhibit considerable similarities in their spatial distribution and moderate similarities in their diet at specific stages in their ontogeny. However, controlled experiments will be needed to ascertain whether recruitment or production of gudgeons is being limited by the exotic mosquitofish.

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