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Improving the ecological understanding of species complexes: the case of piscivory and protracted spawning in the carp gudgeon group *Hypseleotris* spp. (Eleotridae, Teleostei)

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Abstract: Species complexes are a common occurrence in freshwater fish assemblages and may often pose a challenge to the understanding of their ecology. A typical case is the 'cryptic' carp gudgeon group *Hypseleotris* spp. in southeastern Australia, which is thought to comprise four closely related species occurring sympatrically within the Murray–Darling Basin (MDB), where flow delivery scenarios have been proposed for the management and conservation of the native fish faunas. The objective of this study was to provide a deeper insight into the occurrence of piscivory and protracted spawning seasons in *Hypseleotris* spp. based on six years of sampling, and to cast the findings within the broader context of interrelationships between species complexes and their ecology. It is argued that what has been so far referred to as conspecific predation (cannibalism) in *Hypseleotris* spp. could be explained alternatively as 'congeneric' predation, or even as a combination of both. Furthermore, the presence of larvae all year round should be accounted for when assessing the effectiveness of taxon-specific water allocation programs. Better matching of taxonomy with ecology is, therefore, essential for the successful management and conservation of species complexes, and further insights may be provided through the assessment of altricial/precocial forms.

Key words: Cryptic species, cannibalism, Murray–Darling Basin, Bayesian analysis

1. Introduction

In biology, a species complex is a group of closely related species very similar in appearance, such that boundaries between them are often unclear (Mayr, 1970). In fish, several species complexes have been described (e.g., Taylor and Dodson, 1994; Allibone et al., 1996; Klingenberg et al., 2003; Barluenga and Meyer, 2004; Østbye et al., 2006), including those from the freshwater fish fauna of Australia (e.g., Crowley et al., 1986; Crowley and Ivanstoff, 1991; Musyl and Keenan, 1992; Jerry and Woodland, 1997; Hammer et al., 2007), among which the genus *Hypseleotris* has long been regarded as 'cryptic' (Bertozzi et al., 2000; Vilizzi and Kováč, 2014). *Hypseleotris* is widespread and abundant across Australia, with eleven species recognized so far (Unmack, 2000, 2001; Pusey et al., 2004). In eastern and southeastern Australia, there are three described *Hypseleotris* species, namely empire gudgeon *H. compressa*, firetailed gudgeon *H. galii*, and western carp gudgeon *H. klunzigeri*, and at least three undescribed taxa, namely Murray–Darling carp gudgeon *Hypseleotris* sp. 3, Midgley's carp gudgeon *Hypseleotris* sp. 4, and Lake's carp gudgeon *Hypseleotris* sp. 5 (Thacker and Unmack, 2005). Among these, *H. klunzigeri*, together with Murray–Darling, Midgley's, and Lake's carp gudgeon, are believed to occur sympatrically within the Murray–Darling Basin (MDB) in southeastern Australia (Unmack, 2001; Thacker et al., 2007), even though the distributional ranges of *H. klunzigeri* and Midgley's carp gudgeon also extend to the coastal drainages of the east (Thacker et al., 2007).

Yet, taxonomical difficulties in species identification combined with extensive hybridization (Bertozzi et al., 2000; Schmidt et al., 2011) have resulted in the MDB carp gudgeons to be referred to either as western carp gudgeon (in the broad sense) or as a species complex *Hypseleotris* spp., otherwise known as 'carp gudgeon group' (Humphries et al., 1999; King et al., 2003; Vilizzi, 2012). Across the MDB, *Hypseleotris* spp. are generally encountered in slow-flowing or still waters of the littoral zone, normally in association with macrophyte beds or other aquatic vegetation. They comprise generalist predators and opportunistic carnivores known to consume a wide variety of prey (Pusey et al., 2004), including terrestrial insects and micro- and macroinvertebrates (Nielsen et al., 1999, 2000a, 2000b; Meredith et al., 2003; Stoffels and

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Humphries, 2003; Balcombe and Humphries, 2006). In addition, Meredith et al. (2003) were the first to refer to the occurrence of 'conspecific predation' (piscivory) in *Hypseleotris* spp. from littoral riverine environments, and this finding was supported by later studies reporting 'large' individuals feeding occasionally on 'small' individuals within emergent littoral macrophytes (Stoffels and Humphries, 2003; Balcombe and Humphries, 2006).

Both across the MDB and worldwide, environmental flow programs, aimed at the management and conservation of freshwater fish faunas in human-altered water courses, have become an essential component for improved ecosystem services, and have led to the development of flow delivery scenarios tailored to the flow requirements of different fish guilds (Baumgartner et al., 2014). Clearly, for the successful implementation of such intervention measures, an extensive knowledge of the ecology and biology of fish fauna is essential. However, in the case of *Hypseleotris* spp., despite its recent categorization as a foraging generalist with a spawning season lasting from September to April (Baumgartner et al., 2014), more extended spawning periods have been reported (Vilizzi, 2011, 2012), and predictive models for managed inundation events have resulted in lower accuracy compared to other species (Vilizzi et al., 2013).

As part of a long-term investigation on fish larvae responses to in-channel flow pulses (Vilizzi, 2012), the occurrence of piscivory (Vilizzi et al., 2008) and the presence of protracted spawning seasons (Vilizzi, 2011, 2012) in *Hypseleotris* spp. were briefly documented. The objective of the present study is to shed further light on these important ecological aspects of *Hypseleotris* spp. and place them within the wider context of the ecological understanding of species complexes (see Vilizzi and Kováč, 2014). Based on current taxonomical knowledge, the implications of the findings are discussed in terms of their relevance for understanding the ecology of *Hypseleotris* spp. in particular, and of species complexes in general, with a view to management and conservation measures.

2. Materials and methods

2.1. Study area, sampling, and processing

Lindsay Island (34°06′ S, 141°09′ E) is a periodically-inundated 15,000-ha anabranch system of the lower Murray River (VIC, Australia) (Figure 1). Bounded by the Lindsay River to the south and the Murray River to

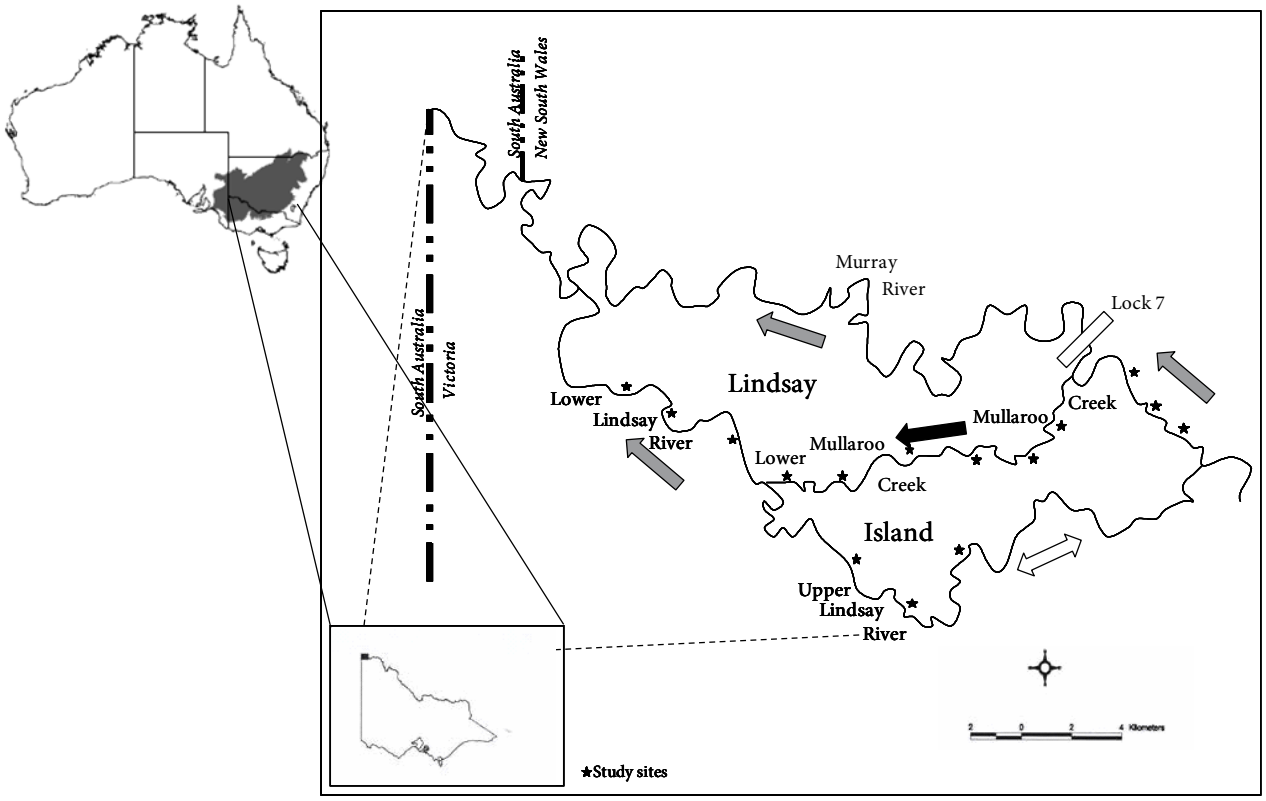

Figure 1. Map of the Lindsay Island anabranch system showing the location of the study sites (marked by asterisks) along four different reaches ('flow habitats'): Upper Lindsay River, Lower Lindsay River, Murray River, Mullaroo Creek. Arrows indicate direction of flow (black: fast flow; grey: slow flow; white-double: no flow).

the north, Lindsay Island is interwoven by a complex anabranch network that is dually regulated by a lock and weir system in the Murray River main channel, and by a series of earthen and concrete structures located at key anabranch effluent points (Vilizzi, 2012). Four reaches make up Lindsay Island: (i) the Upper Lindsay River, a no-flow shallow-ponded habitat; (ii) the Lower Lindsay River, a slow-flow weir pool and weir pool/riverine habitat; (iii) the Murray River, a riverine habitat by definition; and (iv) Mullaroo Creek, a fast-flow anabranch habitat.

From October 2001 to July 2007, fish larvae were sampled from all reaches on Lindsay Island, except for the Murray River reach, where sampling commenced later, in June 2002 (sampling event 12 onwards). There were a total of 76 sampling events over six seasons (each taken to last from August to July; Vilizzi, 2012): 13 in 2001–02, 14 in 2002–03, 12 in 2003–04, 12 in 2004–05, 13 in 2005–06, and 12 in 2006–07. Sampling schedule was every 3 to 5 weeks, with three sites sampled at each reach. At each site, three light traps (22 L × 22 W × 30 H cm) were deployed in the early–mid-afternoon in slackwater areas, left overnight, and reclaimed the next morning. Modified quatrefoil light traps were used during the first season (2001–02), but from the second season onwards (i.e. 2002–03 to 2006–07) a 3-mm knot-to-knot mesh was wrapped around the entrance chambers of the light traps to exclude potentially piscivorous fish, thereby avoiding within-trap predation throughout the rest of the study (Vilizzi et al., 2008). Boat-mounted night trawls and drift nets were also used whenever feasible (details in Vilizzi, 2012). Finally, at each site and on each sampling event, temperature was recorded at a depth of ≈0.3 m along the river bank in the early–mid-afternoon with a Horiba® U-10 multiprobe (Australian Scientific Ltd, Kotara, NSW, Australia), and discharge was obtained for the starting date of each sampling event from data measured at Lock 7 downstream of the Murray River reach (courtesy of the SA Department of Water, Land, and Biodiversity Conservation).

Soon after collection, fish were preserved in 70% ethanol before being returned to the laboratory for later identification and counting under a dissecting microscope. Except for *Hypseleotris* spp., larvae were identified to species level using keys and descriptions from Gerlach (1983), Puckridge and Walker (1990), and Serafini and Humphries (2004). To investigate piscivory, all fish other than larvae collected from October 2001 to February 2002 (first eight sampling events) were also measured for standard length (SL: nearest 1 mm), and prepared for dissection of their gastro-intestinal tract by laying each specimen in a glass petri dish to expose its left-lateral surface. Using surgical scissors under a dissecting microscope, the gut was excised and opened, and any fish larvae ingested were removed. The latter were identified to species level whenever possible, or otherwise categorized as 'unidentified larvae', and the total number and species of larvae consumed by individual predators was then recorded. Finally, to investigate the length of spawning seasons, the abundance of larvae was computed as catch-per-unit-effort (CPUE; details in Vilizzi, 2012).

2.2. Data analysis

Because of the large number of zero values resulting from the absence of larvae in the gut of several *Hypseleotris* spp. individuals, a two-component model was used in which observed absences were modeled separately from observed presences (Kuhnert et al., 2005). Accordingly, in the model for presence/absence:

$z_i \sim \text{Bernoulli}(p)$,

where

$$z_i = \begin{cases} 1 \text{ if } y_i > 0 \\ 0 \text{ otherwise} \end{cases}$$

and in the model for abundance conditional on presence:

$y_i \mid z_i = 1 \sim \text{truncated Poisson}(\lambda)$.

Modeling was within a Bayesian framework, using a Beta(1, 1) and a Gamma (0.001, 0.001) distribution as uninformative priors for p and λ, respectively (Gelman et al., 2004). For model fit comparisons, a Poisson distribution was also fitted to the entire data set (i.e. including zero values), using an uninformative Gamma (0.001, 0.001) prior distribution. Finally, credible intervals for the truncated Poisson distribution in the two-component model were constructed by fitting a categorical distribution (McCarthy, 2007).

Species composition of the larvae ingested by *Hypseleotris* spp. was also modeled by Bayesian estimation using a multinomial distribution, with an uninformative Dirichlet distribution as prior (Gelman et al., 2004). Unidentified larvae were assigned in equal proportions to the identifiable species of larvae, hence assuming that no selection by *Hypseleotris* spp. would occur towards the larvae of any particular species. Finally, the average SL of *Hypseleotris* spp.-consuming larvae was estimated using both an uninformative prior and an informative one, based on length data from Meredith et al. (2003).

All Bayesian models were implemented in OpenBUGS (Spiegelhalter et al., 2007) by sampling 100,000 times from the posterior distribution with the Markov chain Monte Carlo methods, after discarding a 'burn-in' sample of 10,000 (McCarthy, 2007). The Bayesian information criterion (DIC: Spiegelhalter et al., 2002) was then used to compare the fit of the different models.

3. Results

3.1. Piscivory

In total, the gastro-intestinal tracts of 1295 fish were dissected, revealing that 58 of these fish, notably all *Hypseleotris* spp., had consumed larvae (Table 1; Figure 2).

Table 1. Gastro-intestinal contents analysis of the fish caught in light traps on Lindsay Island (southeastern Australia).

Species	Dissected	Fish with larvae	Ingested larvae
Australian smelt	56	0	0
Carp gudgeon group *Hypseleotris* spp.	1051	58	(total) 84
Fly-specked hardyhead (larvae)			5
Hypseleotris spp. (larvae)			15
Crimson-spotted rainbowfish (larvae)			13
Unidentified (larvae)			51
Crimson-spotted rainbowfish	27	0	0
Flathead gudgeon	1	0	0
Fly-specked hardyhead	160	0	0
Total	1295	58	168

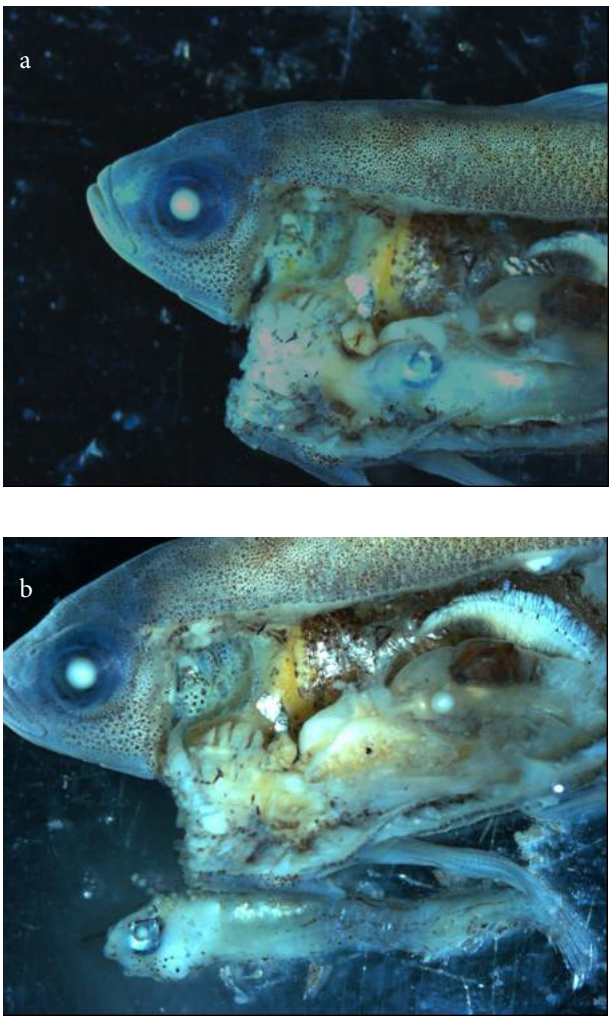

Figure 2. Dissection of an adult predatory *Hypseleotris* spp.: a) eye of *Hypseleotris* spp. larva visible inside gastro-intestinal tract; b) same with removed larva.

All 84 larvae removed from the gut of *Hypseleotris* spp. consisted of unspecked hardyhead *Craterocephalus stercusmuscarum fulvus* (5.9%), *Hypseleotris* spp. (17.9%), and crimson-spotted rainbowfish *Melanotaenia fluviatilis* (15.5%). The large percentage of unidentified individuals (60.7%) was a result of mechanistic damage, likely to have occurred during capture and consumption of prey and/or decay of larvae in the gut of the predator. Bayesian estimates of the species structure of the larvae ingested by *Hypseleotris* spp. (Table 2) showed similar posterior probabilities for predatory *Hypseleotris* spp. ingesting larvae of their own species or of crimson-spotted rainbowfish, and a lower probability of feeding on unspecked hardyhead larvae.

The number of larvae found in the gut of the 58 *Hypseleotris* spp. ranged from 1 to 9, with the majority of predators consuming one or two larvae, and only three individuals with three, seven, and nine larvae (Table 3). A two-component model provided an estimate of the probability of an individual *Hypseleotris* spp. consuming larvae of 0.06 (95% credible interval: 0.04–0.07), whereas the estimated mean number of larvae per predatory fish (i.e. with prey found in their gut) was 1.45, with a 95% credible interval ranging 1.16–1.77. Statistically, the two-component model resulted in a deviance information criterion (DIC) of 614.7, in contrast to a value of 652.6 for the Poisson model based on the entire data set. This indicates better performance of the former model in describing the available data.

Lengths (SL) of predatory *Hypseleotris* spp. (n = 32) ranged 15–40 mm (mean 26.4 ± 0.8 mm SE), including three individuals <22 mm (namely, 15, 17, and 19 mm). Using an uninformative prior for the mean, the mean length of *Hypseleotris* spp. consuming larvae was 26.4 mm (95% credible interval: 24.7–28.1 mm), whereas with an informative prior based on a mean length of 24.7 mm

Table 2. Bayesian posterior probabilities and credibility intervals for the distribution of species of larvae ingested by *Hypseleotris* spp.

		Bayesian estimates			
Species	Observed	Mean	SD	2.5%	97.5%
Fly-specked hardyhead	0.262	0.264	0.047	0.178	0.361
Crimson-spotted rainbowfish	0.381	0.379	0.052	0.281	0.483
Hypseleotris spp.	0.357	0.356	0.051	0.260	0.460

from Meredith et al.'s (2003) data (n = 105), the posterior mean length was 26.2 mm (95% credible interval: 24.6–27.8 mm). As expected, incorporating previous information led to a reduction in the width of the credible interval (from 3.4 mm to 3.2 mm).

3.2. Spawning

During the last five seasons of sampling (i.e. August 2002 to July 2007), larvae of *Hypseleotris* spp. were found throughout the year in the 2005–06 and 2006–07 seasons, and every month, except July and August, in the previous three seasons (Figure 3). This was unlike the larvae of the other taxa (= species), which generally showed shorter spawning seasons, and whose presence/absence and abundance were more closely related to variations in temperature and discharge.

4. Discussion

4.1. Piscivory

The present study has provided the first detailed quantitative analysis of piscivory in a *Hypseleotris* spp. assemblage, the only available information having been so far incidental to previous studies (i.e. Stoffels and Humphries, 2003; Balcombe and Humphries, 2006). In this respect, Stoffels and Humphries (2003) reported large (≥28 mm SL) individuals of Midgley's carp gudgeon feeding on fish (0.2% mean volumetric contribution), whereas Balcombe and Humphries (2006) listed n = 41 large *H. klunzingeri* feeding on small gudgeon (20% total volume) in one sample collected by day, and after dividing their catch into two size classes (i.e. 'small' <25 mm and 'large' ≥25 mm TL), following Balcombe and Closs (2004) (≈21 mm SL threshold; SL = 0.842 TL conversion factor, n = 190 *Hypseleotris* spp. individuals; L Vilizzi, unpublished data). However, even though Balcombe and Humphries (2006) referred to *H. klunzingeri* in their analyses, they also reported the presence of unidentified *Hypseleotris* spp. at their study site, Dugays 2 billabong (= oxbow lake). At that same location, Balcombe and Closs (2004) previously recorded Lake's carp gudgeon, which could only be recognized based on large individuals, and which accounted for 5% of the total *Hypseleotris* spp. population (Balcombe and Closs, 2000). Finally, Meredith et al. (2003) were able to identify with confidence only a proportion of their *Hypseleotris* catch, which was found to consist of *H. klunzingeri* and *H. galii* (a related species limited to coastal drainages of southeastern Australia, but sympatric with *H. klunzingeri* in some areas (Pusey et al., 2004), along with their hybrids.

Although the mean SL of ≈26 mm for predatory *Hypseleotris* spp. reported in the present study is in close agreement with the 'large' *Hypseleotris* spp., found to feed on fish by Stoffels and Humphries (2003) and Balcombe and Humphries (2006), the occurrence of a few predatory individuals < 22 mm SL, hence below the size thresholds for 'small' and 'large' reported in the above studies, deserves attention. To this end, one possible explanation would relate to the possibility that larger/older juveniles may already exhibit piscivorous behavior, which would be supported by published data on size at maturity for *H. klunzingeri* of 26.9 and 29.2 mm SL for ripe (hence, adult) females and males, respectively (Pusey et al., 2004).

A potential confounding factor for the observed occurrence of piscivory in *Hypseleotris* spp., both in the

Table 3. Number of fish larvae found in the gastro-intestinal tract of *Hypseleotris* spp.

Larvae consumed	Number of fish	Proportion of total fish
0	993	0.945
1	45	0.043
2	10	0.010
3	1	0.001
4	0	0.000
5	0	0.000
6	0	0.000
7	1	0.001
8	0	0.000
9	1	0.001

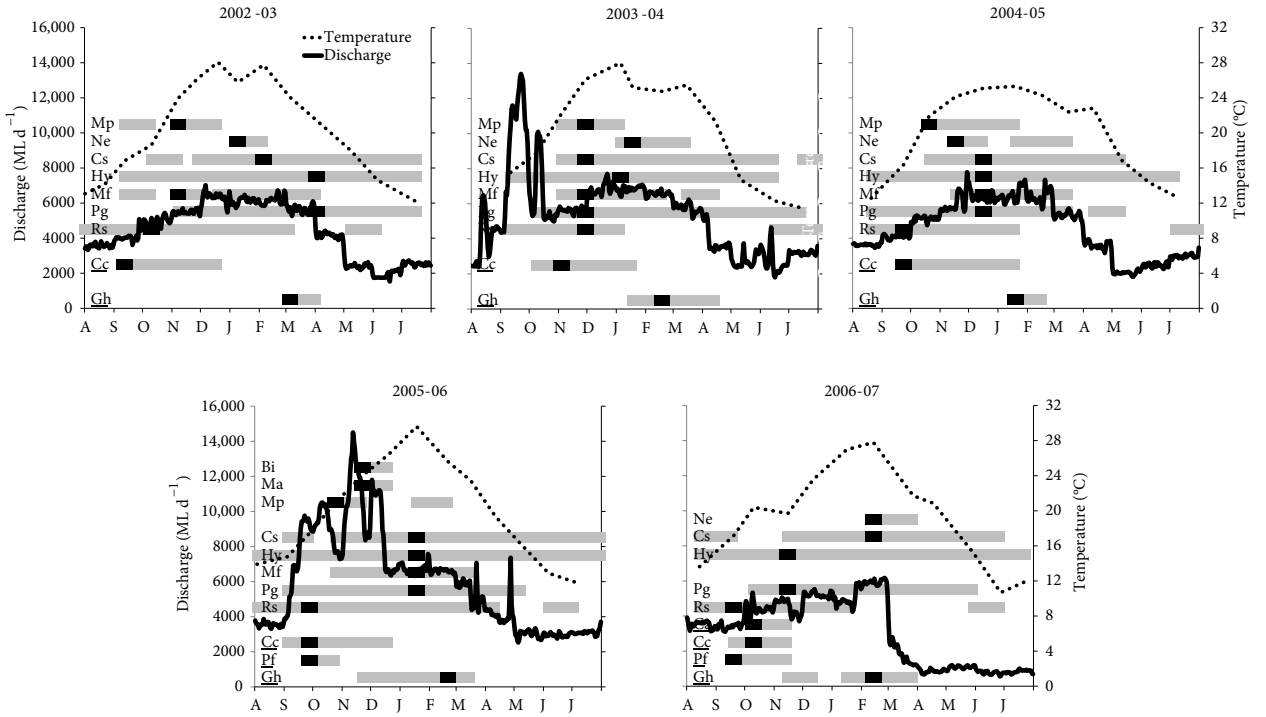

Figure 3. Occurrence (gray) and abundance peaks (black) of the fish larvae sampled on Lindsay Island during five seasons (nonnative species underlined), along with discharge and temperature profiles. Bb = silver perch *Bidyanus bidyanus*; Ma = Murray cod *Maccullochella peelii peeli*; Ma = golden perch *Macquaria ambigua*; Ne = bony herring *Nematalosa erebi*; Cs = unspecked hardyhead *Craterocephalus stercusmuscarum fulvus*; Hy = carp gudgeon group *Hypseleotris* spp.; Mf = Murray-Darling rainbowfish *Melanotaenia fluviatilis*; Pg = flathead gudgeon *Philypnodon grandiceps*; Rs = Australian smelt *Retropinna semoni*; Ca = goldfish *Carassius auratus*; Cc = common carp *Cyprinus carpio*; Pf = European perch *Perca fluviatilis*; Gh = eastern mosquitofish *Gambusia holbrooki*.

current and previous studies (Stoffels and Humphries, 2003; Balcombe and Humphries, 2006), is reliance upon passive collecting gear (sensu Kelso and Rutherford, 1996), justified by the need to sample fish within structurally complex habitats. In this regard, the onset of piscivory and, especially, cannibalism in fish as a result of habitat segregation, has been widely documented in culture environments (cf. Baras and Jobling, 2002). Furthermore, in the only dietary study in which *Hypseleotris* spp. were also sampled by active methods (i.e. dip netting and push net trawls; Meredith et al., 2003), no individuals were found to feed on fish, and this was also true of those caught with bait traps. Conversely, in the present study, *Hypseleotris* spp. was the only 'species' observed to prey on other fish. Therefore, in spite of overall similarities with the trophic ecology of all other (small-body) species sampled (cf. Pusey et al., 2004), the present results reinforce the argument for the occurrence of piscivory in *Hypseleotris* spp. under natural settings and especially in the littoral zone, as postulated by Meredith et al. (2003), and where sampling also took place.

Although the occurrence of piscivory in *Hypseleotris* spp. has been traditionally referred to in terms of 'conspecific' predation (Meredith et al., 2003; Vilizzi et al., 2008), hence cannibalism (e.g., Smith and Reay, 1991), the question remains whether this could be alternatively explained in terms of 'congeneric' predation (or even a combination of both). This is because of the generally documented presence of up to four sympatric species making up *Hypseleotris* spp., even though the likely existence of altricial/precocial interspecific pairs deserves further investigation (Vilizzi and Kováč, 2014).

4.2. Spawning

If the presence of fish larvae is to be regarded as a reliable indicator that fish have spawned (Humphries and Lake, 2000), then the present findings would unarguably point to an extended spawning/breeding season in *Hypseleotris* spp. However, this would be at variance with what was predicted by Humphries et al.'s (1999) classification of the species group as Mode 3b fish (i.e. with a short breeding season; see Vilizzi, 2012). A possible explanation for this apparent contradiction is provided below.

Humphries et al. (2002, Figure 5) displayed 'occurrence bars' for larvae of *Hypseleotris* spp., sampled monthly in 1995–1999 in the highly regulated Campaspe River and in the mildly regulated Broken River (southern MDB).

Whilst the extent of occurrence in the Campaspe River was limited to 1–2 months between November and January, the occurrence of larvae in the Broken River was up to 6–7 months in some years, ranging from late spring (November) to early autumn (April), and this duration was third only to that of flathead gudgeon *Philypnodon grandiceps* and Australian smelt *Retropinna semoni*, two Mode 3a species with longer spawning seasons (Humphries et al., 1999). In a previous paper, based on the first three years of the above data set (i.e. 1995–1998), Humphries and Lake (2000) indicated records of only *H. klunzingeri* larvae from the Campaspe River, and of *H. klunzingeri*, Midgley's carp gudgeon, and Lake's carp gudgeon larvae from the Broken River. In this regard, Humphries et al. (2002, p. 1312) stated that identification of the three species was "extrapolated from the species collected as juveniles and adults in each river […] to the larvae", and that "examination of a number of samples of carp gudgeon by a larval taxonomist unfamiliar with the group and ignorant of how many species were potentially present, suggested that their estimates of the number of species in each river were accurate". Given the above, it can be argued that the longer spawning season for *Hypseleotris* spp. recorded in the Broken River may have been the result of different spawning times by the different species in the group, in which case the apparent contradiction with the life cycle mode of *Hypseleotris* spp. would be reconciled.

4.3. Management considerations

The present study has provided additional supporting evidence for predation by *Hypseleotris* spp. on 'small gudgeons'. Clearly, from a management and conservation perspective orientated especially toward the implementation of water allocation programs, the presence of a 'mosaic' of species may limit, to some extent, the effectiveness of flow delivery scenarios, such as those proposed for *Hypseleotris* spp. (Baumgartner et al., 2014), and as recently testified by the lower accuracy achieved in predictions for this species complex from decision support tools for the management of inundation events (Vilizzi et al., 2013). Given the documented presence of several other species complexes in the freshwater fish fauna of river systems, a better matching of taxonomy with ecology becomes essential for the successful management and conservation of species complexes.

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