Spatial and temporal variability in the distribution and diet of the gudgeon (Eleotridae : *Hypseleotris* spp.) in a subtropical Australian reservoir

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Abstract. The diurnal distribution and diet of *Hypseleotris* spp. was examined over a 14-month period in Maroon Dam, a productive subtropical reservoir in south-east Queensland, Australia. Three distinct size classes of *Hypseleotris* were observed. The smallest (<16 mm standard length (SL)) fish undertake a vertical diurnal migration in the pelagic throughout the year, spending daylight hours near the surface and night hours in deeper waters. The diet of this size class consists almost exclusively of zooplankton (98.6% total prey volume), with cladocera and copepoda dominating the identifiable prey items. A larger (12–20 mm SL) size class group of subadult/adult fish occupies the near-shore littoral throughout the daylight hours but moves out of the sampled area during the night. The diet of this size class is more diverse (zooplankton 58.5%, macro-invertebrate 25.0%, other 16.5%). The largest size class (>20 mm SL) of adult *Hypseleotris* remains in the near-shore littoral throughout seasonal and diurnal cycles and has a more eclectic diet than the other two size classes (zooplankton 28.8%, macro-invertebrate 28.9%, other 42.3%). Spatial and temporal differences in the distribution and diet of these three size class groups are discussed with reference to the abundance and availability of suitable prey, intraspecific competitive exclusion, predator avoidance and water quality.

Extra keywords: diurnal migration, freshwater fish, ontogeny, zooplankton.

Introduction

The genus *Hypseleotris* is widespread and abundant throughout northern and eastern Australia (Hoese and Allen 1983; Herbert and Peeters 1995; Larson and Hoese 1996; Unmack 1997; Allen *et al*. 2002). Consisting of approximately 11 species it is the most widespread genus within Australia (Unmack 2001). Despite this, little is known of their biology with several species remaining undescribed (Unmack 2000; Allen *et al*. 2002). Within south-eastern Australia, *Hypseleotris* often dominate fish communities in terms of abundance (e.g. Gehrke *et al*. 1995) with between two and four species commonly occurring sympatrically (Unmack 2000). Considerable taxonomic uncertainty has surrounded the group because of a lack of easy morphological characters for differentiating each species (Larson and Hoese 1996), which is further complicated by the recently discovered common occurrence of hybrids (Bertozzi *et al*. 2000).

Despite their abundance and likely importance in aquatic ecosystems, the ecology and behaviour of *Hypseleotris* have received only limited attention. Many multispecies studies provide generic catch and distribution data (e.g. Lloyd and Walker 1986; Gehrke *et al*. 1995; Harris 1995; Harris and Silveira 1999; Humphries *et al*. 1999, 2002; Lieschke and Closs 1999; Norris and Thoms 1999; Syarifuddin 2001), yet few provide more detailed analysis. Recently, prey selectivity (Hall 1998) and predation effects on macro-invertebrate (Nielsen *et al*. 1999), and micro-invertebrate (Nielsen *et al*. 2000*a*, 2000*b*) populations have received attention, whereas habitat use by *Hypseleotris* has been examined on only three occasions and in all cases the focus has been on fish in or adjacent to the littoral zone (Stoffels 1998; Balcombe and Closs 2000; Stoffels and Humphries 2003).

In contrast, habitat use by other lake- and reservoir-dwelling fish has been well described. Multispecies studies dominate (e.g. Bohl 1980; Eklov 1997; Kubecka and Wittingerova 1998; Dedual *et al*. 2000; Gido and Matthews 2000; Glova and Sagar 2000; Swierzowski *et al*. 2000; Wanink *et al*. 2001), largely because the often-employed hydro-acoustic methods do not allow for species identification. Single species studies often correlate spatial and temporal patchiness of fish distribution with ontogeny and habitat characteristics in the littoral (e.g. Rossier 1995; Weaver *et al*. 1997; Brown *et al*. 2000) or pelagic (e.g. Bohl 1980; Matthews *et al*. 1985; Hamrin 1986; TeWinkel

and Fleischer 1999; George and Winfield 2000) or both (Mittelbach 1981; Werner and Hall 1988; Imbrock *et al.* 1996; Landry *et al.* 1999). Each of these studies provide one or more of the following four reasons for observed correlations:

(*1*) Abundance and availability of suitable prey; whereby fish are occupying their optimum feeding habitat.

(*2*) Competitive exclusion; whereby fish are forced out of their optimal feeding habitat because of feeding inefficiency or are unwilling to endure acts of aggression from coexisting organisms.

(*3*) Predator avoidance; an extreme form of competitive exclusion whereby smaller age/size classes of fish (prey) are forced out of optimum feeding habitats occupied by larger fish (in the case of piscivory) or other organisms (e.g. birds).

(*4*) Water quality; whereby fish occupy areas of optimum water quality (e.g. temperature, dissolved oxygen) to minimise physiological stress.

The present study examines the relationship between these four descriptors and the diet, distribution and ontogeny of the gudgeon (*Hypseleotris* sp.) in Maroon Dam, a subtropical Australian reservoir.

Materials and methods

Study site

Maroon Dam is a productive irrigation water supply and recreational facility located along Burnett Creek (a tributary of the Logan River) approximately 100 km south-west of Brisbane, Queensland, Australia (152°39′E, 28°10′S). At full supply Maroon Dam has a maximum capacity of 38 400 ML and a maximum depth of 34 m. The Dam is strongly monomictic, stratifying in spring (September–October) and turning over in early winter (June–July). While present, the thermocline and oxycline occur at depths between 5 m and 10 m, typically between 6 m and 8 m. Over the period of the present study, water transparency was relatively high (Secchi depth between 1.4 m and 4.7 m) and surface water temperatures varied from 14.8°C to 29.5°C.

As a result of the unusually high water level in the Dam throughout the study period, the bulk of the normally littoral aquatic vegetation occurred offshore in a dense band approximately 3–8 m from the water's edge at a depth of approximately 1.5–3 m. *Potamogeton* sp. and *Myriophyllum* sp. dominated this vegetation band, with *Ceratophyllum* sp. and *Elodea* sp. more sparsely distributed. This band of water plants extended around the entire perimeter of the Dam and served as the boundary between the near-shore littoral and pelagic zones, belonging to neither. From September 1999 to June 2000, the depth of water available to fish in the pelagic was reduced to 5–8 m because stratification resulted in low dissolved oxygen concentrations ($<2.5\,\mathrm{mg\,L^{-1}}$) in the hypolimnion.

Sampling regimen

With the exception of September 1999, 14 monthly sampling trips were completed between August 1999 and September 2000. All sampling occurred within one week of a full moon to reduce possible lunar effects on fish behaviour (Gaudreau and Boisclair 2000). For each sampling trip, data were collected every 3 h over a 24-h period from noon to noon (nine sampling periods). Sampling was divided into near-shore littoral and pelagic components.

For near-shore littoral sampling, four sites were selected randomly in April 1999 and were resampled each month thereafter. At each site,

one bait trap (square-ended collapsible 45 cm × 25 cm × 25 cm frame, 7-cm opening at each end, 3-mm square mesh) was deployed. Traps were baited with tinned cat food and all baits were refreshed at midnight to reduce the effects of bait potency. Fish caught in the trap were counted and released. The time when each trap was pulled from the water was recorded and the catch expressed as fish per hour. Bait traps have also been used to quantify the relative abundance of *Hypseleotris* by Balcombe and Close (2000) and Stoffels and Humphries (2003).

In addition, five fish were collected from each near-shore littoral site using a dip net (45 cm × 75 cm rectangular frame, 3-mm square mesh) and preserved for stomach content and standard length (SL) analysis. Neither schools of fish nor habitat were targeted during dip netting such that day and night samplings could be standardised. The time that sampling was completed at each littoral site was recorded, and an average 'time per site' was calculated. The SL of 10 fish collected in the dip net at each sampling time was recorded.

In the pelagic, three constant speed ($\sim$10 km h^{-1}) push net trawls were undertaken for 3 min each (trawl distance $\sim$500 m). The push net is a pivoting frame (38 cm × 62 cm) containing a fine mesh (4 mm knot-to-knot) net that is bolted to the boat and samples upto a depth of approximately 50 cm (see also Lieschke and Close 1999). The volume of water sampled during each trawl was approximately 118 m^3. For each sampling time at which catches allowed, the SL of 10 fish collected from the pelagic in the push net was recorded.

Bait traps were also used to sample the pelagic zone. A trap line was anchored to the bottom of the lake and two floats, one at the water surface and one immediately below the surface, kept the line taught and traps stable. Three bait traps were tied to the trap line at depths of 0.5 m, 2 m and at the bottom. Four trap lines were set in the pelagic zone of Maroon Dam each month from August 1999 to March 2000. As in the near-shore littoral, traps were baited with tinned cat food and baits were refreshed every 12 h. Despite co-occurrent catches of *Hypseleotris* with the push net, none were ever caught in zone bait traps set in the pelagic. Therefore, after seven months it was decided to discontinue bait trap sampling in the pelagic zone.

Surface water temperatures were recorded using a Model 95 DO meter (YSI Pty Ltd, http://www.ysi.com) between 1000 hours and 1230 hours at a depth of approximately 15 cm. Surface water temperature data was recorded weekly between November 1999 and May 2000 and fortnightly during the colder months. Monthly average surface water temperatures presented are an average of all surface water temperatures measured within the calendar month.

Hypseleotris *taxonomy*

Fish from the *Hypseleotris* genus dominate the small fish fauna at Maroon Dam, comprising 96% of the total catch in all gear types used (S. Meredith, unpublished data). All dissected fish ($n = 336$) were identified using the morphological descriptions of Larson and Hoese (1996). *Hypseleotris klunzingeri* comprised 23.8% of the catch and *H. galii* comprised 16.4%, whereas 59.8% were unidentifiable. This large proportion of unidentifiable fish was a result of the small size of many fish, but also because many adult fish did not fit neatly into Larson and Hoese's (1996) descriptions. Some of these unidentified adult fish have since been identified genetically as *H. galii* hybrids (M. Adams, unpublished data).

Dietary analysis

Where catches allowed, a minimum of 10 fish were dissected from both near-shore littoral and pelagic zones for each of the nine sampling times during the October 1999 and January 2000 sampling trips. For those time intervals in which fewer than 10 fish were captured, all captured fish were dissected.

The contents of the entire gastrointestinal tract (GIT) of each dissected fish was enumerated using a points method modified from Hynes

(1950). Total GIT fullness was expressed as a percentage (empty = 0%, full = 100%) in increments of 5%. The GIT contents were then separated into prey categories (see Table 1) and each prey category assigned a percentage of the total prey volume (% TPV). The volume (% GIT) occupied by each prey category was then calculated as:

$$\% \text{ GIT} = \text{Total GIT fullness} \times (\% \text{ TPV}/100)$$

The proportional contribution of each prey category to the total prey volume was expressed as a percentage of total prey.

Statistical analysis

Paired sample t-tests were used for diurnal analyses of bait trap and push net catch per unit effort (CPUE), and SL of fish caught in the dip net and push net. Monthly data were separated into day and night pairs based on sunrise and sunset times, and paired day and night means were subjected to analysis. All paired sample t-test results were subjected to Bonferroni correction.

One-way analysis of variance (ANOVA) was used to analyse the differences in total % GIT volumes of the three size classes. Similarly, ANOVA was used to examine the zooplankton, macro-invertebrate and 'other' proportions of total prey volume for the three size classes. These analyses were performed only on those fish with some prey in their GIT ($n = 297$). Fish with empty GITs ($n = 12$) were excluded. All prey volume percentage data were subjected to arcsine transformation before analysis. Tukey post-hoc tests were used to determine the nature of the differences detected. Cladoceran abundance in the diet from the two near-shore littoral size classes was analysed with a Mann–Whitney U-test because data were strongly bimodal and could not meet homoscedasticity assumptions despite transformation. All statistical analyses were performed using SYSTAT (vers. 9.0; SPSS, Chicago, IL, USA).

Results

Spatial distribution

Near-shore littoral v. pelagic

Fish caught in the near-shore littoral zone had a bimodal size class distribution (Fig. 1). The smaller node comprised
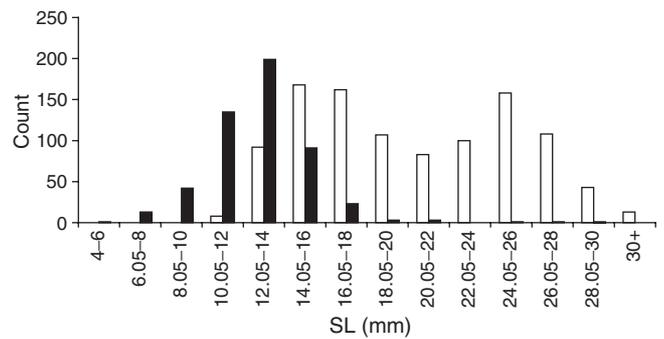

Fig. 1. Standard length (SL) histogram of all *Hypseleotris* collected throughout the sampling period in the near-shore littoral (□) and pelagic (■).

Table 1. Mean prey abundance and volume (± s.e.) in the gastrointestinal tract (GIT) of three *Hypseleotris* size class groups
Combined data from October 1999 and January 2000

Taxa	Pelagic (<16 mm SL) ($n = 121$)			NSL (12–20 mm SL) ($n = 83$)			NSL (>20 mm SL) ($n = 105$)		
	Abundance	Volume (% GIT)	% Total prey volume	Abundance	Volume (% GIT)	% Total prey volume	Abundance	Volume (% GIT)	% Total prey volume
Zooplankton									
Cladocera	2.02 (0.37)	9.7 (1.6)	23.3	14.00 (5.25)	16.7 (2.4)	29.4	32.10 (8.63)	13.3 (2.4)	23.8
Copepoda	1.19 (0.45)	3.4 (1.1)	8.1	4.76 (1.00)	3.5 (0.7)	6.2	0.67 (0.23)	0.5 (0.2)	0.9
Copepoda nauplii	0.13 (0.08)	0.2 (0.1)	0.5	23.52 (5.37)	8.7 (1.8)	15.2	1.47 (1.24)	0.6 (0.4)	1.0
Ostracoda	0.00 (0.00)	0.0 (0.0)	0.0	0.13 (0.06)	0.2 (0.1)	0.3	0.33 (0.12)	0.6 (0.2)	1.0
unidentified fragments	–	27.8 (2.3)	66.8	–	4.2 (0.8)	7.4	–	1.1 (0.5)	2.0
Total (zooplankton)	*3.35 (0.61)*	*41.1 (2.6)*	*98.6*	*42.41 (7.65)*	*33.3 (3.5)*	*58.5*	*34.57 (8.75)*	*16.1 (2.6)*	*28.8*
Macro-invertebrates									
Hemiptera	0.00 (0.00)	0.0 (0.0)	0.0	0.16 (0.13)	0.9 (0.6)	1.5	0.42 (0.14)	1.7 (0.5)	3.1
Coleoptera	0.00 (0.00)	0.0 (0.0)	0.0	0.00 (0.00)	0.0 (0.0)	0.0	0.01 (0.01)	0.0 (0.0)	0.0
Gastropoda	0.00 (0.00)	0.0 (0.0)	0.0	0.02 (0.02)	0.3 (0.2)	0.5	0.05 (0.02)	0.3 (0.2)	0.6
Diptera larvae	0.00 (0.00)	0.0 (0.0)	0.0	0.78 (0.22)	4.9 (1.3)	8.5	2.11 (0.42)	5.8 (1.1)	10.4
Odonata larvae	0.00 (0.00)	0.0 (0.0)	0.0	0.00 (0.00)	0.0 (0.0)	0.0	0.01 (0.01)	0.1 (0.1)	0.1
Ephemeroptera larvae	0.00 (0.00)	0.0 (0.0)	0.0	0.00 (0.00)	0.0 (0.0)	0.0	0.04 (0.02)	0.6 (0.3)	1.1
Trichoptera larvae	0.00 (0.00)	0.0 (0.0)	0.0	0.07 (0.04)	0.1 (0.1)	0.2	0.27 (0.06)	3.2 (0.8)	5.7
Acarina	0.00 (0.00)	0.0 (0.0)	0.0	0.17 (0.11)	0.1 (0.1)	0.2	0.07 (0.04)	0.1 (0.1)	0.2
Unidentified fragments	–	0.0 (0.0)	0.0	–	8.2 (2.2)	14.4	–	4.3 (1.2)	7.7
Total (Macro-invertebrates)	*0.00 (0.00)*	*0.0 (0.0)*	*0.0*	*1.20 (0.30)*	*14.4 (2.4)*	*25.0*	*2.97 (0.49)*	*16.2 (2.2)*	*28.9*
Other									
Filamentous algae	–	0.0 (0.0)	0.0	–	0.0 (0.0)	0.0	–	5.0 (1.6)	8.9
Unidentified/unidentifiable	–	0.6 (0.3)	1.4	–	9.2 (1.4)	16.5	–	18.7 (2.0)	33.4
Total (Other)	–	*0.6 (0.3)*	*1.4*	–	*9.2 (1.4)*	*16.5*	–	*23.6 (2.5)*	*42.3*
Total GIT fullness		**41.7 (2.6)**	**100.0**		**56.9 (2.9)**	**100.0**		**55.9 (2.8)**	**100.0**

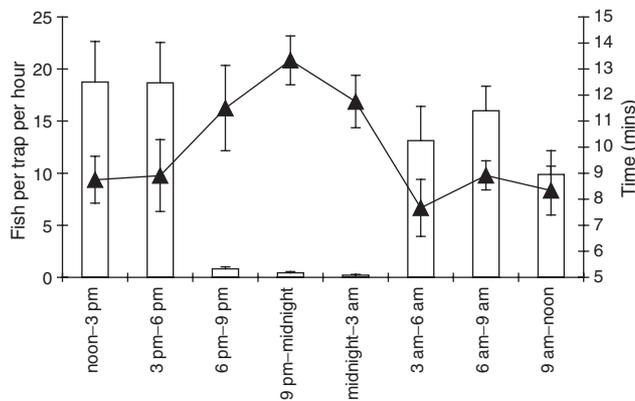**Fig. 2.** Diurnal variation in abundance of *Hypseleotris* collected in the near-shore littoral (□, bait traps—fish per trap h^{-1}) and mean time spent per sampling site (▲, minutes), averaged throughout the study period (±s.e.).

Fig. 3. Diurnal (□, day; ■, night) variation in standard length (SL) of *Hypseleotris* in near-shore littoral (dip net) throughout the study period.

mainly fish of 12–20 mm SL, with a modal peak at 14.05–16 mm SL. The second near-shore littoral node is made up of fish >20 mm SL, with a modal peak at 24.05–26 mm SL. No fish <10 mm SL were caught in the near-shore littoral zone. In contrast, the size class distribution of fish in the pelagic zone for the whole year was approximately normal, the modal size class being 12.05–14 mm SL (Fig. 1). Ninety-five per cent of all *Hypseleotris* caught in the pelagic were <16 mm SL.

Hypseleotris *diet*

Pelagic (<16 mm SL) fish had a significantly lower Total % GIT volume (mean 41.7%) than the 12–20 mm SL (mean 56.9%) and >20 mm SL (mean 55.9%) near-shore littoral size classes ($F_{2,303} = 9.692$, $P < 0.001$). No difference in the Total % GIT volume was found between the two near-shore littoral size classes.

The volumetric proportion of zooplankton in the diet of *Hypseleotris* decreased significantly with increasing size class (mean 98.6%, 58.5% and 28.8% for the <16 mm SL pelagic, 12–20 mm SL and >20 mm SL near-shore littoral size classes, respectively; $F_{2,291} = 139.78$, $P < 0.001$). Cladocera made up the greatest volume of all identifiable zooplankton in each of the size classes (mean 23.3%, 29.4% and 23.8% of total prey volume for the pelagic <16 mm SL, 12–20 mm SL and >20 mm SL near-shore littoral size classes, respectively). Cladoceran abundance data was skewed strongly and no significant difference between the means of the 12–20 mm SL (mean 14.00 cladocerans) and the >20 mm SL (mean 32.10 cladocerans) size classes was found (Mann–Whitney $U = 4898$, $P = 0.131$). Adult copepoda made the next highest % GIT volume contribution to the diet of the pelagic (<16 mm SL) fish (mean 8.1%), whereas copepod nauplii comprise the next highest volume in the 12–20 mm SL near-shore littoral *Hypseleotris* (mean 15.2%).
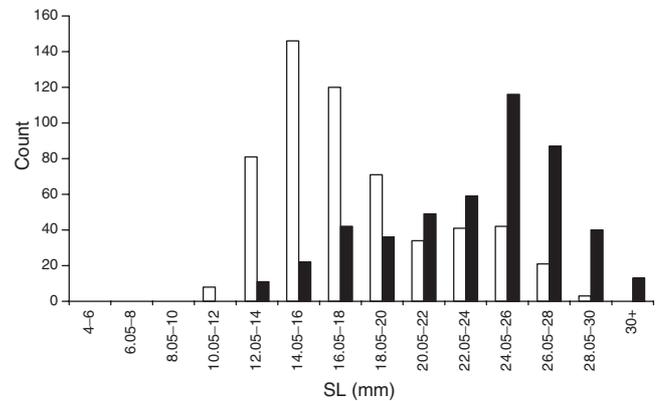
Macro-invertebrates were not found in the GIT of *Hypseleotris* collected from the pelagic (<16 mm SL). The volumetric proportion of macro-invertebrates in the near-shore littoral size classes (mean 25.0% and 28.9% for the 12–20 mm SL and the >20 mm SL size classes, respectively) were not significantly different ($F_{2,291} = 29.47$, $P < 0.001$). Dipteran larvae comprised the highest volumetric proportion of identifiable prey in both near-shore littoral size classes (mean 8.5% and 10.4% for the 12–20 mm SL and the >20 mm SL size classes, respectively).

In contrast to zooplankton, the volumetric proportion of 'other' items in the diet of *Hypseleotris* increased significantly with increasing size class (mean 1.4%, 16.5% and 42.3% for the <16 mm SL pelagic, 12–20 mm SL and >20 mm SL near-shore littoral size classes, respectively; $F_{2,291} = 35.63$, $P < 0.001$).

Temporal distribution

Diurnal: near-shore littoral zone

Significantly more fish were caught in the bait traps in the near-shore littoral zone during daylight hours (mean 14.4 fish per trap per hour) than in the night hours (mean 3.7 fish per trap per hour) ($t = 4.501$, d.f. = 11, $P = 0.001$) (Fig. 2). Fish caught in the dip net during daylight hours (mean 17.9 mm SL) were smaller than fish caught during the night (mean 23.3 mm SL) ($t = -10.08$, d.f. = 11, $P < 0.001$) (Fig. 3).

Diurnal: pelagic zone

Push net catch rates in the pelagic were greater during daylight (mean 16.8 fish per trawl) than during night sampling (mean 2.4 fish per trawl) ($t = 2.76$, d.f. = 11, $P = 0.019$) (Fig. 4). The size of fish caught in the pelagic was unaffected by light/dark cycles (mean daylight SL = 12.6 mm, night SL = 13.0 mm) ($t = -0.884$, d.f. = 10, $P = 0.397$) (Fig. 5).
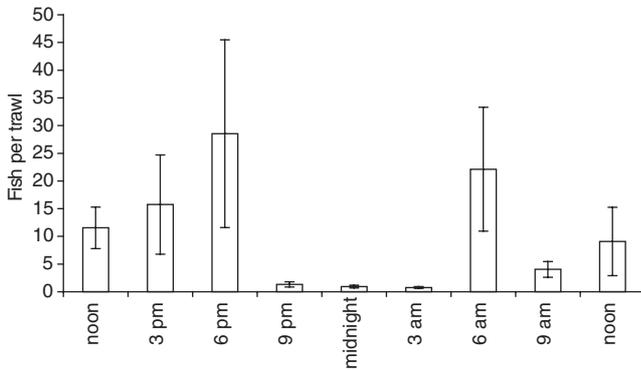
Fig. 4. Diurnal variation in abundance of *Hypseleotris* collected in the pelagic (push net—fish per trawl) throughout the study period (± s.e.).
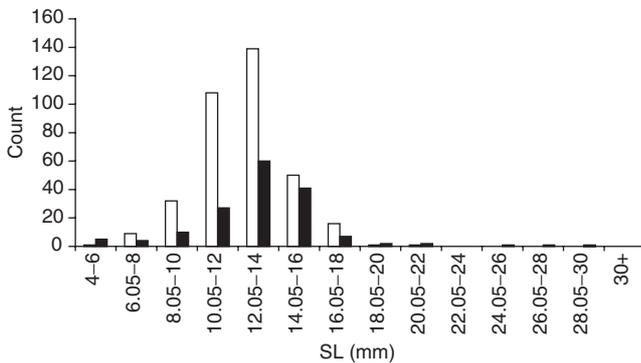

Fig. 5. Diurnal (□, day; ■, night) variation in standard length (SL) of fish caught in the pelagic (push net) throughout the study period.
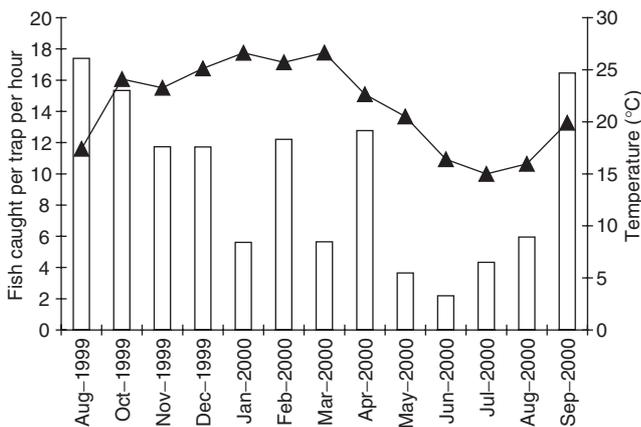

Fig. 6. Monthly near-shore littoral bait trap catch (□, fish per trap h^{-1}) and average monthly water temperature (▲) throughout the study period.

Seasonal: near-shore littoral zone catch rate

Catches of *Hypseleotris* in bait traps were generally lower during the colder winter months than in the warmer months (Fig. 6). It is not clear if this is because of temporal variability
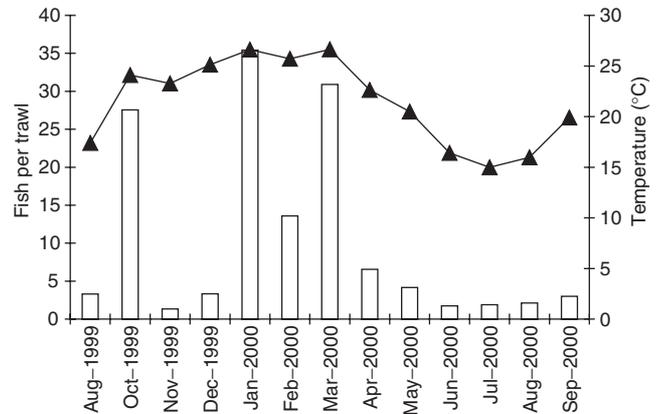

Fig. 7. Monthly pelagic push net catch (□, fish per trawl) and average monthly water temperature (▲) throughout the study period.

of fish numbers in the near-shore littoral, inactivity of fish during the winter months or both.

Seasonal: pelagic zone catch rate

Hypseleotris were collected from the pelagic throughout the year, with greatest catches occurring in October 1999, January 2000 and March 2000 (Fig. 7). Seasonal push net catch data appear to follow water temperature trends, with each downturn in average monthly temperature producing a lesser catch than the previous month, and each upturn in temperature producing a greater catch. Yet, as with bait traps, it is not clear if catch rate reflects changes in fish activity or abundance.

Discussion

Spatial and temporal distribution

Three spatially and temporally defined size groups of *Hypseleotris* were identified in Maroon Dam. A smaller (<16 mm SL) size class was caught in the pelagic, a 12–20 mm SL size class dominated the catch in the near-shore littoral during daylight hours and a larger >20 mm SL size class dominated the catch in the near-shore littoral during the night.

Although different sampling techniques were used in the near-shore littoral and pelagic areas, this is thought not to have biased results. The dip net, bait trap and push net have been shown individually to be able to collect the entire size class range of *Hypseleotris* and other fish (notably Australian smelt) in other published (Lieschke and Closs 1999; Stoffels and Humphries 2003) and unpublished studies (S. Meredith, unpublished data; B. Ebner, unpublished data). Furthermore, push and dip netting are both active capture techniques, and the smaller mesh size (3 mm knot-to-knot) of the dip net caught the larger fish in the near-shore littoral whereas the larger mesh in the push net (4 mm knot-to-knot) captured the smaller fish in the pelagic. The effect of the speed at which the push net is propelled on catch has also

been explored; for boat speeds of 2.7–9.9 km h^{-1} no differences in the abundance or SL of *Hypseleotris* were detected (B. Ebner, unpublished data). Therefore, the consistently, almost exclusive catch of smaller *Hypseleotris* in the pelagic and larger *Hypseleotris* in the near-shore littoral is considered to reflect the true size class distribution of fish rather than any bias implicit in the sampling design.

Pelagic

The catch of early juvenile *Hypseleotris* in the pelagic throughout the year is consistent with recent observations of an extended breeding season (Humphries *et al.* 2002) but conflicts with earlier conclusions that *Hypseleotris* undertake a single spawning between October and January (Hoese *et al.* 1980; Larson and Hoese 1996). It is worth noting that studies by Hoese *et al.* (1980) and Larson and Hoese (1996) were based on limited data obtained largely under experimental conditions. As further field-based life-history studies are undertaken (including recent otolith analyses; C. Sharpe, unpublished data), it is becoming apparent that *Hypseleotris* are serial, protracted or repeat spawners (Humphries *et al.* 1999).

The presence of only smaller *Hypseleotris* (<16 mm SL) in the pelagic, with larger fish generally restricted to the near-shore littoral (Fig. 1), indicates that the pelagic zone of Maroon Dam acts as a nursery for juveniles (*Hypseleotris* collected from Maroon Dam contained mature gonads only after attaining a minimum size of 19.85 mm SL: $n = 164$; S. Meredith, unpublished data). Because the demersal eggs of *Hypseleotris* are laid, fertilised and hatch in the littoral zone (Anderson *et al.* 1971; Mackay 1973*a*, 1973*b*; Konagai and Rimmer 1985), larval/early juvenile fish must undertake a horizontal migration from the littoral to the pelagic. Such a migration has been observed for larval bluegill sunfish (*Lepomis macrochirus*) (Werner and Hall 1988). The advantage of undertaking such an energetically expensive migration has been described by a combination of optimum prey availability and size-related predator avoidance (Mittelbach 1981; Werner and Hall 1988). Such justification is also applicable to larval/early juvenile *Hypseleotris*, for whom conspecific predation is known to occur in littoral riverine environments (Meredith *et al.* 2002) and suitable zooplankton prey is both abundant and available in the pelagic of Maroon Dam (discussed further in *Diet*).

There was also a strong diurnal catch pattern in the surface waters of the pelagic (Fig. 4), with *Hypseleotris* abundant in the warmest most well-lit layer during the day, and moving into the unsampled areas of either the deep pelagic (vertical migration) or the dense band of aquatic macrophytes separating the near-shore littoral and the pelagic (horizontal migration) at night. It is considered that this catch pattern is representative of a short (<10 m) diurnal vertical migration by pelagic *Hypseleotris* as this is more likely to be bioenergetically sustainable for a 16-mm SL fish than

the required diurnal horizontal migration of approximately 100–500 m.

Such a diurnal migration conflicts with that observed in most lakes and contradicts the predator avoidance/light intensity (e.g. Hamrin 1986) or thermal foraging optimum (Burczynski *et al.* 1987) hypotheses suggested for many small pelagic fish. Yet, Swierzowski *et al.* (2000) found a similar pattern of diurnal fish abundance in the surface waters of a Polish reservoir. They concluded that in their oligotrophic, unproductive lake, daylight foraging by prey fishes in the optimal light intensity conditions of the epilimnion is more important for survival than the risks associated with predator avoidance. This may also be the case in Maroon Dam. The diet of Australian bass (*Macquaria novemaculeata*) collected concurrently from the Dam consists almost entirely of littoral macro-invertebrates and larger (>16 mm SL) *Hypseleotris* (P. Mayes, unpublished data). The dominance of larger *Hypseleotris* in the stomachs of bass, coupled with the presence of other predators such as *Philypnodon grandiceps* in the littoral (S. Meredith, unpublished data) and the potential for conspecific predation (Meredith *et al.* 2002) indicates that predation on *Hypseleotris* occurs mainly in or near the littoral zone. Therefore, predator avoidance does not appear to be an important life history consideration for larval/early juvenile *Hypseleotris* in the pelagic of Maroon Dam. Diurnal vertical migrations of these fish out of pelagic surface waters at night are likely to be linked to either temperature preference (cf. Burczynski *et al.* 1987) or similar diurnal movements of prey (cf. Dini and Carpenter 1991). The information required to examine these hypotheses was not collected, thus they remain the subject for future work.

Near-shore littoral

Dip netting in the near-shore littoral was not employed in discrete temporally defined units, rather it was continued until five fish were captured. Therefore, the presented near-shore littoral size class distributions (Fig. 3) reflect the relative abundance of size classes only at the time of sampling, and diurnal changes in this distribution represents the migration of a whole size class of *Hypseleotris* into or out of the sampled area. Three hypotheses can explain the observed diurnal variability in size class of fish collected in the near-shore littoral: (*i*) larger (>20 mm SL) fish move into the near-shore littoral at dusk and remain until dawn; (*ii*) smaller (12–20 mm SL) fish move out of the near-shore littoral at dusk and return at dawn; or (*iii*) hypotheses (*i*) and (*ii*) are both occurring.

A considerably greater sampling effort was required to catch fish in the dip net during night sampling than during daylight sampling (S. Meredith and P. Mayes, personal observation). This is reflected in the average time spent at sites over the diel sampling period and the lower catch of *Hypseleotris* in bait traps during the night (Fig. 2), and leads to the conclusion that fewer *Hypseleotris* occupy the near-shore littoral

during the night than during the day. This refutes hypothesis (*i*) above, but is consistent with hypotheses (*ii*) and (*iii*). Thus, although the movements of the larger size class (>20 mm SL) remain unknown, the fish belonging to the 12–20 mm SL size class occupy the near-shore littoral during the day and move into an area outside of that sampled during the night.

Hamrin (1986) found a similar horizontal migration for vendace (*Coregonus albula*), and concluded that this was because of ontogenetic changes in temperature and light preferences and size-related intraspecific competition. Holker *et al*. (2002) found a similar diurnal horizontal migration pattern for roach (*Rutilus rutilus*), concluding that this was a response to predator avoidance in the pelagic, where roach feeding conditions were optimal. The physiological (i.e. water quality preference) and ecological (i.e. inter- and intraspecific interaction, optimal foraging conditions) data required to reach the conclusions of either Hamrin (1986) or Holker *et al*. (2002) are not yet available for *Hypseleotris*, thus the basis for diurnal horizontal migrations by the 12–20 mm SL size class of *Hypseleotris* in Maroon Dam remains unresolved. The unusually high water levels during the sampling period did, however, create an uncharacteristic habitat for *Hypseleotris*. A 'normal' year, during which the densest vegetation is located in the shallower and more thermally unstable near-shore littoral, may produce different diurnal horizontal migration patterns. Further examination of these patterns would shed significant light on whether diurnal migrations by *Hypseleotris* represent physiological, predator avoidance or competitive interaction strategies.

Diet

The observed variability in spatial and temporal distributions of the three different size classes of *Hypseleotris* is well reflected in their diets. The decreasing proportion of zooplankton prey and the similarly increasing proportion of 'other' prey items in the GIT of <16 mm SL (pelagic), 12–20 mm SL (near-shore littoral), and >20 mm SL (near-shore littoral) fish, respectively, combined with the presence of macro-invertebrates only in fish caught in the diet of near-shore littoral describes well the ontogenetic niche (Werner and Gilliam 1984) occupied by *Hypseleotris* in Maroon Dam.

Juvenile *Hypseleotris* in the pelagic appear to be almost exclusively zooplanktivorous (Table 1). This is consistent with the early life stages of most fish species, which rely on the zooplankton as a small, easily digestible and abundant protein source (Lazzaro 1987). As well as the availability of food, the pelagic also offers little structural complexity in the form of aquatic macrophytes that might hamper feeding (Landry *et al*. 1999) and, therefore, appears to represent an ideal feeding environment for juvenile *Hypseleotris*.

Once they attain a size of 12–20 mm SL, juvenile *Hypseleotris* migrate back into the near-shore littoral during daylight hours. The presence of benthic macro-invertebrates in the GIT of this size class indicates they are foraging during the

day when they are in the near-shore littoral. Although macro-invertebrates are slower moving, higher energy density and larger prey than zooplankton (Wootton 1998; Holker *et al*. 2002), it is not clear how forage efficiency interacts with these characteristics to determine an optimum feeding habitat for *Hypseleotris*. Bluegill studies that show similar ontogenetic niche shifts to those observed in the current study conclude that the pelagic offers the most energetically advantageous feeding habitat for all size classes of fish, and that larger bluegill move back into the littoral only as a predator avoidance strategy (Mittelbach 1981; Werner and Hall 1988). Such conclusions cannot be drawn from the current study until further examination of optimal foraging requirements for *Hypseleotris* are undertaken.

Larger (>20 mm SL) *Hypseleotris* have the most diverse diet, including three macro-invertebrate taxa (Coleoptera, Ephemeroptera and Odonata) not found in the 12–20 mm SL size class. The presence of these taxa in the diet contradicts previous descriptions of the *Hypseleotris* diet as one that contains zooplankton and benthic dipteran larvae only (Nielsen *et al*. 1999, 2000*a*), but concurs with the more diverse diet described by Stoffels and Humphries (2003). The greater diversity of prey in the >20 mm SL size class is likely to be a result of their larger gape size (mean vertical gape ± s.e. for 12–20 mm SL = 1.14 ± 0.01 mm ($n = 81$), and for >20 mm SL = 1.98 ± 0.01 mm ($n = 104$); S. Meredith, unpublished data), whereby larger fish have access to a more diverse range of prey (cf. Mansfield and McArdle 1998).

Conclusion

Recent work on *Hypseleotris* in floodplain billabongs (Stoffels and Humphries 2003) has identified similar ontogenetic niche shifts to those observed in Maroon Dam and, as such, patterns observed in the present study may have a wider spatial context. As in the current study, Stoffels and Humphries (2003) were also unable to describe causal mechanisms behind the *Hypseleotris* size class partitioning because of a paucity of information on the genus. Further work on ontogenetic niche shifts of *Hypseleotris* is necessary before these studies can be interpreted adequately, whereby the determination of optimal foraging conditions and physiological water quality preferences are the highest priority.

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