

## Diet of the western carp gudgeon (*Hypseleotris klunzingeri* Ogilby) in an Australian floodplain lake: the role of water level stability

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To examine temporal variation in diet, two size classes of western carp gudgeon *Hypseleotris klunzingeri* were collected from macrophyte habitats in Dugays 2 billabong, a floodplain lake on the River Murray, Victoria, Australia, for 1 year. Fish were collected bimonthly during the day and at night between October 1995 and September 1996. Western carp gudgeon consumed a range of prey, including caddisflies, odonates, shrimps and detritus. The bulk of their diet volume, however, consisted of chironomids and zooplankton. The diets of small and large western carp gudgeon were similar and did not change from day to night. There was, however, high variability across sampling trips in fish diets, both at the community level and among selected prey groups, particularly chironomids, zooplankton and detritus. Community analysis revealed that diets of fish collected from the billabong following stable antecedent water levels were similar and showed little variation, while those collected following fluctuating antecedent water levels showed much more variation. These patterns were mirrored in the volumes of individual diet components. © 2006 The Authors

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Key words: billabong; diet; food resources temporal variability; *Hypseleotris*; water levels.

### INTRODUCTION

Temporal variation in abundance or availability of prey can have major effects on energy input for fishes that have limited ability to move between environments having different quality or quantities of food. Fishes in temporally closed systems, such as disconnected floodplain environments, must withstand seasonal variation in available resources as best they can (King *et al.*, 2003). Temporal fluctuations in food resources in such situations may be predictable and associated with temperature, *e.g.* winter declines in invertebrate production, or

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patterns in hydrology, *e.g.* seasonal connection with the main channel of the river (Walker, 1992; Walker & Thoms, 1993; Balcombe, 2002). Thus, it is likely that highs and lows of food availability have been a component of the environmental within which floodplain-resident fishes have evolved. Relatively recent anthropogenic changes to river hydrology, however, have altered patterns in connectivity between floodplain habitats and the river channel. These changes have impacted on natural patterns of water levels, particularly temporally (Walker & Thoms, 1993; Ward & Stanford, 1993).

In aquatic systems where water levels are highly variable, such as in lakes and reservoirs, the quality and quantity of food resources for fishes can vary markedly through time, particularly in littoral areas containing macrophytes (Gasith & Gafny, 1998; Piet, 1998; Welianje & Amarasinghe, 2003). Examination of the diets of fishes can reveal changes in food resource levels, which are manifested as diet-switching from high energy food to lower energy foods as better quality foods become scarce (Persson, 1983; Lobon-Cervia & Rincon, 1994). Fish dietary studies in relation to a seasonal changes in water levels in aquatic systems are rare. It is not known, therefore, whether the impacts of these changes on fish food resources are greater when fluctuations occur aseasonally than when they occur at more predictable times of the year.

Recent work has indicated that significant fluctuations in the abundance of a common south-eastern Australian floodplain fish species, western carp gudgeon *Hypseleotris klunzingeri* (Ogilby) in a large billabong (oxbow lake) were associated with aseasonal water level fluctuations (Balcombe & Closs, 2004). It was hypothesized that water level fluctuations had a deleterious impact on available food resources. Carp gudgeon *Hypseleotris* spp. are often in high abundance in waterbodies throughout the Murray-Darling Basin, and are particularly associated with macrophytes and snags (Balcombe & Closs, 2004). They are generalist predators with broad diets (Balcombe, 2002; Meredith *et al.*, 2003; Stoffels & Humphries, 2003; Pusey *et al.*, 2004) and their diet composition should, therefore, reflect temporal variation in food resources in their environment (Lobon-Cervia & Rincon, 1994; Garcia-Berthou & Moreno-Amich, 2000).

In this paper, the diet of western carp gudgeon associated with emergent littoral macrophytes (giant rush *Juncus ingens*) of a River Murray billabong was examined, with the aim of investigating temporal variability in its diet and testing the hypothesis that the temporal variability will be driven by water level stability. Specifically, the hypotheses that there will be greater volumes of high quality prey and fish will have fuller stomachs during periods following stable water levels than during periods following fluctuating water levels were tested. The stability of water levels in this billabong can either be driven by natural occurrences (typically seasonal spring flooding, between July and November), or unnaturally as a result of flow regulation for irrigation (usually December to April).

## MATERIALS AND METHODS

### STUDY LOCATION

Dugays 2 (36° 02' 30" S; 146° 20' 30" E), is a eutrophic billabong (*c.* 7.2 ha) of the River Murray (between Lake Hume and Lake Mulwala), situated near Rutherglen,

Victoria, south-east Australia. The billabong is *c.* 40 km downstream of Lake Hume, a storage reservoir whose role is to regulate the River Murray for downstream irrigation use. There are no channel diversions ('offtakes') between Lake Hume and Dugays 2. Lying alongside the River Murray, water level fluctuations in the billabong largely mirror that of the river channel (Balcombe, 2002; Balcombe & Closs, 2004), hence outflows from Lake Hume have a large influence on the hydrology of Dugays 2 billabong. The dominant macrophyte in Dugays 2 billabong is giant rush, which grows in monospecific stands, generally along the shore in water <1 m deep. It can occur in clumps as small as 2 m in diameter to long, continuous stands. The stems of this plant support an encrusting biofilm of varying thickness and complexity that can include diatoms, filamentous algae and inorganic matter (S.R. Balcombe, pers. obs.). Apart from European perch *Perca fluviatilis* L. and gudgeon (*H. Klunzingeri* and *Hypseleotris* spp.), the other abundant fish species of Dugays 2 are the exotic common carp *Cyprinus carpio* L. and the native planktivorous Australian smelt *Retropinna semoni* Weber.

### COLLECTION OF FISH AND ANALYSIS OF GUT CONTENTS

Fish were collected bimonthly between October 1995 and September 1996 using inverted cone, 1 mm mesh Gansell (Gansell, Milperra, Australia) fish traps (Balcombe & Closs, 2000, 2004). Three sampling occasions took place during periods of stable water levels and three sampling occasions took place during or just after fluctuating water levels (see Table I). Water level stability was assessed on daily water level variation, and weekly average giant rush habitat availability at the end of each of the 4 weeks prior to sampling. Daily measurements of water levels were recorded with a Unidata Starlogger (Unidata Pty Ltd, O'Connor, Australia). Weekly changes in available habitat (plant surface area of giant rush) were calculated by applying average weekly water depth measurements to measured macrophyte stand attributes (Balcombe & Closs, 2004).

On each sampling visit, 30 traps were deployed between 0900 and 1200 hours ('day' traps) and 30 traps were deployed between 2100 and 2400 hours ('night' traps), and in each case, left to fish for 3 h. Subsamples of fish were retained for gut contents analysis from eight randomly chosen 'day' traps and eight randomly chosen 'night' traps. For traps with >10 fish in them, 10 fish were retained, whereas all fish were retained when fewer fish were captured. Fish were killed immediately with an overdose of benzocaine, measured for total length ( $L_T$ ; mm) fixed in 10% buffered formalin and transferred to 70% ethanol after 24–48 h, following immersion in water to remove residual formalin.

The entire length of the alimentary canal was removed from each fish and placed under water on a watch glass for a visual assessment of per cent fullness. The gut was subsequently dissected and its contents placed in a Petri dish, whose base was lined with 1 mm graph paper. The relative volumetric contribution of individual items in the gut was assessed using an indirect volumetric method (Hyslop, 1980). Contents were squashed to a constant depth and each food type scored according to the number of graph squares covered. Points allotted to each food type were summed and expressed as a percentage of the total points for each fish group on each sampling date. The gut contents of two size classes of western carp gudgeon were examined: small (<25 mm  $L_T$ ) and large (>25 mm  $L_T$ ), following Balcombe & Closs (2004).

The contents of fish guts were placed into 10 prey categories: chironomids, zooplankton, shrimp (*Paratya australiensis* and *Caridina mccullochi*), non-chironomid dipterans, non-dipteran insects (mainly odonate and trichopteran larvae), terrestrial invertebrates, fishes, unidentified eggs, detritus and unidentified material. These categories were chosen because they constituted clear prey items that accounted for at least 10% of the total prey volume on at least one sampling trip, or accounted for at least 10% of the total prey across all sampling trips. A total of 879 western carp gudgeon guts were examined for the 6 day and 6 night periods.

Community analysis of the full range of prey items consumed by western carp gudgeon over the six sampling occasions was examined using non-metric multidimensional scaling (NMDS). Gut content data were first square-root transformed and then a dissimilarity

TABLE I. Antecedent conditions and their probable source for the 28 days prior to each sampling trip

Sampling trip number (date)	Water stability	General conditions	Influence on general conditions
1 (October 1995)	Stable	Very stable, with levels almost constant for previous 28 days.	Natural period of stability due to low spring rainfall.
2 (December 1995)	Fluctuating	Large fluctuations up until 6 days prior to sampling. Relatively stable from then. Early in irrigation season.	Unnatural fluctuations resulting from managed flows for irrigation.
3 (March 1996)	Fluctuating	Large fluctuations up until 2 days prior to sampling. Late in irrigation season.	Unnatural fluctuations resulting from managed flows for irrigation.
4 (April 1996)	Stable	Minor fluctuations up until 16 days prior to sampling then relatively stable.	Some unnatural influence from managed flows, followed by natural autumn stability due to low rainfall.
5 (June 1996)	Stable	Very stable, with levels almost constant for previous 28 days.	Natural winter stability with low evaporation and little runoff.
6 (September 1996)	Fluctuating	Highly fluctuating until 7 days prior to sampling, then a steady decline.	Natural spring flooding, although some management influence on total flow volume (proportion held in Lake Hume).

matrix was constructed using the Bray-Curtis dissimilarity measure. One-way analysis of similarity (ANOSIM) was used to look for community-level differences in the prey of small and large western carp gudgeon, between day and night time periods and sampling trips. ANOSIM was also used to test the hypothesis that fish diets in stable water levels would be different to those in fluctuating water levels. All multivariate analyses were performed using Primer v5 (Clarke & Warwick, 2001).

Multivariate analysis of invertebrate assemblages and diet components, above, revealed that chironomids, zooplankton and detritus were indicative of the dietary components most likely to be affected by water level change. So, one-way ANOVA was used to compare the percentage contribution of chironomids, zooplankton and detritus and per cent gut fullness among sampling trips. Unplanned multiple comparisons were performed where appropriate, using Tukey's HSD tests. To subsequently test any differences between stable and fluctuating diets, *t*-tests were undertaken on the same diet components used in the ANOVAs for each of the two sampling trips. Data were arcsine transformed to meet the assumptions of normality and heteroscedacity, and this was confirmed by screening after transformation of the data. Analysis was performed using SPSS© 11.5 (SPSS inc, 1989–2002).

## RESULTS

Chironomids contributed consistently to the diet of large and small western carp gudgeon, ranging from 13 to 90% by volume across sampling occasions (Table II). Zooplankton also contributed a considerable proportion to the diet on at least four of the six sampling dates, both day and night. Large western carp gudgeon also fed upon shrimps and occasionally small gudgeon, while small western carp gudgeon occasionally fed upon unidentified eggs. Both size classes of fish also fed on detritus, particularly in December and March.

The NMDS revealed no particular pattern in diet in relation to either western carp gudgeon size or diel period (Fig. 1), which was also confirmed by non-significant ANOSIMS (fish size ANOSIM, global  $r = 0.085$ ; diel period ANOSIM, global  $r = -0.053$ ). Diets were, however, significantly different among sampling trips (ANOSIM, global  $r = 0.541$   $P < 0.01$ ). Pair-wise comparisons revealed nine sampling trips that were significantly different from each other (trips: 1 v. 3 and 6; 2 v. 3; 3 v. 4, 5 and 6; 4 v. 5 and 6; 5 v. 6). When these comparisons are placed in the context of water level stability (see Table I), of the nine significantly different times, six were fluctuating v. stable conditions, one stable v. stable and two fluctuating v. fluctuating. Clear differences in diets can be seen in multidimensional space, with a grouping of the gut contents of fish associated with stable water level periods in the centre, whereas the gut contents of fish associated with fluctuating water levels were more dispersed, mostly in the horizontal plane (Fig. 1). The difference in diet between the two water stability periods was significant (ANOSIM global  $r = 0.239$ ,  $P < 0.01$ ).

Mean stomach fullness and percentage volume in the diet of detritus, chironomids and zooplankton were all significantly different among sampling trips (Table III). The greatest variation among pairs of sampling trips was for zooplankton, chironomids and detritus. Each of these components had seven, five and five pair-wise differences, respectively. Stomach fullness had the least variation across sampling trips, with only two significant pair-wise differences: trip 2 v. 1 and 5. Of all significant pairwise comparisons (19 in total), 14 were between

TABLE II. Summary of diet composition (per cent of total volume) and per cent mean stomach fullness for small (S) and large (L) western carp gudgeon during two diel periods: day (D) and night (N) and for six sampling trips (see Table I for dates)

Sample	n	Full	Shrimp	Chiro	Diptera	Zoop	Terr	Fish	Eggs	Detri	Aquins	Unid
L1D	80	23	0	62	3	12	2	0	5	1	16	0
L1N	55	34	11	55	2	17	1	0	0	1	6	7
L2D	59	2	23	24	1	11	0	0	19	10	8	5
L2N	63	17	0	46	0	52	0	0	2	0	0	0
L3D	39	38	4	28	0	0	7	0	0	56	1	4
L3N	39	15	0	61	0	0	1	0	0	37	2	0
L4D	41	26	1	66	2	3	2	20	0	3	1	1
L4N	32	27	0	90	0	4	0	0	0	4	2	0
L5D	99	31	0	47	4	40	1	0	5	0	3	1
L5N	25	35	0	51	2	38	0	0	5	0	2	2
L6D	30	27	0	35	2	59	2	0	1	2	0	0
L6N	12	31	0	4	0	49	0	0	0	0	0	11
S1D	21	3	0	83	0	17	0	0	0	0	0	0
S1N	21	35	0	83	0	17	0	0	0	0	0	0
S2D	22	12	0	42	0	27	0	0	12	19	0	0
S2N	14	12	0	41	0	59	0	0	0	0	0	0
S3D	25	34	0	33	0	7	6	0	0	46	0	8
S3N	20	13	0	73	0	0	0	0	0	14	0	13
S4D	34	18	0	88	0	11	0	0	0	1	0	0
S4N	32	24	0	71	2	10	0	0	15	2	0	0
S5D	17	39	0	57	0	41	0	0	2	0	0	0
S5N	13	3	0	55	4	22	0	0	19	0	0	0
S6D	36	2	0	16	2	78	0	0	4	0	0	1
S6N	50	24	0	13	0	87	0	0	0	0	0	0

Chiro, chironomids; Dipt, other dipterans; Zoop, zooplankton; Terr, terrestrial insects; Fish, gudgeon; Eggs, unidentified eggs; Detri, detritus; Aquin, other aquatic insects; Unid, unidentified material.

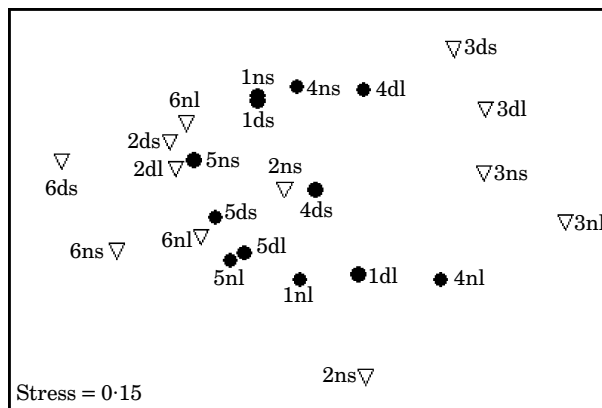


FIG. 1. NMDS plot of western carp gudgeon diet in stable (●) and fluctuating (▽) water levels. 1, October, 1995; 2, December 1995; 3, March 1996; 4, April 1996; 5, June 1996; 6, December 1996; d, day; n, night; s, small western carp gudgeon; l, large western carp gudgeon.

TABLE III. One-way ANOVA results examining variation among sampling times stomach fullness, detritus, chironomids and zooplankton (note sampling trips 1 to 6 as in Table I)

	Mean square	d.f.	<i>F</i>	<i>P</i>	Significant pair-wise differences among sampling trips (at $P < 0.05$ )
Stomach fullness	0.017	5	3.627	0.019	(1-2) (2-5)
Detritus	0.098	5	12.886	<0.001	(3-1,2,4,5,6)
Chironomids	1.232	5	8.226	<0.001	(1-2,6) (2-4) (3-4) (4-6)
Zooplankton	1.565	5	14.485	<0.001	(1-6) (2-3,6) (3-5,6) (4-6) (5-6)

stable and fluctuating water levels, while five were between fluctuating and fluctuating water levels.

When diets were compared between contrasting water level conditions, there were significantly greater volumes of chironomids (Fig. 2; *t*-test, d.f. = 11,  $P < 0.001$ ) in the western carp gudgeon diets during stable than fluctuating water levels. By contrast, fish consumed less detritus (Fig. 2; *t*-test, d.f. = 11,  $P < 0.05$ ) and zooplankton (Fig. 2; *t*-test, d.f. = 11,  $P < 0.05$ ) during stable water levels than during fluctuating water levels. There was no significance difference in mean stomach fullness between the two contrasting water level conditions (Fig. 2; *t*-test, d.f. = 11,  $P > 0.05$ ).

## DISCUSSION

Western carp gudgeon fed upon a wide range of invertebrates, including chironomids, zooplankton, caddisflies, odonates and shrimp, fishes and detritus; confirming their generalist feeding habit (Stoffels & Humphries, 2003; Pusey *et al.*, 2004). The volume of chironomids consumed by western carp gudgeon in Dugays 2 billabong was higher than in comparable diet studies of carp gudgeon (Meredith *et al.*, 2003; Stoffels & Humphries, 2003) and was probably due to the presence of dense macrophyte stands. These dense stands support highly conspicuous biofilm assemblages and probably represent the most significant source of benthic production in Dugays 2 billabong (Balcombe, 2002).

Although there were some differences in prey items consumed, small and large western carp gudgeon diets were similar across all sampling periods. This contrasted with large ontogenetic differences in the diets of carp gudgeon in both natural billabongs (Stoffels & Humphries, 2003) and man-made lakes (Meredith *et al.*, 2003). There was also little difference in diets between the two diel periods, which is, perhaps, not surprising, given that fish were most likely feeding within the same habitat type, giant rush, regardless of diel period (Balcombe, 2002).

The major source of variability in western carp gudgeon diets was sampling trip, with the most variation being between trips preceded by fluctuating water levels and those preceded by stable water levels. This result confirmed the initial hypothesis that water level stability would be the major driver of temporal variability in diets. The hypothesis that the higher quality food (in this case chironomids) would be reduced and lower quality food (in this case detritus) greater in times of fluctuating compared to stable water levels was also

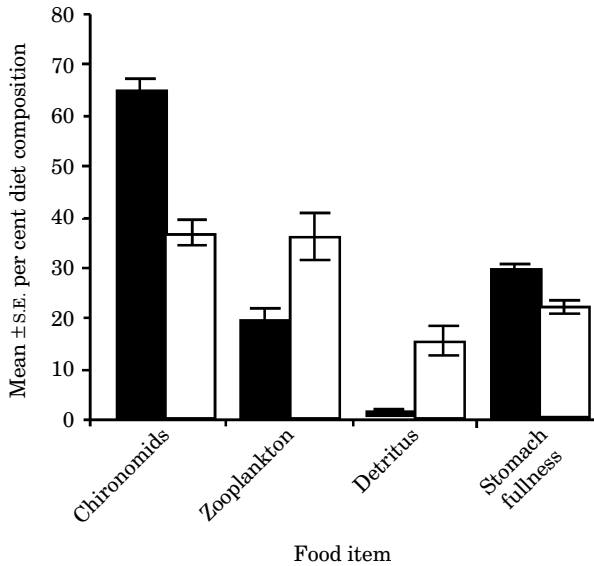


FIG. 2. Mean  $\pm$  S.E. per cent of diet composition and stomach fullness for stable (■) and fluctuating (□) water levels,  $n = 6$  for each water level condition.

confirmed. Stomach fullness did not, however, differ between fluctuating and stable conditions and this hypothesis was rejected. Although power would have been low to detect a difference in stomach fullness, it is probable that fish can maintain consistent levels of food by eating greater volumes of lower quality prey items (Balcombe *et al.*, 2005).

Detritus is generally considered to be low in nutritional quality (Bowen, 1979). A number of studies in lotic and lentic systems elsewhere in the world have considered that an increased consumption of detritus is a prime compensatory response to a decline in higher value primary food resources (McNeely, 1987; Grimm, 1988; Balcombe *et al.*, 2005). The combination of higher consumption of detritus and fewer chironomids, suggests that indeed western carp gudgeon diets were energetically poorer as a consequence of water level fluctuation. Piet (1998) found *Barbus* spp. consumed fewer insects, more detritus and ate less during low water levels than during high water levels in a Sri Lankan reservoir. In that study, high water levels represented resource-rich times, while low levels represented resource-poor times, suggesting water level variability may be an important driver of the trophic dynamics of lentic fish species.

Western carp gudgeon diets in Dugays 2 billabong appeared to be poorer when water levels had been fluctuating than when they had been stable prior to sampling. Most of the water level instability in the billabong is not due to natural river flow, but is a result of water release for irrigation (Balcombe, 2002). In response to regulation of river flows, two major changes to the natural water level patterns in this billabong take place. The first is that the billabong now experiences larger fluctuations from November to March than pre-regulation, when naturally, rainfall would have been low. Previously this would have been a period of very slow drawdown as a result of evaporation at the end of the spring

peaks. Secondly, the billabong is now more stable and lower from April to November as runoff is retained in Lake Hume for later release. If water level stability has such a profound effect on resources available to fishes, as suggested here and in Balcombe (2002), it is possible that the impacts on natural river flows through the irrigation season could override natural patterns of food supply to the resident fishes. Such changes would then be expected to impact on other natural processes, such as larval and juvenile recruitment, and ultimately survivorship (King *et al.*, 2003; Balcombe & Closs, 2004). Further investigation of the relationship between flow variability and its impact on fish food webs could result in better management of flow releases to minimize the impact on fish food resources. This knowledge could help to address the continued decline of native fish stocks in the Murray-Darling Basin (Norris *et al.*, 2001).

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