Diets of gudgeons (*Hypseleotris* spp.) in an Australian floodplain lake : the role of water level stability

S.R. Balcombe^{1,2} P. Humphries^{3,4}

1. CRC for Freshwater Ecology, Department of Environmental Management and Ecology,
LaTrobe University, PO Box 821, Wodonga, Victoria 3689 Australia.

3. CRC for Freshwater Ecology, Monash University, Department of Biological Sciences,
c/- MDFRC, PO Box 921, Albury, NSW 2640 Australia.

Running Headline: Fish diet in a floodplain billabong

2. Author to whom correspondence should be addressed, current address: CRC for
Freshwater Ecology, Centre for Riverine Landscapes, Faculty of Environmental Sciences,
Griffith University, Nathan, Qld 4111 Australia.

4. Present address: The Johnstone Centre, School of Environmental and Information
Sciences, Charles Sturt University, PO Box 789, Albury, New South Wales 2640
Australia.

ABSTRACT

Temporal variability in the diets of fish can indicate temporal changes in prey resources at both seasonal and diel scales. To examine temporal variation in diet, two size classes of western carp gudgeon (*Hypseleotris klunzingeri* Ogilby) were collected from macrophyte habitats in Dugays 2 billabong, a floodplain lake on the River Murray, Victoria, Australia, for one year. Fish were collected bimonthly during the day and at night between October 1995 and September 1996. Gudgeons consumed a range of prey, including caddisflies, odonates, shrimps and detritus. The bulk of their diet volume, however, consisted of chironomids and zooplankters. The diets of small and large gudgeon were similar and did not change from day to night. There was, however, high variability across sampling trips in gudgeon 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.

Keywords: *Hypseleotris* diet, billabong, food resources temporal variability, water levels

INTRODUCTION

Temporal variation in abundance or availability of prey can have major effects on energy input for fish 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 ride out 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 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 context within which floodplain-resident fish have evolved. However, relatively recent anthropogenic changes to river hydrology 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 fish can vary markedly through time, particularly in littoral areas containing macrophytes (Gasith & Gafny, 1998; Piet, 1998, Weliange & Amarasinghe, 2003). Examination of the diets of fish 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 aseasonal 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

southeastern Australian floodplain fish species, western carp gudgeon (*Hypseleotris klunzingeri*), in a large billabong (oxbow lake) were associated with aseasonal water level fluctuations (Balcombe & Closs, 2004). It was hypothesised that water level fluctuations had a deleterious impact on available food resources. Carp gudgeons (*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, we examine the diet of western carp gudgeons associated with emergent littoral macrophytes (giant rush, *Juncus ingens*) of a River Murray billabong, with the aim of investigating temporal variability in gudgeon diets and testing the hypothesis that the temporal variability will be driven by water level stability. Specifically, we test 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. The stability of water levels in this billabong can either be driven by natural occurrences (typically seasonal spring flooding, between July and November), or unnatural 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 (approximately 7.2 ha) of the River Murray (between Lake Hume and Lake Mulwala), situated near Rutherglen, Victoria, S.E. Australia. The billabong is approximately 40 km downstream of Lake Hume, a storage reservoir whose role is to regulate the River Murray for downstream irrigation use. There are no offtake channels 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, *Juncus ingens*, which grows in monospecific stands, generally along the shore in water less than 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 gudgeons, 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 (see 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 four 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 measures to measured macrophyte stand attributes (see Balcombe & Closs, 2004).

On each sampling visit, 30 traps were deployed between 0900 and 1200 ('day' traps) and 30 traps were deployed between 2100 and 2400 ('night' traps), and in each case, left to fish for three hours. Subsamples of fish were retained for gut contents analysis from 8 randomly chosen 'day' traps and 8 randomly chosen 'night' traps. For traps with more than 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, 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 percent 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 gudgeon were examined: (small [< 25 mm T.L.] western carp gudgeons, large [>25 mm T.L.] western carp gudgeon), following Balcombe & Closs (2004).

The contents of fish guts were placed into 10 prey categories: Chironomidae, zooplankton, shrimp (*Paratya australiensis* & *Caridina mccullochi*), non-chironomid diptera, non-dipteran insects (mainly odonate and trichopteran larvae), terrestrial invertebrates, fish, 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 carp gudgeon guts were examined for the six day and six night periods.

Community analysis of the full range of prey items consumed by carp gudgeons 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 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 gudgeons, 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 analysis of variance (ANOVA) was used to compare the percentage contribution of chironomids, zooplankton and detritus and percent 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 gudgeons, 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 gudgeons also fed upon shrimps and occasionally small gudgeons, while small gudgeons occasionally fed upon unidentified eggs. Both size classes of fish also fed on detritus, particularly in December and March.

NMDS revealed no particular pattern in diet in relation to either gudgeon size or diel period (Fig. 1), which was also confirmed by non-significant ANOSIMS (gudgeon 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 $p < 0.005$). Pairwise comparisons revealed nine sampling trips that were significantly different from each other (trips: 1 v 3&6; 2v3; 3v4,5&6; 4v5&6; and 5v6). 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 2 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 pairwise differences, respectively. Stomach fullness had the least variation across sampling trips, with only two significant pairwise differences: trip 2 v 1 and 5. Of all significant pairwise comparisons (19 in total), 14 were between 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.1, $t = -5.555$, $df = 11$, $p < 0.001$) in the carp gudgeon diets during stable than fluctuating water levels. By contrast, gudgeons consumed less detritus (Fig.1, $t = -2.548$, $df = 11$, $p < 0.05$) and zooplankton (Fig.1, $t = 2.411$, $df = 11$, $p < 0.05$) 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. 1, $t = -2.124$, $df = 11$, $p = 0.057$).

DISCUSSION

Western carp gudgeons fed upon a wide range of invertebrates, including chironomids, zooplankton, caddisflies, odonates, shrimp, fish and detritus; confirming their generalist feeding habit (Stoffels & Humphries, 2003; Pusey *et al.*, 2004). The volume of chironomids consumed by western carp gudgeons in Dugays 2 billabong was higher than in comparable diet studies of carp gudgeons (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 likely represent the most significant source of benthic production in Dugays 2 billabong (Balcombe, 2002).

Although there was some differences in prey items consumed, small and large gudgeon diets were similar across all sampling periods. This contrasted to large ontogenetic differences in the diets of carp gudgeons 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 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 contribution of chironomids would be lower and detritus higher in times of fluctuating compared to stable water levels was also 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.*, in press).

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.*, in press). The combination of higher consumption of detritus and fewer chironomids, suggests that indeed 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 fish, 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 fish. 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).

ACKNOWLEDGEMENTS

This study was supported by LaTrobe University and CRC for Freshwater Ecology Postgraduate Stipends. The research was conducted under Department of Conservation and Natural Resources Permit No. FSP/CW/145 and LaTrobe University Ethics Permit LSB95/21. The authors wish to thank Gerry Closs for help and guidance throughout the study.

REFERENCES

Balcombe, S.R. (2002). Resource use by *Hypseleotris* (Pisces: Gobiidae) in the littoral macrophytes of a floodplain billabong. Unpubl. PhD thesis. Department of

Environmental Management and Ecology, LaTrobe University, Albury/Wodonga, Australia.

Balcombe, S.R. & Closs, G.P. (2000). Variation in carp gudgeon (*Hypseleotris* spp.) catch rate in dense macrophytes. *Journal of Freshwater Ecology* **15**, 389-385.

Balcombe, S.R. & Closs, G.P. (2004). Spatial relationships and temporal variability in a littoral macrophyte fish assemblage. *Marine and Freshwater Research* **55**, 609-617.

Balcombe, S.R., Bunn, S.E., Davies, P.M., & McKenzie-Smith, F.J. (in press) Variability of fish diets between dry and flood periods in an arid zone floodplain river. *Journal of Fish Biology*.

Bowen, S.H. (1979). A nutritional constant in detritivory by fishes: the stunted population of *Sarotherodon mossambicus* in Lake Sibaya, South Africa. *Ecological Monographs* **49**, 17-31.

Clarke, K. R., & Warwick, R. M. (2001). 'Change in Marine Communities: An Approach to Statistical Analysis and Interpretation'. 2nd Edition. (PRIMER-E Ltd: Plymouth, United Kingdom.)

Garcia-Berthou, E. & R. Moreno-Amich (2000). Food of introduced pumpkinseed sunfish: ontogenetic diet shift and seasonal variation. *Journal of Fish Biology* **57**, 29-40.

Gasith, A. & Gafny, S. (1998). Importance of physical structures in lakes: The case of Lake Kinneret and general implications. In *The Structuring Role of Submerged Macrophytes in Lakes* (Eds. E. Jeppesen, Ma. Sondergaard, Mo Sondergaard and K. Christoffersen) pp. 331-338. New York:Springer.

Grimm, N.B. (1988). Feeding dynamics, nitrogen budgets, and ecosystem role of a desert stream omnivore, *Agostia chrysogaster* (Pisces: Cyprinidae). *Environmental*

- Biology of Fishes* **21**, 143-152.
- Hyslop, E. J. (1980). Stomach contents analysis - a review of methods and their application. *Journal of Fish Biology* **17**, 411-429.
- King, A.J., Humphries, P., & Lake, P.S. (2003). Fish recruitment on floodplains: the roles of patterns of flooding and life history characteristics. *Canadian Journal of Fisheries and Aquatic Sciences* **60**, 773-86.
- Lobon-Cervia, J. & Rincon, P.A. (1994). Trophic ecology of red roach (*Rutilus arcasii*) in a seasonal stream; an example of detritivory as a feeding tactic. *Freshwater Biology* **32**, 123-132.
- Meredith, S.N., Matveev, V.F. & Myes, P. (2003). Spatial and temporal variability in the distribution and diet of the gudgeon (Eleotridae : *Hypseleotris* spp.) in a subtropical Australian reservoir. *Marine and Freshwater Research* **54**, 1009-10017.
- McNeely, D.L. (1987). Niche relations within an Ozark stream cyprinid assemblage. *Environmental Biology of Fishes* **3**, 195-208.
- Norris, R.H., Liston, P., Davies, N., Coysh, J., Dyer, F., Linke, S., Prosser, I. & Young, W. (2001) Snapshot of the Murray-Darling Basin. 48pp. Canberra: Murray-Darling Basin Commission.
- Persson, L. (1983). Food consumption and the significance of detritus and algae to intraspecific competition in roach *Rutilus rutilus* in a shallow eutrophic lake. *Oikos* **41**, 118-125.
- Piet, G.J. (1998). Impact of environmental perturbation on a tropical fish community. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 1842-1853.
- Pusey, B.J., Kennard, M.J. & Arthington, A.H. (2004). *Freshwater fishes of north-eastern Australia*. Collingwood, Victoria: CSIRO Publishing,. 684pp.

- Stoffels, R.J. & Humphries, P. (2003). Ontogenetic variation in the diurnal food and habitat associations of an endemic and an exotic fish in floodplain ponds: consequences for niche partitioning. *Environmental Biology of Fishes* **66**, 293-305.
- Walker, K.F. (1992) The River Murray, Australia: a semiarid lowland river. In *The Rivers Handbook : Hydrological and Ecological Principles*. **VI**, pp. 271-292. (Eds P.Calow & G.E. Petts). Oxford: Blackwell.
- Walker, K.F. & Thoms, M.C. (1993) Environmental effects of flow regulation on a semi-arid lowland river: the River Murray, South Australia. *Regulated Rivers: Research and Management* **7**, 103-119.
- Ward, J.V. & Stanford, J.A. (1993) Research needs in regulated river ecology. *Regulated Rivers Research and Management* **8**, 205-209.
- Weliange, W.S. & Amarasinghe, U.S. (2003). Seasonality in dietary shifts in size-structured freshwater fish assemblages in three reservoirs of Sri Lanka. *Environmental Biology of Fishes* **68**, 269-282.

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).

Table II. Summary of diet composition (percent of total volume) and percent mean stomach fullness for small (S) and large (L) western carp gudgeons (two diel periods: day (D) and night (N) for six sampling trips (see Table 1 for dates). Key: chiro=chironomids, dipt

= other dipterans, zoop = zooplankton, terr = terrestrial insects, fish = gudgeons, eggs = unidentified eggs, detri = detritus, aquin = other aquatic insects, unid = unidentified material.

sample	N	full	shrimp	chiro	dipter	zoops	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

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

	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)

FIGURES

Figure 1. NMDS plot of western carp gudgeon 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.

Figure 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.