

Short communication

Diel patterns of feeding and prey selection in giant kokopu (*Galaxias argenteus*)

ERIC A. HANSEN

Department of Zoology
University of Otago
P.O. Box 56
Dunedin, New Zealand
email: haner436@student.otago.ac.nz

BRUNO O. DAVID

Department of Conservation
P.O. Box 842
Whangarei, New Zealand
email: bdaavid@doc.govt.nz

GERARD P. CLOSS

Department of Zoology
University of Otago
P.O. Box 56
Dunedin, New Zealand
email: gerry.closs@stonebow.otago.ac.nz

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INTRODUCTION

Diel patterns of feeding and prey selection by drift-feeding fish in small streams are determined by various interacting factors including prey abundance, ease of prey capture, visibility, water velocity, fish size, and social status (Fausch 1984; Closs 1994; Nakano & Furekawa-Tanaka 1994; Grossman et al. 2002). Nocturnal fish species face different challenges with respect to prey detection and capture (Montgomery & Milton 1993), and significant differences in the abundance and composition of potential invertebrate prey (Sagar & Glova 1992) relative to species that feed by day. Efficient feeding at night may require special adaptations including well-developed lateral line systems (Montgomery & Milton 1993; McDowall 1997) and a high level of visual acuity under low light conditions (Meyer-Rochow & Coddington 2003).

In New Zealand, various species of galaxiid, including giant kokopu (*Galaxias argenteus*), banded kokopu (*Galaxias fasciatus*), shortjaw kokopu (*Galaxias postvectis*), koaro (*Galaxias brevipinnis*), and common river galaxias (*Galaxias vulgaris*) are considered to be primarily nocturnal (McDowall 1990). Studies of gut fullness over a diel cycle also indicate that koaro (*G. brevipinnis*) and common river galaxias (*G. vulgaris*) feed primarily at night (Cadwallader 1975; Glova & Sagar 1991). In these fish, prey detection under low light conditions may be facilitated by an accessory lateral line (McDowall 1997). However, various fish species may also exhibit a degree of plasticity with respect to patterns of diel activity (Alanara et al. 2001; David & Closs 2003). Koaro have been observed to feed during the day (Hayes 1996), and giant kokopu may be active for long periods by day during warmer months (David & Closs 2003; David & Stoffels 2003). Differences in the composition of available prey and the ability of fish to detect that

Abstract We examined diel variation in prey selection by giant kokopu, *Galaxias argenteus*, in relation to diel variation in the abundance of drifting invertebrates in a second order stream in Otago, New Zealand in summer. Clear differences in both the quantity and composition of prey consumed was evident. Greater numbers of aquatic insects were consumed at night relative to the day, whereas more terrestrial insects were consumed by day relative to the night. Giant kokopu were selective in the prey consumed. Trichoptera dominated giant kokopu diet at night even though drift samples collected at night were dominated by *Deleatidium* mayflies. Results suggest that giant kokopu feed actively during night and day in summer, and that prey selection is influenced by interactions between factors including prey availability, prey characteristics and light.

prey would seem likely to lead to significant differences in the diet of fish feeding by day or night.

In this study, we compared the gut contents of giant kokopu collected by either day or night. Giant kokopu have previously been described as a relatively non-specialised predator, feeding on a wide variety of terrestrial and aquatic invertebrates, and occasionally fish (Jellyman 1979; Bonnett & Lambert 2002; David & Closs 2003). However, no study to date has examined diel variation in the diet of giant kokopu.

METHODS

A total of 37 giant kokopu (16 night, 21 day) were captured along Alex Stream, a second order stream that drains into Lake Waiholo, c. 50 km south of Dunedin, South Island, New Zealand between 1 and 27 February 2002 (see David 2002 for details of site). Fish were randomly captured along a 300 m reach of stream on the same day or consecutive days for day and night samples. Fish for day gut samples were caught between 1630 and 1820 h by angling (flyfishing), and between 2300 and 0300 h for night gut samples with a spotlight and dip net. Giant kokopu are often active during the day in the summer season (David & Stoffels 2003) and invariably were caught when presented with a fly. Also, a crepuscular peak in feeding activity has previously been observed (David & Closs 2003), therefore sampling between 2300 and 0300 h was considered to give an accurate representation of the quantity and types of food items that were eaten throughout the night. Fish <15 cm in length were seldom active at night and hence could not be collected for sampling. Invertebrate samples were identified to species whenever possible and dry weights of stomach contents determined.

Upon capture each fish was transferred to a bucket containing 135 µl/litre of 2-phenoxyethanol dissolved in stream water. Once anaesthetised, fish were measured to the nearest mm and stomach flushed. Water was pumped directly into the stomach with a single tube causing food items to be flushed out. This technique has been shown in previous studies to be an efficient method of removing food items while ensuring the safety of fish (Giles 1980; Quist et al. 2002). We used either a 25 ml syringe (2 mm diam. tube) for fish between 10 and 14 cm in length or a 60 ml syringe (3 mm diam. tube) for fish between 15 and 30 cm. Fish under 10 cm in length were deemed too small to safely stomach

flush without causing injury. Stomach contents were flushed into a sorting tray and transferred to a pottle containing 90% ethanol. After flushing, fish were placed in fresh streamwater to aid their recovery. Once a fish had regained equilibrium (usually within 30 s), it was returned to its point of capture. A record of the unique pattern of markings along the back of each fish was kept (see David & Stoffels 2003 for methods) to ensure each fish was sampled only once over the study period. Stomach flushed fish recovered rapidly from the procedure and were regularly sighted over a 2-month period post-flushing.

To determine the selectivity of feeding giant kokopu, macroinvertebrates were sampled with up to four drift nets placed upstream and downstream of sampled fish each day and night. Drift nets (1-mm-mesh size) reached the bottom of the stream to the water surface and were positioned in the same locations of the stream on each sampling date. Upon collection the retrieval time was noted and collected items preserved in 90% ethanol and identified using Winterbourn et al. (2000). The volume of water that passed through drift nets was calculated by taking a water velocity reading (centre of each net's opening, range 0.10–0.29 m/s), then multiplying this value by the duration nets were in the water and by the surface area of water covering the mouth of drift nets. Day and night drift samples were compared using paired *t* tests.

Feeding selectivity of giant kokopu was estimated using the the Manly-Chesson index (Mittelbach 2000):

$$\alpha_i = (d_i / N_i) / \sum_{j=1}^k (d_j / N_j)$$

Where $i = 1, 2, \dots, k$ and k is the number of prey categories, d_i is the number (or proportion) of prey type i in the diet, and N_i is the density (or proportion) of prey of type i in the environment. The index α_i ranges from 0 to 1. Prey types that are consumed in proportion to their abundance in the environment have $\alpha_i = 1/k$, $\alpha_i > 1/k$ indicates selection for a prey type, and $\alpha_i < 1/k$ indicates selection against a prey type (Mittlebach 2000).

RESULTS

Invertebrate drift was dominated by three orders of insects: Ephemeroptera, Trichoptera, and Diptera (Table 1). Overall terrestrial and aquatic insects accounted for 15.1% and 84.9% of the drift

respectively; and Ephemeroptera, Trichoptera, and terrestrial Diptera accounted for 64.0%, 12.4%, and 13.6% of the total drift respectively. Over 99% of mayfly fauna consisted of *Deleatidium* and *Nesameletus* spp. and over 90% of the caddis fly fauna consisted of *Olinga*, *Hudsonema*, and *Pychnocentria* sp. Significantly more Ephemeroptera were found in night drift samples compared to day samples ($t = 8.52$, $P < 0.0001$, d.f. = 21), whereas terrestrial Diptera were found in larger numbers in day drift samples than night samples ($t = 1.75$, $P < 0.10$, d.f. = 21).

The mean number of total invertebrates found in gut samples of giant kokopu sampled during day and night time hours was 27.49 and 36.57 respectively (Table 1). All fish sampled during the night had at least three food items present and only one fish sampled during the day had zero food items present. The majority of invertebrates found in stomachs of giant kokopu consisted of cased Trichoptera (mostly *Olinga* spp.), Ephemeroptera (mostly *Deleatidium* spp.), and adult terrestrial Diptera (Table 1). Five times more aquatic invertebrates were consumed by giant kokopu at night than terrestrial insects, although as small fish remained hidden during the night, gut samples were not taken from fish under 15 cm (Fig. 1). Small fish (size 10–15 cm) consumed significantly more terrestrial insects than larger fish (size 15–25 cm) during the day ($t = 2.127$, $P < 0.05$). The mean dry weights of stomach contents of fish larger than 15 cm were 0.056 g and 0.063 g in day and night samples respectively.

Ephemeroptera were found c. 13 times more often in the drift than in gut samples of giant kokopu,

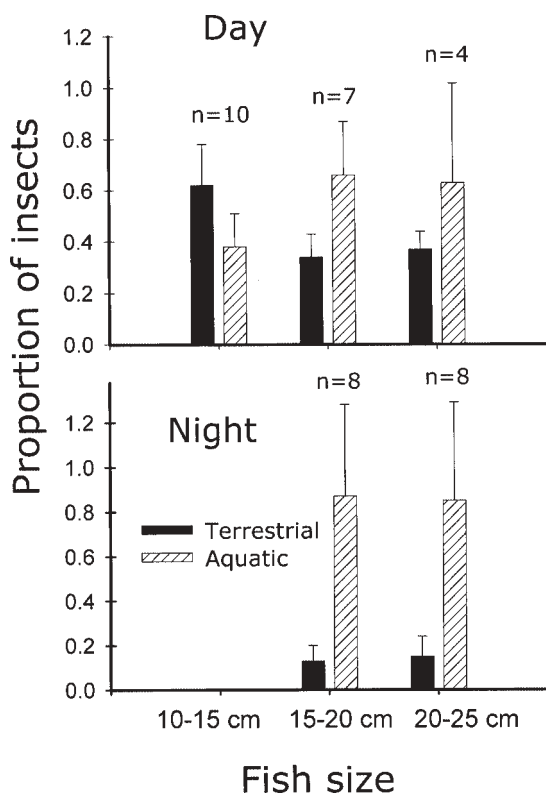


Fig. 1 Proportion (+1 SE) of terrestrial and aquatic insects flushed from the stomachs of small, medium, and large giant kokopu (*Galaxias argenteus*).

Table 1 Mean number of invertebrates collected in day and night drift samples/100 litre per h and mean number of invertebrates collected in day and night stomach samples. (SE, standard error.)

Food item	Day drift samples		Day stomach samples		Night drift samples		Night stomach samples	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Ephemeroptera	0.155	0.04	0.50	0.21	18.78	2.91	1.44	0.59
Trichoptera	0.95	0.37	12.18	4.22	2.67	0.36	29.06	8.31
Terrestrial Diptera	2.98	0.71	8.32	1.65	0.89	0.33	2.75	0.66
Aquatic Diptera	0.284	0.12	1.0	0.44	0.78	0.18	0.94	0.36
Plecoptera	0.03	0.03	0.00	0.00	0.18	0.08	0.13	0.085
Arachnids	0.266	0.098	0.91	0.30	0.457	0.28	0.56	0.20
Terrestrial Coleoptera	0.126	0.044	1.63	0.51	0.28	0.17	0.69	0.22
Terrestrial Hemiptera	0.128	0.044	2.27	0.71	0.14	0.064	0.69	0.40
Other aquatic invertebrates	0.064	0.032	0.68	0.25	0.62	0.224	0.31	0.11
All aquatic invertebrates	1.48	0.46	14.36	5.12	23.04	3.76	31.89	9.45
All terrestrial invertebrates	3.51	0.59	13.13	3.17	1.82	0.86	4.68	1.46

whereas cased Trichoptera were found in gut samples c. 10 times more often than in drift samples. In both day and night comparisons of available drift to gut contents of giant kokopu the food item that was most strongly selected for was cased Trichoptera, where $\alpha_i = 0.686$ and 0.928 respectively. In contrast, Ephemeroptera larvae were selected against with $\alpha_i = 0.107$ and 0.0064 for day and night respectively. During both day and night, caddis were found in the stomachs of all giant kokopu 86% and 88% of the time respectively. In contrast mayflies were only found 33% and 63% of the time in day and night stomach samples respectively.

DISCUSSION

Consistent with other studies of giant kokopu (Jellyman 1979; Bonnett & Lambert 2002; David & Closs 2003), giant kokopu consumed a range of aquatic and terrestrial invertebrate prey. Significantly, readily identifiable prey items were recorded in both day and night gut samples, indicating that giant kokopu of varying sizes were actively feeding over the entire diel cycle. Recent studies of giant kokopu behaviour have observed high levels of diurnal activity (David & Closs 2003; David & Stoffels 2003). This study confirms that such activity is at least partly associated with feeding. Similar patterns of diel feeding activity have also been observed in koaro (Hayes 1996).

The highest number of prey items per gut were recorded at night demonstrating that feeding rates are highest then, at least for fish >15 cm. Clearly giant kokopu are able to feed effectively under low light conditions, an observation that corresponds with the morphology of their lateral line system (McDowall 1997). Variation in the composition of the gut contents over the diel cycle was observed, specifically in the number of terrestrial invertebrates consumed during the day. However, giant kokopu showed continuous selectivity towards Trichopterans with 44% and 79% of all food items sampled in guts consisting of cadis during the day and night respectively. Diel variation in the composition of prey is likely to be determined by changes in prey availability (Sagar & Glova 1992) and the capacity of fish to detect prey under variable light conditions (Montgomery & Milton 1993).

The mean number of terrestrial dipterans per gut was higher by day relative to night, a pattern that also corresponded with the increased availability of such prey in the drift. Small fish fed predominantly on

terrestrial invertebrates during the day. Previous studies have shown that the heaviest individuals position themselves at the heads of pools (David & Closs 2003; David & Stoffels 2003), whereas smaller fish are forced to take up positions at the downstream end of pools where access to drift may be limited (Fausch 1984). Small fish may therefore be denied access to the most profitable positions for feeding on aquatic drift and thus prey opportunistically on terrestrial invertebrates that fall directly into pools from overhanging vegetation.

Giant kokopu have been previously described as non-specialised feeders (Bonnett & Lambert 2002), although this study indicates that they are selective at least at the scale of a single stream. Cased Trichoptera were clearly the most preferred prey item, a pattern of feeding that corresponds closely with observations of prey selection in short-jawed kokopu where cased Trichoptera were also the preferred prey item (McDowall et al. 1996). In this study giant kokopu consumed cased Trichoptera over 10 times more frequently than Ephemeroptera even though mayflies were present in higher numbers in the drift, at least at night. It is possible that giant kokopu use their lateral line as a primary means of detecting prey and therefore feed predominantly on benthic Trichoptera, whereas mayflies effectively drift at low light levels unnoticed. Although the benthos was not sampled in this study, fish were rarely observed feeding off the stream bottom but were commonly seen drift feeding during both day and night.

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REFERENCES

- Alanara, A.; Burns, M. D.; Metcalfe, N. B. 2001: Intraspecific resource partitioning in brown trout: the temporal distribution of foraging is determined by social rank. *Journal of Animal Ecology* 70: 980–986.
- Bonnett, M. L.; Lambert, P. W. 2002: Diet of giant kokopu, *Galaxias argenteus*. *New Zealand Journal of Marine and Freshwater Research* 36: 361–369.

- Cadwallader, P. L. 1975: Feeding habits of two fish species in relation to invertebrate drift in a New Zealand river. *New Zealand Journal of Marine and Freshwater Research* 9: 11–26.
- Closs, G. P. 1994: Feeding of *Galaxias olidus* (Günther) (Pisces: Galaxiidae) in an intermittent Australian stream. *Australian Journal of Marine and Freshwater Research* 45: 227–232.
- David, B. O. 2002: Ecology of the giant kokopu. Unpublished PhD thesis, University of Otago, Dunedin, New Zealand.
- David, B. O.; Closs, G. P. 2003: Seasonal variation in diel activity and microhabitat use of an endemic New Zealand stream-dwelling galaxiid. *Freshwater Biology* 48: 1765–1781.
- David, B. O.; Stoffels, R. J. 2003: Spatial organisation and behavioural interaction of giant kokopu (*Galaxias argenteus*) in two stream pools differing in fish density. *New Zealand Journal of Marine and Freshwater Research* 37: 315–322.
- Fausch, K. D. 1984: Profitable stream positions for salmonids: relating specific growth rate to net energy gain. *Canadian Journal of Zoology* 62: 441–451.
- Giles, N. 1980: A stomach sampler for use on live fish. *Journal of Fish Biology* 16: 441–444.
- Glova, G. J.; Sagar, P. M. 1991: Dietary and spatial overlap between stream populations of a native and two introduced fish species in New Zealand. *Australian Journal of Marine and Freshwater Research* 42: 423–433.
- Grossman, G. D.; Rincon, P. A.; Farr, M. D.; Ratajczak R. E. Jr. 2002: A new optimal foraging model predicts habitat use by drift-feeding stream minnows. *Ecology of Freshwater Fish* 11: 2–10.
- Hayes, J. W. 1996: Observations of surface feeding behaviour in pools by koaro, *Galaxias brevipinnis*. *Journal for the Royal Society of New Zealand* 26: 139–141.
- Jellyman, D. J. 1979: Observations on the biology of the giant kokopu, *Galaxias argenteus* (Gmelin 1789). *Mauri Ora* 7: 53–61.
- McDowall, R. M. 1990: New Zealand freshwater fishes: a natural history and guide. Auckland, Heinemann Reed.
- McDowall, R. M. 1997: An accessory lateral line in some New Zealand and Australian galaxiids (Teleostei: Galaxiidae). *Ecology of Freshwater Fish* 6: 217–224.
- McDowall, R. M.; Main, M. R.; West, D. W.; Lyon, G. L. 1996: Terrestrial and benthic foods in the diet of the shortjawed kokopu, *Galaxias postvectis* Clarke (Teleostei: Galaxiidae). *New Zealand Journal of Marine and Freshwater Research* 30: 257–269.
- Meyer-Rochow, V. B.; Coddington, P. E. 2003: Eyes and vision of the New Zealand torrentfish *Cheimarrichthys fosteri* Von Haast (1874): histology, photochemistry and electrophysiology. In: Val, A. L.; Kapoor, B. G. ed. Fish adaptations. Pp. 337–381.
- Mittlebach, G. G. 2000: Fish foraging and habitat choice: a theoretical perspective. In: Hart, P. J. B.; Reynolds, J. D. ed. Handbook of fish biology and fisheries. Malden, MA, Blackwell Publishing. Pp. 251–266.
- Montgomery, J. C.; Milton, R. C. 1993: Use of the lateral line for feeding in the torrent fish (*Cheimarrichthys fosteri*). *New Zealand Journal of Zoology* 20: 121–125.
- Nakano, S.; Furukawa-Tanaka, T. 1994: Intra- and interspecific dominance hierarchies and variation in foraging tactics of two species of stream dwelling chars. *Ecological Research* 9: 9–20.
- Quist, M. C.; Guy, C. S.; Bernot, R. J.; Stephen, J. L. 2002: Efficiency of removing food items from walleyes using acrylic tubes. *Journal of Freshwater Ecology* 17: 179–184.
- Sagar, P. M.; Glova, G. J. 1992: Diel changes in the abundance and size composition of invertebrate drift in five rivers in the South Island, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 26: 103–114.
- Winterbourn, M. J.; Gregson, K. L. D.; Dolphin, C. H. 2000: Guide to the aquatic insects of New Zealand. Bulletin of the Entomological Society of New Zealand.